ECOLOGICAL AND COGNITIVE INFLUENCES ON ORANGUTAN SPACE USE

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Abstract

Many primates depend on resources that are dispersed non-uniformly. Primates able to encode the locations of such resources and navigate efficiently between them would gain a selective advantage. However, little is currently known about the cognitive mechanisms that help primates achieve this efficiency in the wild. The presence habitual route networks in some primate species suggests they may navigate using route-based “cognitive maps” for encoding spatial information. However, little is known about factors that influence where such route networks are established. Recent evidence of habitual route networks in wild orangutans makes them ideal candidates for examining factors that affect the establishment and use of such networks. I completed three studies using new methodology to examine ecological and cognitive factors that may affect habitual route networks in wild orangutans living in Kutai National Park, East Kalimantan, Indonesia. Results suggest that orangutan habitual route networks are likely the product of both local ecological considerations and how they cognitively encode and use spatial information. Results imply that the spatial configuration of habitual route networks may primarily be a product of local ecology, whereas how orangutans use them day-to-day may be a product of both local ecology and sophisticated cognitive strategies that may include cognitive maps. These studies demonstrate the utility of using modern mapping software and machine learning technology for applications in primate behavior and ecology.

Dedication

For my Mother, who sat with me on rainy days by the orangutan exhibit at the zoo at the start of my research

For my Father, who helped me navigate the sometimes-frustrating complexities of the academic world,

For my Sister, who tolerated my constant venting while she was busy watching TV.

For Rachel, whose unwavering love and support helped me through the times when the light at the end of the tunnel had faded from view.

For Putri the orangutan, whose hate for me just made me lover her more, and her son Pur who, despite his mother's hate always watched me with curiosity.

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A very large thanks to my supervisor Anne Russon, for imparting in me her love of orangutans and her appreciation for their quirks and personality through her orangutan stories. There are few people (especially bosses!) with whom I could spend months in the jungle and still be on speaking terms. Her guidance and help in formulating and developing my research was a huge part of my success and is much appreciated. Thanks to committee members Kristin Andrews and Suzanne MacDonald, whose feedback, support, and extreme positivity helped me get through the final stretch of my dissertation. Kristin, thanks for facilitating a much-need trip to Africa at my most stressed-out time. Suzanne, thanks for the zoo tour when I was young, where I got my first taste of primate intelligence (by being charged by a jealous silverback).

Thanks to my Indonesian friends and coworkers who made the jungle a fun place. Misters (Pak): Ahmad, Pardi, Yunus, Suriadi, Kasih, Daman, Arbain, Supiani, Rizal, and Mardiensa. An extra-huge thanks to Purwo Kuncoro whose knowledge was invaluable and whose friendship and fellow-nerdiness were a welcome break from loneliness, and to Agnes Ferisa, who was always willing to share her vast orangutan knowledge and whose friendship and constant jokes eased me into Indonesian, culture, language, and bureaucratic intricacies.

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Thanks to the orangutans who (sometimes unwillingly – looking at you, Putri) allowed me to follow and observe their fascinating behavior.

I would never have been able to complete these long 7 years without the love and support of **all** my colleagues, friends, and extended family. Thanks especially to Rachel and my family, finishing this dissertation would have been impossible without your love, guidance, and advice.

Table of Contents

List of Tables

List of Figures

Chapter 1: General Introduction

Orangutan habitual route networks: Ecological and cognitive influences on orangutan space use

Wild primates travel daily to fulfil a variety of needs including but not limited to searching for food, accessing suitable nesting/sleeping sites, and social reasons. Such travel is not uniform. Even within regions of homogeneous habitat, primates can revisit certain areas frequently, while avoiding other areas entirely (Di Fiore & Suarez, 2007; Hopkins, 2010; Lührs, Dammhahn, Kappeler, & Fichtel, 2009; Noser & Byrne, 2010; Porter & Garber, 2012). Identifying factors that influence primate travel decisions can contribute to understanding what spatial information primates encode cognitively. This in turn has important applications in conservation and habitat management by contributing to the identification of areas on which to focus conservation efforts.

Many primates depend on resources that are dispersed non-uniformly in space and time and whose availability may be hard to predict, especially species primarily dependent on ripe fruit (Milton, 1981). At a given time, fruit may be available from only a small portion of trees even within a single species and those trees may be distant from each other (Masi, Cipolletta, & Robbins, 2009; Tomoko et al., 2010; van Schaik, Marshall, & Wich, 2009). Although the availability of resources can vary considerably, the locations of many important primate resources, in particular fruit trees, remain stable over long periods of time offering some degree of predictability (Milton, 1981). Many frugivorous primates also inhabit large home ranges and eat at thousands of feeding sites (Di Fiore & Suarez, 2007; Janmaat, Byrne, & Zuberbühler, 2006; Knott et al., 2008; Normand

& Boesch, 2009). Such large home ranges combined with reliance on patchy resources that are available unpredictably means that primates may have to travel relatively long distances to find food resources.

Since the locations of such recurring resources remain stable over time, primates able to encode the locations in memory and adopt strategies to navigate efficiently between them could increase their access to such resources, thereby gaining a selective advantage. The benefits of efficient travel between stable resource patches may have presented a significant pressure to evolve sophisticated cognitive abilities for spatial processing in the primate order (Galdikas & Vasey, 1992; Milton, 1981; Normand & Boesch, 2009). A growing body of evidence demonstrates that primates can indeed remember and travel efficiently between many locations in their habitat (Janson & Byrne, 2007). However, little is currently known about how primates handle these difficulties cognitively to help them achieve this efficiency in the wild. In the context of this paper, cognition refers to “all forms of knowing and awareness, such as perceiving, conceiving, remembering, reasoning, judging, imagining, and problem solving” (American Psychological Association, 2007). Spatial cognition is then these same mental processes applied to locations and directions in space, including spatial memory, navigation, and decisions based on spatial information.

Primates have been theorized to use “cognitive maps” to encode locations and spatial relationships between resources in their home ranges in memory, but how such maps are organized remains poorly understood (Garber & Dolins, 2014; Janson & Byrne, 2007). There are two main hypotheses: route-based or coordinate-based organization, or some combination of both (Dolins & Menzel, 2012; Garber & Porter, 2014; Poucet, 1993).

Coordinate-based cognitive maps encode information about the relative angles and distances between locations. This knowledge would allow individuals to navigate by using direct straight-line travel routes between out-of-sight locations (Normand & Boesch, 2009; Poucet, 1993). Route-based cognitive maps encode information about how to recognize repeatedly used travel routes, how these routes interconnect, and information about which locations are along which routes (Di Fiore & Suarez, 2007). Route-based cognitive maps would allow individuals to navigate by following a series of known routes and changing routes where they intersect (Di Fiore & Suarez, 2007; Poucet, 1993).

To determine the nature of primate cognitive maps, researchers examine their travel routes for indicative patterns consistent with either type of proposed cognitive map. For example, travel patterns consistent with coordinate-based cognitive maps could include primates taking travel routes directly to out of sight resources, more linear travel, and more flexible range use, and would be able to plot novel (never before travelled) travel routes (Poucet, 1993). In contrast, route-based cognitive maps would likely yield travel patterns clustered along frequently re-used pathways, with infrequent travel away from such pathways, and would not be able to plot novel routes (Poucet, 1993). Route-based maps would allow for novel *combinations* of known route segments, but such combinations would be selected from a set of known, previously travelled routes. Primates using a combination of such strategies would likely yield travel patterns that appear intermediate between these two extremes.

Few studies have found evidence supporting coordinate-based cognitive maps, except for preliminary evidence from chimpanzees (*Pan troglodytes*) who may be able to plot novel routes in their home ranges (Garber & Dolins, 2014; Janson & Byrne, 2007; Normand & Boesch, 2009). There has been more evidence in support of route-based cognitive maps. Several primate species use networks of repeatedly reused pathways (hereafter habitual route networks), including several New World monkeys (Di Fiore & Suarez, 2007; Hopkins, 2010; Porter & Garber, 2012), at least one species of lemur (*Microcebus murinus*) (Lührs et al. 2009), chacma baboons (*Papio ursinus*) (Noser & Byrne, 2007a), and Bornean orangutans (*Pongo pygmaeus*) (Bebko, 2012).

Although the presence of such habitual route networks has been established for some species, little is known about factors that influence where such routes are established. Although primate travel decisions are likely influenced by constraints and affordances resulting from cognitive mechanisms (i.e. spatial memory), their decisions are likely also based in part on current local ecological factors (Di Fiore & Suarez, 2007; Hopkins, 2010; Lührs et al., 2009; Noser & Byrne, 2010; Porter & Garber, 2012). The spatial distribution of resources in primates' ranges is likely an important ecological factor influencing their travel. Primates that target travel towards particular locations repeatedly could generate habitual travel routes leading to and from such locations. Resource patches (e.g. fruits) are likely to be especially important travel targets compared to more uniformly distributed resources that are available more readily (e.g., bark) (Milton, 1981). Trees of certain species could also be travel targets as nest sites or as sources of other foods (e.g., leaves, flowers). Food producing trees may be important travel targets even when they lack resources, since visits to monitor a tree's phenological status could aid in accessing its resources before competitors once they become available (Di Fiore & Suarez, 2007).

Ecological factors such as topography (e.g., rivers, hills, cliffs, etc.) could also affect primate travel decisions since they can constrain or prevent travel through particular areas; some may create "bottlenecks" that could funnel travel routes along particular pathways, contributing to the formation of habitual routes (Di Fiore & Suarez, 2007). Bottlenecking effects could be especially pronounced in arboreal species whose travel is constrained by the presence of sufficient canopy connectivity when maintaining arboreal travel (Di Fiore & Suarez, 2007; Hopkins, 2010; Lührs et al., 2009; Thorpe & Crompton, 2009). Terrestrial travel may provide an alternative in cases when no arboreal routes are available.

Although the spatial configuration of habitual route networks may be linked to ecological factors, variation in how primates use such networks remains poorly understood. The presence of humans could disrupt normal use of habitual route networks if primates attempt to avoid or flee from them. Few studies have examined how human disturbances affect use of habitual route networks, but such encounters may provide one window into how primates encode spatial information in cognitive maps. Evidence for cognitive maps could be examined if primates target particular areas of habitat or use their habitual networks differently when fleeing from humans. If primates are able to plan their travel in advance, we would expect that they would systematically change their behavior leading up escaping from humans. Such changes may include changes in activity budget, travel targets, travel speed, and their use of their habitual route networks. Furthermore, if primates who primarily show evidence for route-based cognitive maps deviate from their typical habitual route networks when fleeing humans, it could show evidence that they also use other types of cognitive maps.

Many studies on primate ranging have examined spatial scales that affect entire populations (i.e. 10 – 1000 km) (Hickey et al., 2013; Palminteri, Powell, Asner, & Peres, 2012). Although important, such modelling does not provide a description of local conditions at spatial scales pertaining to individual animals or small groups. Modelling animals' space use on a more local scale would allow for examining specific factors that affect individual travel routes. Such high-resolution ranging analyses open additional avenues for examining cognitive mechanisms relating to travel choices. High resolution knowledge of habitat preferences could also have added benefit of improving assessments of usable habitat size and quality within larger ecosystems. However, higher resolution data are more affected by measurement error, especially travel routes recorded using handheld GPS devices, compared to low-resolution data. However, studies of primate spatial cognition and ranging at spatial scales pertaining to individual primates have typically not accounted for GPS error in their analyses, which can be substantial in densely forested and uneven terrain typical of primate habitat.

Environmental effects including atmospheric noise, humidity, and moisture can create stochastic errors causing waypoints to scatter about their true location. GPS signals can also reflect off nearby dense surfaces. The slight time delay from these reflections can cause travel routes recorded from GPS devices to shift by several meters in one direction. Multipathing is more likely to occur near large dense objects (i.e. vehicles, buildings, cliffs, mountains), large tree trunks, or under dense forest canopy. As a consequence of GPS error, recorded primate travel routes are typically noisier, longer, and slightly offset from actual travel routes. Therefore, GPS records may incorrectly meander back and forth and backtrack when travel was straight. For these reasons, it is important to develop methodology for field studies of primate travel patterns in fine-scale space that account for GPS error.

In addition to developing methodology to address GPS error, the increased availability of free high-resolution satellite imagery combined with state-of-the-art free machine learning packages opens up new avenues for analysis of primate space use at smaller spatial scales. Using machine learning, computers may be able to learn complex patterns in satellite images that may be unrecognizable to humans (Ng, 2018). Animal researchers have been slow to adopt machine learning as an analysis tool, and to my knowledge primatologists have yet to apply machine learning to ranging behavior. Machine learning has the potential to contribute to understanding primate ranging and habitat use by modelling primate space use in well-studied areas and then extrapolating the models to areas where in-situ research is difficult or impractical.

Orangutans’ intelligence and flexible behavioral repertoire make them ideal candidates for examining spatial cognition. I recently found empirical evidence that a population of wild East Bornean orangutans (*Pongo pygmaeus morio*) use habitual route networks in at least part of their habitat (Bebko, 2012). Although the presence of this network has been established, factors that affect its spatial configuration and how orangutans use the network remain unknown.

Orangutans are primarily frugivores, among the largest primates, and highly arboreal (Leighton, 1993; Pontzer & Wrangham, 2004; Thorpe & Crompton, 2009). Orangutans can also inhabit large home ranges with most sites reporting adult female home ranges between 150-600ha (Singleton, Knott, Morrogh-Bernard, Wich, & van Schaik, 2009). High frugivory (patchy resources), large body size, and high arboreality mean orangutans may face more difficulties meeting their daily energetic needs than many other primates (Milton, 1981; Pontzer & Wrangham, 2004). Indeed, orangutans’ caloric balance can be negative for large portions of the year (Knott, 1998). Consequently, orangutans may have some of the most sophisticated foraging strategies among primates, relying on a combination of many factors to make decisions about where to travel.

Assessing factors that influence orangutan travel and space use is increasingly important since orangutans are critically endangered, with wild populations declining rapidly throughout their range due to extensive habitat loss (IUCN, 2018). Orangutans are now predominantly found in protected areas and small forest fragments disconnected from larger populations (Husson et al., 2009; Utami-Atmoko et al., 2017). Better understanding orangutan spatial cognition and ranging could have important applications for managing their remaining habitat and highlighting areas important for orangutan conservation.

To assess factors that influence orangutan travel route networks, I completed studies on wild orangutans in Kutai National Park, East Kalimantan, Indonesia. The extent of intact orangutan habitat within the park's boundaries is unknown, and parts of the park experience severe human damage and encroachment. For this reason, it is a key location to assess habitat quality and orangutan space use to highlight areas important for orangutan conservation and areas where habitat may be degraded. I completed three studies on orangutans ranging within one area of Kutai National Park for evidence of ecological and cognitive factors that may affect their travel decisions.

Chapter 2 presents a two-part study that examined ecological factors that contribute to the spatial configuration of the orangutans' habitual route network. I examined behavioral and ecological ranging data from wild orangutans in Kutai National Park for evidence whether the spatial distribution of resources and other ecological factors in the nearby local habitat were associated with intersections and routes in their habitual travel route network.

Chapter 3 presents a study that examined how orangutans vary use of their habitual route network flexibly in response to human disturbances. This study examined changes in behavior and travel prior to wild orangutans escaping from human observers for evidence they may plan such escapes in advance. I examined ranging and behavioral data from wild in Kutai National Park for differences in ranging and activity between days when orangutans escaped from our observation team and compared them to days when they did not escape. I also examined changes in behavior in the hours leading up to an escape for evidence of advanced planning of their escapes.

Chapter 4 presents a study that developed and tested new methodology for modelling orangutan space use from ecological variables derived from visual characteristics in satellite imagery. In this study, I applied deep machine learning to model ecological predictors of space use in wild orangutans in Kutai National Park. I compared several architectures of deep convolutional neural networks and trained them using behavioral and ranging data paired with raw visual-wavelength satellite imagery of the area.

Chapter 2: Research Paper 1: Ecological factors associated with the spatial configuration of habitual route networks in wild orangutans (*Pongo pygmaeus morio*)

Adam O. Bebko, Anne E. Russon

Abstract

Primates' use of habitual travel route networks has often been interpreted as evidence that they cognitively encode and represent information using a route-based mental map. Ecological factors such as travel targets, travel bottlenecks and heuristic foraging strategies likely contribute to the spatial configuration of their route networks. To examine such ecological factors, we completed two studies on behavioral and ecological ranging data from wild orangutans (*Pongo pygmaeus morio*) in Kutai National Park, East Kalimantan, Indonesia (Jan. 2010 - Dec. 2012). Intersections (Nodes) in their habitual travel route network were associated with nearby feeding bouts of key fruit taxa, and orangutan travel routes passed by more resources than control (adjacent parallel) routes through the same area. Our results suggest that the establishment of habitual route networks may in part be a product of repeated travel between nodes located near key fruit trees, and routes connecting nodes are selected to maintain consistent access to resources during travel. Our results combined with satellite imagery also suggest that some such connecting arboreal routes may be highly constrained due to arboreal bottlenecking, so orangutans must select from a small number of possible arboreal connections to maintain arboreal travel. Our evidence suggests that environmental affordances and constraints contributed substantially to the configuration of these orangutans' habitual arboreal route network.

Keywords: Ecology, Route Networks, Cognitive Maps, Orangutan, Ranging.

Ecological factors associated with the spatial configuration of habitual route networks in wild orangutans (*Pongo pygmaeus morio*).

Wild primates travel daily to fulfil a variety of needs including but not limited to searching for food, accessing suitable nesting/sleeping sites, and for social reasons (e.g. territory defense, seeking/avoiding social partners, etc.). Strategies that aid primates efficiently navigate their ranges would allow primates to maximize access to such resources, while minimizing time and energy spent on travel. Many important primate resources, in particular fruit trees, are accessed repeatedly from the same locations over long periods of time (Milton, 1981). Although over the span of several years resources can disappear due to deaths and damage to trees and other vegetation (i.e. storms, El Niño Southern Oscillation events), overall, resources such as large fruit trees remain in the same location for long periods of time and over many fruiting cycles. Primates that are able to encode the locations of such recurring resources and navigate between them would increase their access to such resources, thereby gaining a selective advantage.

While little is currently known about primate navigation strategies, a growing body of evidence demonstrates that primates can remember and efficiently travel between many locations spread of long distances (Janson & Byrne, 2007). Although difficult to test empirically, primates have been theorized to encode such spatial information in a “cognitive map”, but how such maps are organized remains poorly understood (Garber & Dolins, 2014; Janson & Byrne, 2007). There are two main hypotheses regarding how such cognitive maps are organized: route-based, coordinate-based, or some combination of both (Dolins & Menzel, 2012; Garber & Porter, 2014; Poucet, 1993).

Coordinate-based cognitive maps involve memory of the relative angles and distances between locations. This allows individuals to navigate using novel straight-line travel routes to out-of-sight locations (Normand & Boesch, 2009; Poucet, 1993). Route-based cognitive maps involve memory about how to recognize repeatedly used routes, how the routes interconnect, and information about which locations are along which routes (Di Fiore & Suarez, 2007). This allows individuals to navigate by following a series of known routes and changing routes where they intersect (Di Fiore & Suarez, 2007; Poucet, 1993).

Researchers examine primate travel routes for evidence consistent with such mental maps. Researchers have proposed several indicative travel patterns that could provide support for either type of cognitive map. Travel patterns consistent with coordinate based cognitive maps could include primates taking novel travel routes directly to out of sight resources, more linear travel, and more flexible use ranges (Poucet, 1993). In contrast, route-based cognitive maps would likely yield travel patterns clustered along frequently re-used pathways, with infrequent travel away from such pathways (Poucet, 1993). Primates using a combination of strategies would likely yield travel patterns that appear intermediate between these two extremes.

Few studies have found evidence supporting coordinate-based cognitive maps, except for preliminary evidence from chimpanzees (*Pan troglodytes*) (Garber & Dolins, 2014; Janson & Byrne, 2007; Normand & Boesch, 2009). Such chimpanzees appeared to plot direct and apparently novel paths between resources. More evidence has been found consistent with route-based cognitive maps. Several primate species have been found to have travel routes that are clustered along networks of repeatedly reused pathways (hereafter habitual route networks), including several New World monkeys (Di Fiore & Suarez, 2007; Hopkins, 2010; Porter & Garber, 2012), at least one species of lemur (*Microcebus murinus*) (Lührs et al., 2009), chacma baboons (*Papio ursinus*) (Noser & Byrne, 2010), and Bornean orangutans (*Pongo pygmaeus*) (Bebko, 2012). Such habitual route networks consist of two components: habitual travel routes that are reused over a long period, and intersections of these routes called nodes (Di Fiore & Suarez, 2007).

In addition to how primates cognitively represent information, ecological factors likely influence primate travel decisions. Topographical features (i.e. hills, ridges, etc.) and local resource distribution could influence travel decisions by reducing the likelihood of travel through certain areas (possibly preventing it entirely), while increasing the likelihood of travel through other areas. Several studies that found evidence for habitual route networks also cited possible ecological influences, although the importance of such factors remains poorly understood (Di Fiore & Suarez, 2007; Lührs et al., 2009; Noser & Byrne, 2010; Porter & Garber, 2012). Therefore, primate travel choices may be the result of decisions based on both spatial cognition and current ecological factors.

The spatial distribution of resources in primates’ ranges is likely an important ecological factor influencing primate travel patterns. The locations of resource patches (e.g. fruits) are likely more important travel targets than the locations of resources that are more uniformly distributed (e.g., bark and leaves), especially for primates that rely on ripe fruit (Milton, 1981). Trees of certain species could also be travel targets as nest sites or as sources of other foods (e.g., leaves, flowers, bark). Food producing trees may be important travel targets even when they lack resources, since visits to monitor a tree's phenological status could aid in accessing its resources before competitors once they become available (Di Fiore & Suarez, 2007).

Ecological factors such as topography (e.g., rivers, hills, cliffs, etc.) can also affect primate travel patterns since they can constrain or even prevent travel through particular areas; some may create "bottlenecks" that could funnel travel routes along particular pathways, contributing to the formation of habitual routes (Di Fiore & Suarez, 2007). Bottlenecking effects could be especially important in arboreal primate species whose arboreal travel is constrained by the presence of trees that have sufficient canopy connectivity (Di Fiore & Suarez, 2007; Hopkins, 2010; Lührs et al., 2009; Thorpe & Crompton, 2009).

It is therefore important to examine how ecological factors interact with cognitive processes to gain a better understanding of primate navigation strategies. In this study, we examine ecological factors that may influence travel patterns in a population of wild orangutans. There have been reports of wild orangutans reusing arboreal travel routes (Galdikas & Vasey, 1992; Mackinnon, 1974; Thorpe & Crompton, 2009), although few studies have tested this empirically. We recently found empirical evidence that a population of wild East

Bornean orangutans (*Pongo pygmaeus morio*) in Kutai NP, East Kalimantan, Indonesia use habitual route networks in at least part of their habitat (Bebko, 2012). Although the presence of this network has been established, factors that affect its spatial configuration (i.e. the locations of the routes and nodes in the network) remain unknown.

This paper presents two studies in which we examined how ecological factors may contribute to the spatial configuration of these orangutans' habitual route network. In Study 1, we assessed what factors may influence the locations of nodes (intersections) in these orangutans' habitual route network. In Study 2, we examined factors that may influence the locations of orangutans' habitual routes.

Study 1

Many primate species have shown evidence of goal-directed travel towards important resources in their home range (Asensio, Brockelman, Malaivijitnond, & Reichard, 2011; Noser & Byrne, 2014; Porter & Garber, 2012; Valero & Byrne, 2007), including travel to "inspect" important resource sources (visit and inspect but do not feed or otherwise use that source) (Galdikas pers. comm., Russon pers. obs.). Orangutans are primarily frugivores, preferring some fruit species over others, and preferring large food patches over smaller ones (Leighton, 1993). Accordingly, large trees of preferred fruit species are likely to be more important travel targets than smaller trees of the same species since they tend to contain more total fruit.

Repeated goal-directed travel to such important resources could lead to many travel routes intersecting at their locations, resulting in the establishment of nodes at important resources. In several other arboreal frugivorous primates and terrestrial chacma baboons (*Papio ursinus*), intersections of travel routes were associated with important resources (Asensio et al., 2011; Garber & Porter, 2014; Hopkins, 2010; Noser & Byrne, 2010; Porter & Garber, 2012). We therefore predicted that nodes (intersections) in wild KNP orangutans' habitual route network would be more strongly associated with the locations of feeding bouts on important fruit taxa than with the locations of other activities (e.g., rest, travel, feed on other food items/taxa).

Method

Subjects and setting

We observed wild orangutans (*P. p. morio*) in Kutai National Park, East Kalimantan, Indonesia. The study area, Bendili, is situated along ~8km of the south bank of the Sangatta River, with a 200m grid transect system covering approximately 4-5 km^2 (Figure 2.1). The area had not been commercially logged as of the 1990s (Campbell, 1992; Leighton, 1993) but shows recent signs of small-scale illegal logging and hunting (pers. obs.). The study area was heavily damaged by Borneo-wide forest fires in 1982/83 and 1997/98 that affected the majority of the park, but at the time of this study the area had been regenerating naturally from this fire damage for around 12-15 years (Russon, Kuncoro, & Ferisa, 2015). The original forest in this area includes two forest types, riparian and upland mixed dipterocarp forest which experiences masting (Leighton, 1993); it now consists of a mix of primary and secondary forest of both forest types (Russon et al., 2015). By the end of this study period, we had encountered over 30 orangutans and repeatedly observed, identified, and named 18 of them.

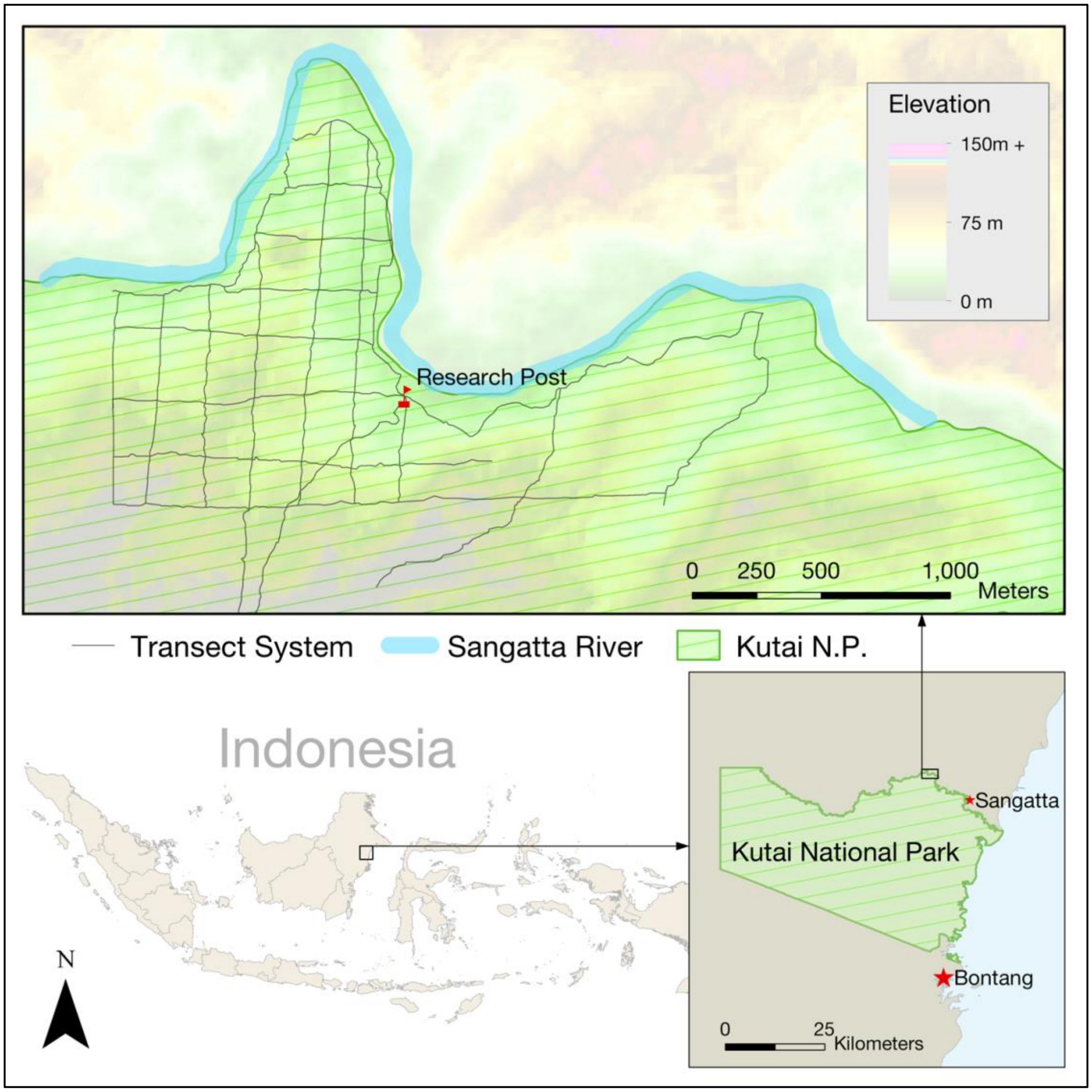

Figure 2.1: Kutai National Park in Borneo, Indonesia, with Bendili study area highlighted.

Sampling and Data collection

The authors and local field staff located orangutans by searching the forest on foot. Trained observers collected data within the standard framework of nest-to-nest focal individual follows, using continuous event-based sampling of the focal orangutan's behavior. We collected travel and other behavioral data for this study between January 2010 and December 2012. Behavioral data included the orangutan's activity (feed, rest, travel and other, plus start and end times of each activity bout), height in the trees, foods eaten, any social partners, and detailed descriptive notes. For foods eaten, we attempted to identify the taxon (local and scientific names). We also recorded which species part (or item) was consumed (i.e. leaf - young or mature, inner bark (cambium), fruit (ripe or unripe), flower, animal part etc.). If field identification was not possible we collected samples for later identification by botanical experts; if neither was successful we coded food items as unknown.

To record orangutans' location during travel, we also created GPS waypoints every 15 minutes throughout a follow near the trunk of the tree that the orangutan occupied using Garmin 60Cs and 60Csx handheld units. Analyses of these waypoint data incorporated corrections for GPS device error (per error assessments below).

Measures

GPS Error

To estimate GPS device error formally, we collected additional waypoints from stationary locations every 15 minutes during 3-hour sessions. We completed 20 such sessions on 12 days over 3 months (Feb, Mar, Jul 2011). To control for temperature, moisture, multipathing, and satellite position, we scheduled these error estimation sessions during daylight hours but at different times of the day and split these sessions between three locations: one in a clearing, one under heavy forest cover, and one next to a stream. We analyzed data from these sessions to estimate the average distance that the recorded GPS points deviated over time. We estimated GPS error from the device error data collection sessions. The first two waypoints were usually inaccurate because the GPS signal had not yet been acquired, so if they were >40 m away from the session's centroid we deleted them. We drew 1-standard-deviation error ellipses around remaining waypoints for each session (Ministry of Environment B.C., 2001) and then converted the ellipses into 95% error circles (Department of Natural Resources WA., 2004). We used the mean circle radius as an estimate of GPS error that represented a 95% confidence limit on the deviation of a point from its true location.

Travel Route

We created travel routes by connecting all GPS waypoints from a day's observation period. We then "noise-cleaned" all travel routes of GPS error by combining all waypoints that clustered within the estimated error of the GPS device into their centroid (Bebko, 2012, 2017). Our devices could not accurately represent or even detect small-scale movements within the GPS error threshold. Due to such error, small scale movements could be recorded as movement the wrong direction. Therefore, to reduce possible error in travel distance and direction, we performed this noise-cleaning even in cases where our behavioral data indicated the orangutan moved.

Habitual route network

We defined habitual travel routes as overlapping clusters of travel routes that followed the same path (Di Fiore & Suarez, 2007). We mapped all travel routes recorded during the study period. Bebko (Bebko, 2012, 2017) created a computer algorithm programmed in Python for ESRI ArcGIS 10 to detect overlapping travel routes while accounting for the error in GPS devices (Figure 2.2A). Although overlaps can occur between two or more travel routes, to be conservative, we considered only habitual routes where at least three travel route segments overlapped over a length of at least 25% of the mean daily travel distance of the individuals followed (Bebko, 2012, 2017). 25% was selected since it represents a travel distance that is important for orangutans since it represents a substantial portion of their daily travel.

Nodes

We defined a node as a location where several travel routes intersected (Di Fiore & Suarez, 2007). We flagged all roughly circular areas where at least five travel routes intersected (Figure 2.2B). To ensure that such areas represented intersections of travel routes (and not short segments of habitual travel routes) we only considered locations where the number of overlaps at that location was higher than individual habitual route segments entering that location (Bebko, 2012, 2017). The radii of these circular node areas were set to the estimated GPS error.

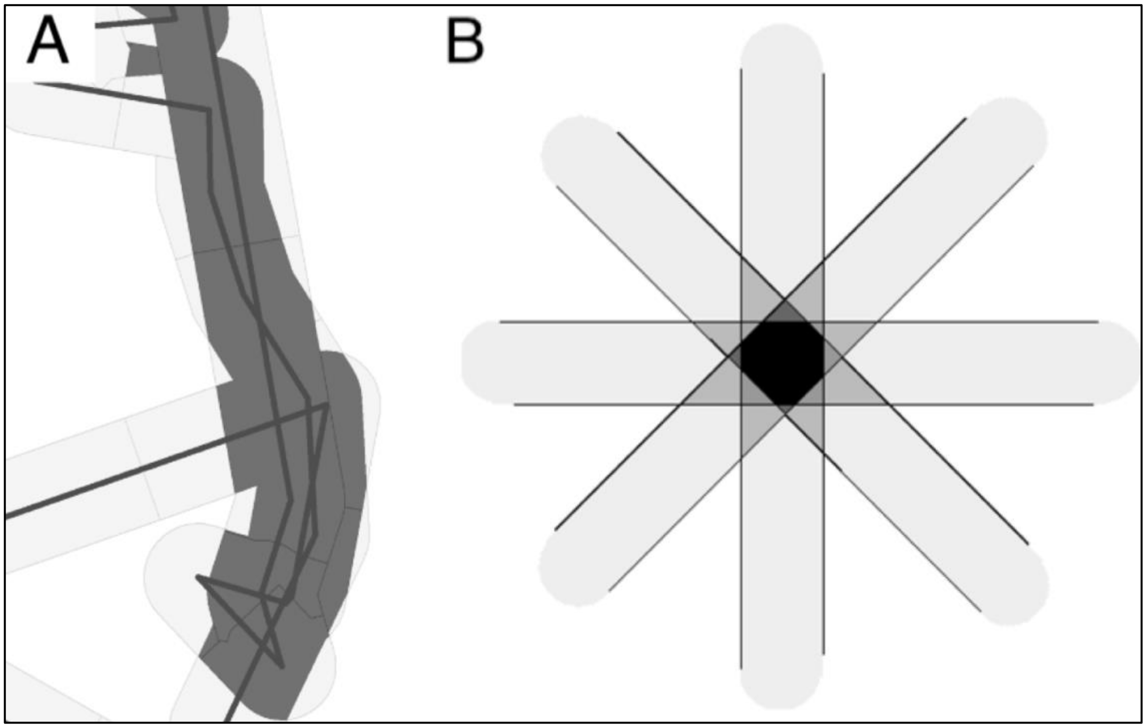

Figure 2.2: Hypothetical habitual route network features. (A) Overlapping travel routes detected as putative habitual travel route (B) Circular overlap area representing a putative node location.

Key fruit taxa

We selected four taxa that represent key fruit sources for local orangutans: *Dracontomelon dao*, *Diospyros sp.*, *Castanopsis sp.*, *Ficus spp.* (Table 2.1). Selection was based on analyses of our observational data for Bendili 2010-12 (Russon et al., 2015), the experience of local field staff, and previous studies of *P. p. morio* in the area (Campbell, 1992; Leighton, 1993; Rodman, 1973). We grouped all figs as one taxon for analyses due to the difficulty of identifying figs to the species level, a common practice in research on orangutans and other primate species (Hanya & Chapman, 2013; Hardus et al., 2013; Leighton, 1993; Morrogh-Bernard et al., 2009; Wich, Utami-Atmoko, Mitra Setia, Djoyosudharmo, & Geurts, 2006).

Table 2.1
Scientific and Local Names of Key Species

Taxa	Species	Local Name
Anacardiaceae	*Dracontomelon dao*	sengkuang
Ebenaceae	Diospyros spp.	baleu[1]
Fagaceae	*Castanopsis sp.*	pelele
Moraceae	*Ficus spp.*	multiple names[1]

1: Local name may include more than one species

Locations of feeding bouts on key taxa

Due to the 15-minute interval between recording GPS waypoints, we were not always able to record the exact locations of short feeding bouts. We estimated the location of each feeding bout as the GPS waypoint closest in time to the feeding bout. Long feeding bouts (> 15 min) were accurately located since any such bouts were necessarily recorded with at least one GPS point. The location of such feeding bouts was represented by the centroid of all associated GPS waypoints. The approximated locations of short feeding bouts (< 15 m) were also relatively accurate since orangutans typically travelled slowly (avg. 2-4 m/min during travel [unpublished data]). For this reason, such short feeding bout locations were typically less than 25 m away from their associated GPS point.

Control locations

Control locations represented locations where orangutans were recorded not feeding on key food taxa (i.e., travel, rest, feed on other taxa, etc.). Due to the enormous number of control locations (> 7500), we did not condense the locations into centroids (as we did above) in cases where multiple GPS points represented the same activity, although we did noise-clean the data for GPS error. Therefore, it is possible that there were multiple control points that represented the same activity at the same location. However, this omission would over-represent the control locations in the statistical models used, making this method of selecting control points extremely conservative statistically.

Nearness to nodes in the habitual route network

We considered that a location was near a node in the habitual route network if it was within the estimated GPS error distance from that node (Bebko, 2012, 2017). We use the term “near” since due to GPS error, locations at the node could be recorded as within the 20 m radius of the node itself, or within the estimated GPS accuracy of the node’s 20 m circle.

Analyses

Relationship between node location and key resource trees

Data include multiple observations per day and per individual, so they fail statistical assumptions of independence. Therefore, we used a multilevel logistic regression model with data nested by date of observation and individual. Our model assessed whether feeding bouts on key food taxa were more likely than the control locations to be near a node. Using R statistics software, we fit the model with the *glmer* function of *lme4* package (Model 1).

Model 1
R-Statistics code for the logistic regression model of nearness-to-node predicted by feeding bout species.

```
Near Node ~ Key Taxa + (1 | Orangutan) + (1 | Date)
```

Where *Key Taxa* was a dummy-coded variable with 4 contrasts: locations of feeding bouts on the four key fruit taxa were contrasted with control locations; *Orangutan* was the identity of the orangutan; and *Date* was the date of observation.

Results and Discussion

We observed 18 identified and several unidentified orangutans on a total of 304 days resulting in a total of 7776 useable GPS locations. The data represent a total of 329 feeding bouts on *Dracontomelon dao*, 69 on *Diospyros sp.*, 48 on *Castanopsis sp.*, and 50 on *Ficus spp*. The pool of useable control points was 7000 locations.

The mean radius of 95% GPS error circles was 20.34 m (sd. = 9.97 m, range = 6.37 - 45.20 m) therefore we estimated the GPS error to be 20 m instead of the error estimate reported by the devices themselves, which usually ranged between 5 m and 14 m.

For a given orangutan on a given day, feeding bouts on all key taxa were significantly more likely to have occurred near nodes than near control locations (Table 2.2). We also calculated odds ratios for all predicted parameters. *Dracontomelon dao* was associated with an odds ratio of 1.80, indicating that for a given orangutan on a given day, feeding bout locations were 1.80 times more likely than other activity locations to be near a node (95% C.I. = 1.16 - 2.80). Similarly, *Castanopsis sp.* was associated with an odds ratio of 15.20 (95% C.I. =

5.86 - 39.43), *Diospyros sp.* 1.84 (95% C.I. = 1.01 - 3.37), and *Ficus sp.* 1.63 (95% C.I. = 1.14 - 2.33).

The random effects in the model, date and individual, both had non-zero variances, indicating that both contributed to the variation in likelihood of GPS locations being near nodes. This implies that individuals differed in their amount of travel near nodes, and that orangutans travelled near nodes on some days more than others.

Table 2.2
Regression coefficients for distance from node of key species eaten.

Parameter	Est.	S. E.	*z*	*p*	Odds ratio (95% CI)
(Intercept)	-1.92	0.44	-4.34	< 0.001 ***	
Dracontomelon dao	0.59	0.22	2.63	0.008 **	1.80 (1.16 - 2.80)
Diospyros sp.	0.61	0.31	1.99	0.047 *	1.84 (1.01 - 3.37)
Castanopsis sp.	2.72	0.49	5.60	< 0.001 ***	15.20 (5.86 - 39.43)
Ficus spp.	0.49	0.18	2.70	0.007 **	1.63 (1.14 - 2.33)

Note: * significant at $\alpha = 0.05$, ** significant at $\alpha = 0.01$, *** significant at $\alpha = 0.001$.

We mapped the locations of significant key taxa with respect to node locations (Figure 2.3). Several nodes were associated with feeding bouts on key taxa.

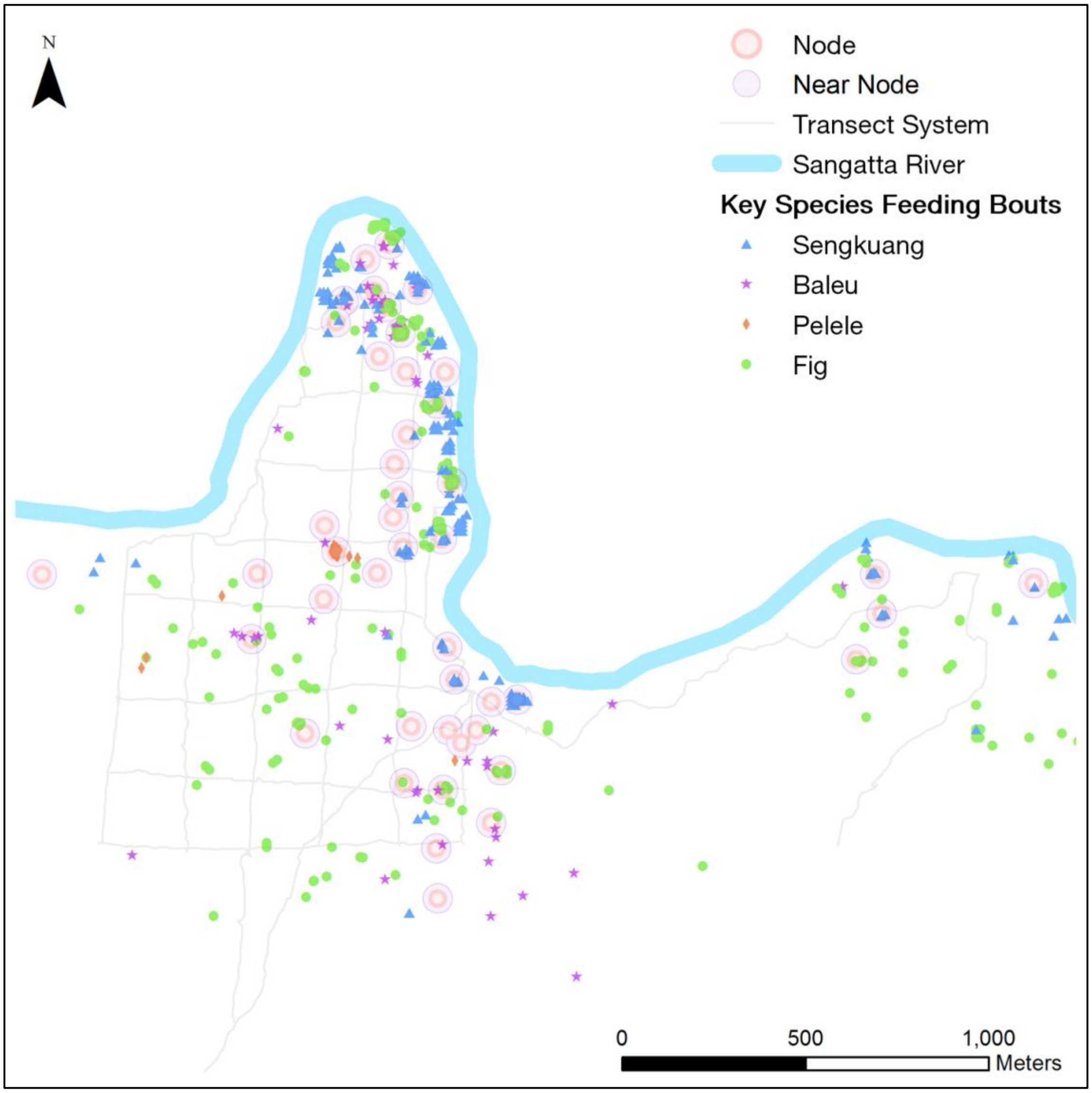

Figure 2.3: Locations of orangutan feeding bouts on key taxa in relation to node locations in Kutai National Park, Indonesia (Jan 2010 – Dec 2012).

We compared Model 1 to a simpler model in which there were random intercepts for individual but not for date, since we had few days in which we observed multiple orangutans. This simpler model was a significantly poorer fit to the data (BIC = 8208) than was the original model (BIC = 6390), lower BIC being preferable (Log Likelihood test: $\chi^2(1) = 1826.6$, $p < 0.001$).

As predicted, feeding bouts on all four specified key taxa were more likely to be near nodes of the habitual route network than near control locations. Our findings are consistent with those for other arboreal frugivorous primates and terrestrial chacma baboons (*Papio ursinus*), for whom intersections of travel routes were associated with important resources (Asensio et al., 2011; Garber & Porter, 2014; Hopkins, 2010; Noser & Byrne, 2010; Porter & Garber, 2012).

We did not differentiate between fig species, but some species may be more important for orangutans than others. Therefore, we also analyzed a model similar to the above, but separating the *Ficus sp.* category into two categories that local experts used based on local traditional knowledge: “kayu ara” – tree fig taxa, and “other figs” (epiphytic climbers, stranglers, creepers, lianas). Nearly all such “kayu ara” trees were large relative to other trees nearby, we observed orangutans feeding on many of their parts (leaves, cambium, fruit), and many of these trees contained orangutan nests.

This division should be interpreted with caution since, as discussed above, fig taxa are very difficult to identify. Nevertheless, in this model “kayu ara" figs were significantly associated with nodes (B = 1.17, p = 0.007), whereas “other figs” were not (B = 0.22, p = 0.31). This suggests that certain large fig trees are preferred travel targets for orangutans, while many other figs are not. Many primates’ have preferred food resources, especially ripe fruit, many of which are only available seasonally, and in their absence, individuals increase consumption of less-preferred “fallback” resources (Marshall & Wrangham, 2007). Orangutans often consume fig fruits as fallback foods, mainly where or when other fruits are scarce (Morrogh-Bernard et al., 2009; Tomoko et al., 2010). Although these findings using local traditional classification hint at the possibility that certain fig taxa may be more important for the establishment of habitual route networks than others, more detailed identification of fig taxa is needed to assess how each contributes to the establishment of habitual route networks.

One limitation of this study was that short feeding bouts were treated the same statistically as feeding bouts lasting several hours. In particular, we observed orangutans feeding from individual *D. dao* trees continuously for several consecutive days, which suggests they represent extremely important food resources for orangutans. Note that our analyses did not adjust for feeding bouts based on their duration: it was the locations of such food resources (not the time spent at them) that were important in relation to the locations of nodes in the network. We aim to examine duration of feeding bouts in future studies assessing how primates *use* habitual route networks.

Overall, many node locations were associated with large individual trees of key fruit taxa, consistent with orangutan preferences for fruit in large crops (Leighton, 1993) and suggesting that the spatial configuration of nodes in these orangutans' habitual route network can be explained in part by the presence and location of such trees. However, not all nodes were associated with such trees, implying that there may be other important taxa not included here or that some nodes may be primarily determined by other factors, such as forest composition or nesting preferences. For example, we have identified several locations in the study area were we consistently found new, old, and repaired nests, suggesting long-term reuse of these nesting sites, so some nodes may represent nesting sites. Further examination of these non-fruit-taxa nodes is needed to determine other factors that may explain their location.

Overall, our results from Study 1 suggest that distribution of key resources in this orangutan population can partially explain the spatial configuration of the habitual route network. However, additional ecological factors likely also contribute to the configuration of habitual travel routes that connect nodes, which we examine in Study 2.

Study 2

Orangutans' primarily arboreal lifestyle and large body size may result in their travel routes being more constrained compared to smaller-sized or more terrestrial primates. Orangutans require relatively large branches or lianas to travel between neighboring trees, trees spaced closely enough for large branches to interconnect, and/or trees or lianas that can be swayed close enough to neighboring trees so that orangutans can cross these gaps (Campbell, 1992; Povinelli & Cant, 1995; Thorpe & Crompton, 2009). Accordingly, orangutan arboreal travel routes may be more likely to pass through areas of larger trees with large overlapping branches or interconnecting lianas and less likely to pass through areas with poorer arboreal connectivity.

Although large fruit resources are likely orangutans' major travel targets (as shown in Study 1), access to other resources during travel between large fruit resources could be important in choosing certain paths over others. Orangutans repeatedly selecting travel routes through areas rich in less-preferred resources while on their way to more important resources may also contribute to the establishment of habitual travel routes.

As a second approach to examining ecological factors that influence the establishment of habitual routes along particular pathways, we examined the number of large trees and large resource trees (i.e. trees in which local orangutans ate or nested) along the travel routes that orangutans took compared to those along computer-generated “control” routes. For our purposes, a control route was a route passing through the same area as an orangutan’s actual travel route but offset from it by a small distance (30 m). We predicted that orangutans’ travel routes would pass through areas with more large food resource trees and more large trees overall than the computer-generated control routes.

Method

Subjects and research setting

The subjects and research setting were the same as for Study 1

Measures

Measures defined in study 1 have the same definition in Study 2.

Large orangutan resource trees

An orangutan resource was defined as any tree or liana of a taxon that orangutans were known to use for food or nesting at our study area. Forest fires had burned much of the area 12-14 years ago, so large trees were relatively uncommon in the study area. Therefore, all trees with trunk-diameter-at-breast-height (DBH) greater than 50cm were considered large trees.

Control routes

To determine the availability of orangutan resources along orangutan travel routes compared to nearby areas, we created matched “control” routes for each selected orangutan day travel route. A control route represented another possible travel route passing through the same area as its paired orangutan travel route, but one that the orangutan *did not* take.

Data collection

We collected data for this study from June - September 2011. From the pool of all previously recorded full-day orangutan travel routes (Jan. 2010 – Sep. 2011), we first identified all observation days on which the orangutan’s behavior appeared little impacted by the presence of the observation team (i.e. low levels of aggression or annoyance and the majority of activity was food or travel oriented). Among them, we selected days on which travel routes represented different areas of the study site and sampled orangutans of both sexes and several age classes. We selected 19 travel routes that met these criteria.

Using ESRI ArcGIS and GPS TrackMaker we created control routes by translating (offsetting) each actual route waypoint to one side of the route by a distance of 30m, perpendicular to the direction of travel (Figure 2.4). Since two parallel control routes were possible (one on each side of the actual route), we selected one side at random to use as the matched control. In cases where the original route turned back on itself we simplified the parallel control route so that it remained offset and never crossed the actual route. We did not use straight-line control routes, since we were comparing orangutan’s routes with adjacent possible routes through the same territory, and straight-line routes would not follow realistic trajectories through the habitat.

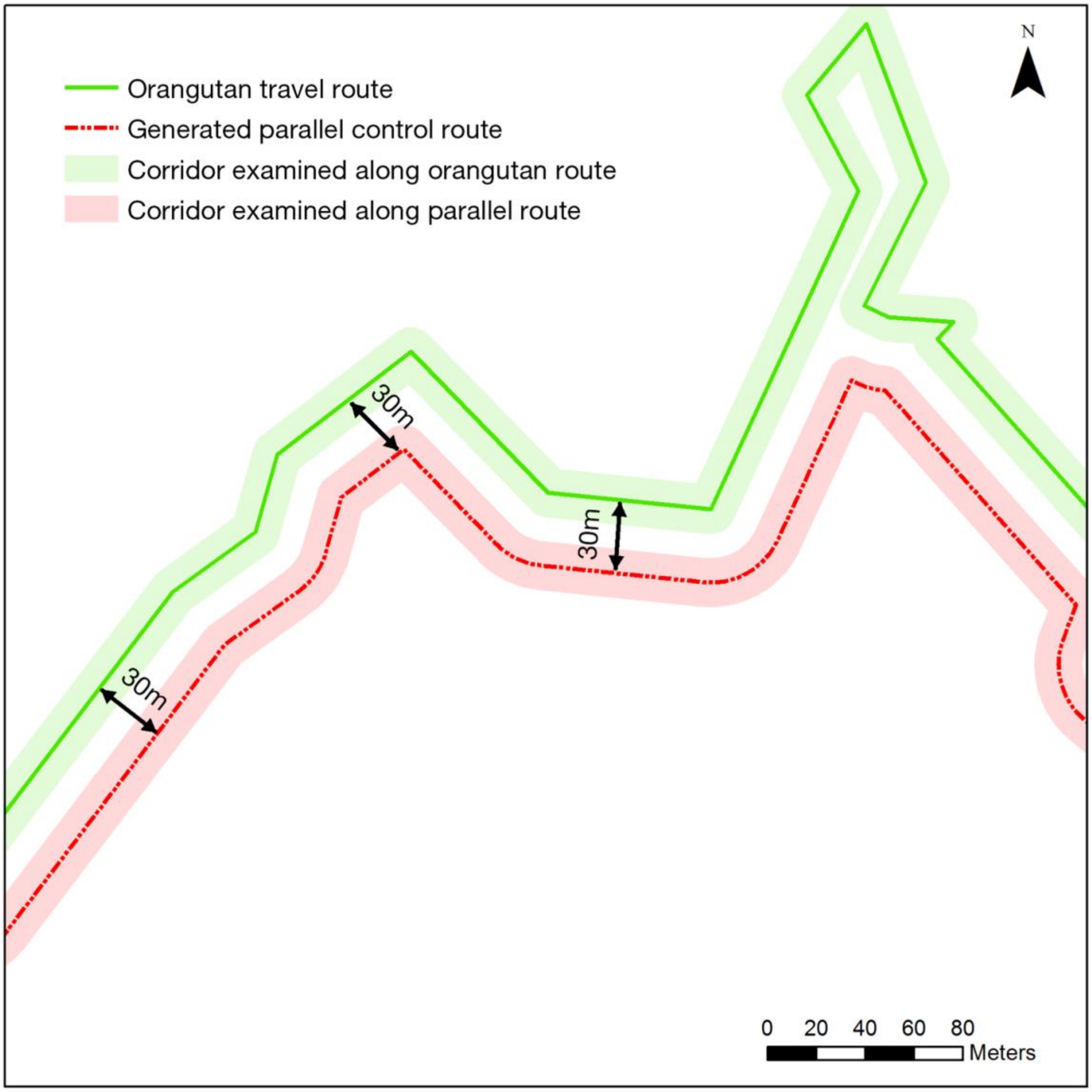

Figure 2.4: Example control route creation. We constructed parallel control routes by translating the original travel routes by 30m to one side such that the two routes never overlapped.

The 30 m offset was chosen because in this study area, 30 m represented the closest distance between arboreal travel routes that was likely to be measurably distinct. Experienced field assistants who followed these orangutans regularly estimated the largest tree crowns in the study area were less than 30 m wide, therefore individuals travelling 30 m apart were unlikely to access the same resources or trees.

To assess resources along both orangutan and control routes, we walked both routes using the GPS devices' route-guidance function and assessed the range and density of orangutan food resources accessible along each route with the help of knowledgeable field assistants. We recorded and identified all large trees (>50 cm DBH) within a 20m corridor (i.e., 10 m to the left and 10 m to the right) along each route and whether they were local orangutan food resources. We used 20m corridors since (1) resources within 10m of the actual route are close enough to be accessible by orangutans travelling along that route (in this forest, crowns of large trees can often extend 10m or more from their trunks), (2) this left a gap of 10m between the actual and control corridors, preventing double-counting.

These spacing criteria (30 m separation between actual and control routes, 20 m wide corridor centered along each) had the added benefit that while retracing the routes for data collection, we were unlikely to accidentally meander into the matched comparison route because of GPS error.

Along both actual and control routes, we also recorded *ad lib* qualitative notes on changes in forest cover (open vs. canopy), ground vegetation density, habitat quality/nature (forest vs. bamboo vs. shrubs), and physical features (rivers, steep inclines, cliffs, etc.).

Analyses

We compared actual orangutan travel routes with their matched parallel control routes on the frequency of all large trees (including non-resource trees) and large resource trees (food, nesting). To account for routes of differing length, we used the relative frequency of trees and resources along each route per kilometer. We also completed similar comparisons treating nest and food resources separately. We tested all comparisons using Wilcoxon signed-rank tests (Wilcoxon, 1945).

Results and Discussion

Overall, we collected data along 19 travel routes and their matched parallel control routes that totaled 9.3km in length. Data were from five adult females (with dependent offspring), one flanged adult male, three unflanged adult males (sexually mature but lacking flanges and other sexual characteristics), and 5 adolescent males (independent, but not yet sexually mature). We recorded 735 large trees, including 510 large resource trees of which 500 were food resources and 420 were nest resources (Figure 2.5). Many species were identified as both food and nest resources.

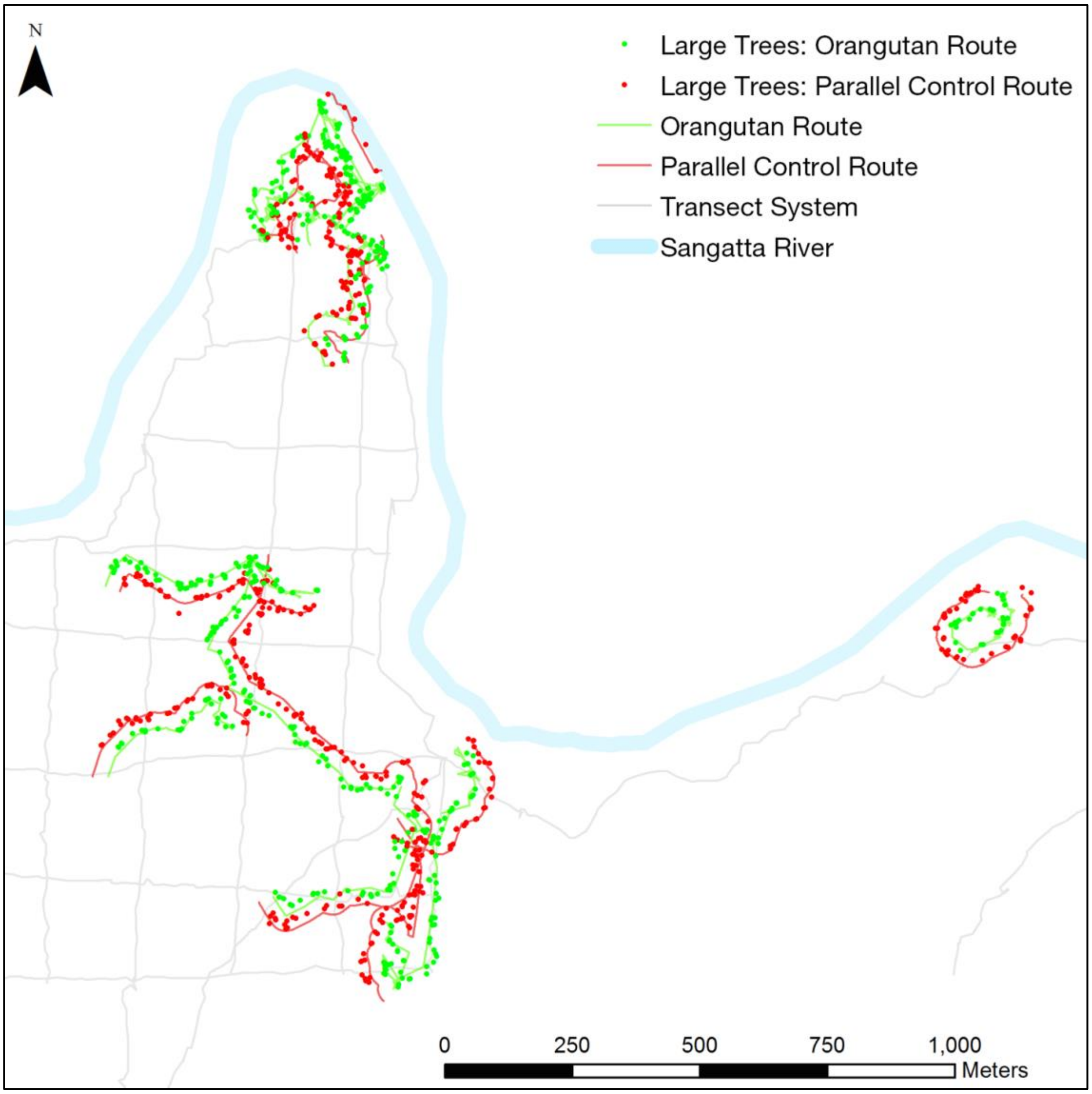

Figure 2.5: Locations of selected orangutan travel routes and matched parallel control routes. All trees DBH > 50cm within 20m along the routes are shown. Data collected in Kutai National Park, Indonesia (Jun – Sep 2011).

As predicted, there were significantly more large trees (including both resource and non-resource trees) per km along actual routes vs. matched control routes (Figure 2.6) (Wilcoxon signed-rank test: $Z = 3.14$, $N = 19$, $p = 0.002$) and significantly more large resource trees per km along actual vs. matched control routes (Wilcoxon signed-rank test: $Z = 2.58$, $N = 19$, $p = 0.010$). Examining large food trees and nest trees separately yielded similar results; there were significantly more large food trees (Wilcoxon signed-rank test: $Z = 2.50$, $N = 19$, $p = 0.012$) and large nest trees (Wilcoxon signed-rank test: $Z = 2.58$, $N = 19$, $p = 0.010$) per km along actual travel routes than along matched control routes. There was one route (8/8/2011 Putri) that was an outlier with many more trees per km than its matched control, since a section of the control route passed along the Sangatta river, meaning no trees were present. We considered deleting this outlier, however, it was representative of possible reasons orangutans may avoid accessing riverbanks and rivers since they contain few trees. Furthermore, the statistical test was not overly affected by this outlier since it required conversion to ranks.

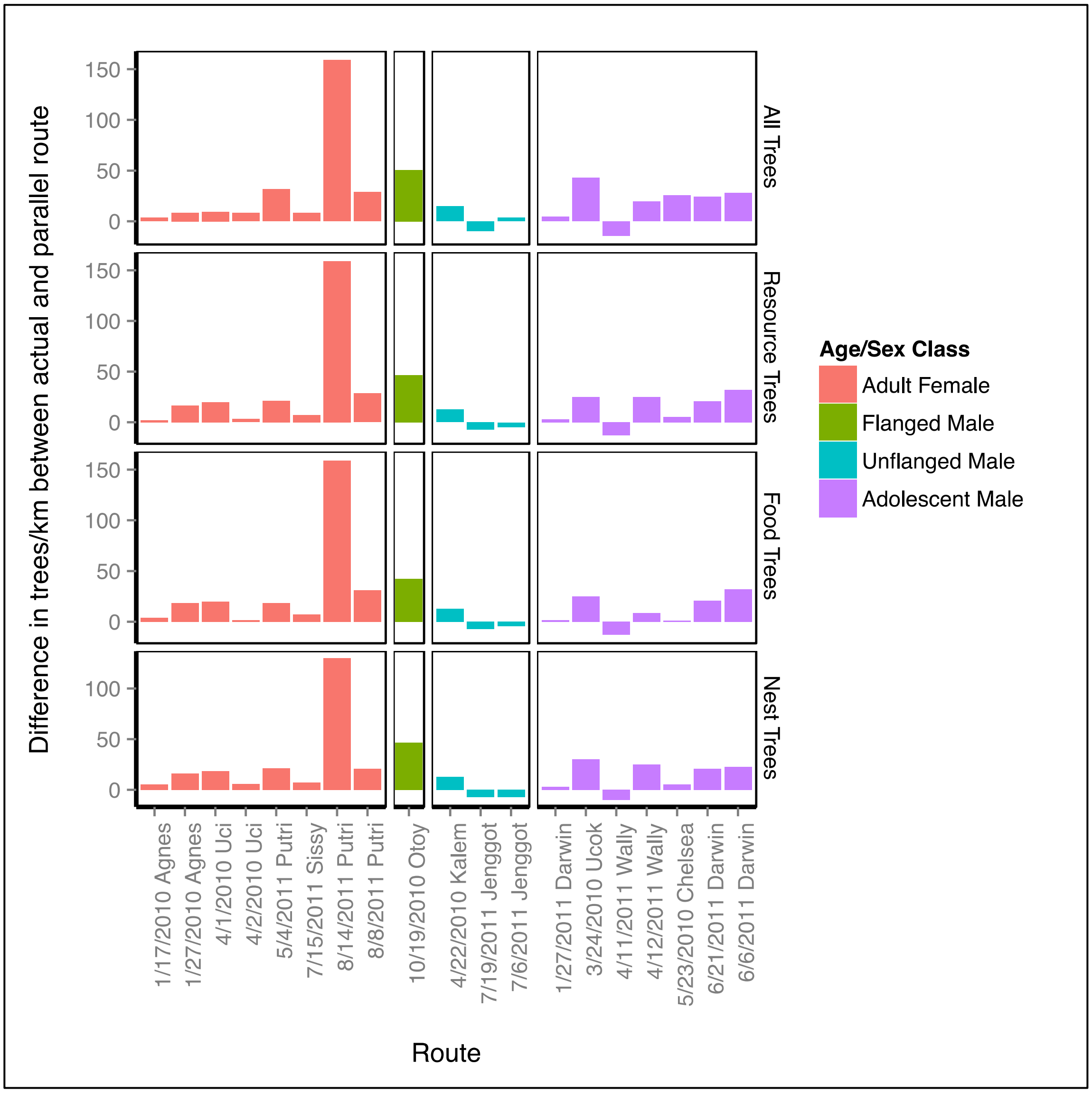

Figure 2.6: The difference in the number of large resource trees (DBH > 50cm) per km along orangutan travel routes and matched parallel control routes in Kutai National Park, Indonesia (Jan 2010 – Aug 2011). Data were split by age/sex class and resource type.

Overall, as predicted, there were more orangutan resources (both food and nest resources) along actual orangutan travel routes compared to parallel routes passing nearby. However, there were also significantly more large trees (combined resource and non-resource) along orangutan travel routes compared to along control routes. Our results suggest that on a very local scale, orangutans may target travel through areas with more large trees generally and more resource trees than nearby areas.

However, length of study is highly correlated with the total number of resource species identified at orangutan study sites (Russon et al., 2009), and our study is based on only 1.5 years of data. For this reason, we may have under-reported the actual number of resource species. Over time, as more local orangutan resources are identified, resource trees may represent a larger proportion of all trees than currently estimated.

The only three cases where actual routes had fewer tree resources than control routes were from an adolescent male (Wally) and an unflanged adult male (Jenggot). Although this is a small sample size, these young-male-low-resource travel routes could reflect a combination of lacking knowledge of the study area (van Noordwijk, Sauren, Morrogh-Bernard, Atmoko, & van Schaik, 2009), disturbance from human observers (Cipolletta, 2003), and/or differing importance of nutrition compared to other age/sex classes (Bates & Byrne, 2009; Normand, Ban, & Boesch, 2009). The last scenario seems to be most likely since both young males were longer-term residents of the area and displayed less disturbance from and more curiosity towards the human observers than newcomers typically did.

Finally, we compared orangutans’ habitual routes with satellite imagery showing forest cover and qualitative notes taken during data collection. This comparison indicated that many orangutan routes passed near edges of forest clearings but still within forest cover (Figure 2.7). Clearings in the study area were typically very sunny and populated by dense understory vegetation including lianas, shrubs, ferns, and bamboo that was difficult for humans to traverse. In contrast to the actual orangutan travel routes, parallel control routes often passed directly through these open areas, and several control routes had little forest cover over the length of the entire route. The orangutans' actual travel routes rarely passed through clearings, and in at least two instances when orangutans did enter clearings, behavioral notes indicate they displayed increased agitation toward the human observers just before entry (i.e. threat vocalizations, branch throwing, etc.), suggesting that they may have been fleeing from or warning/threatening the observers, and not travelling for foraging purposes.

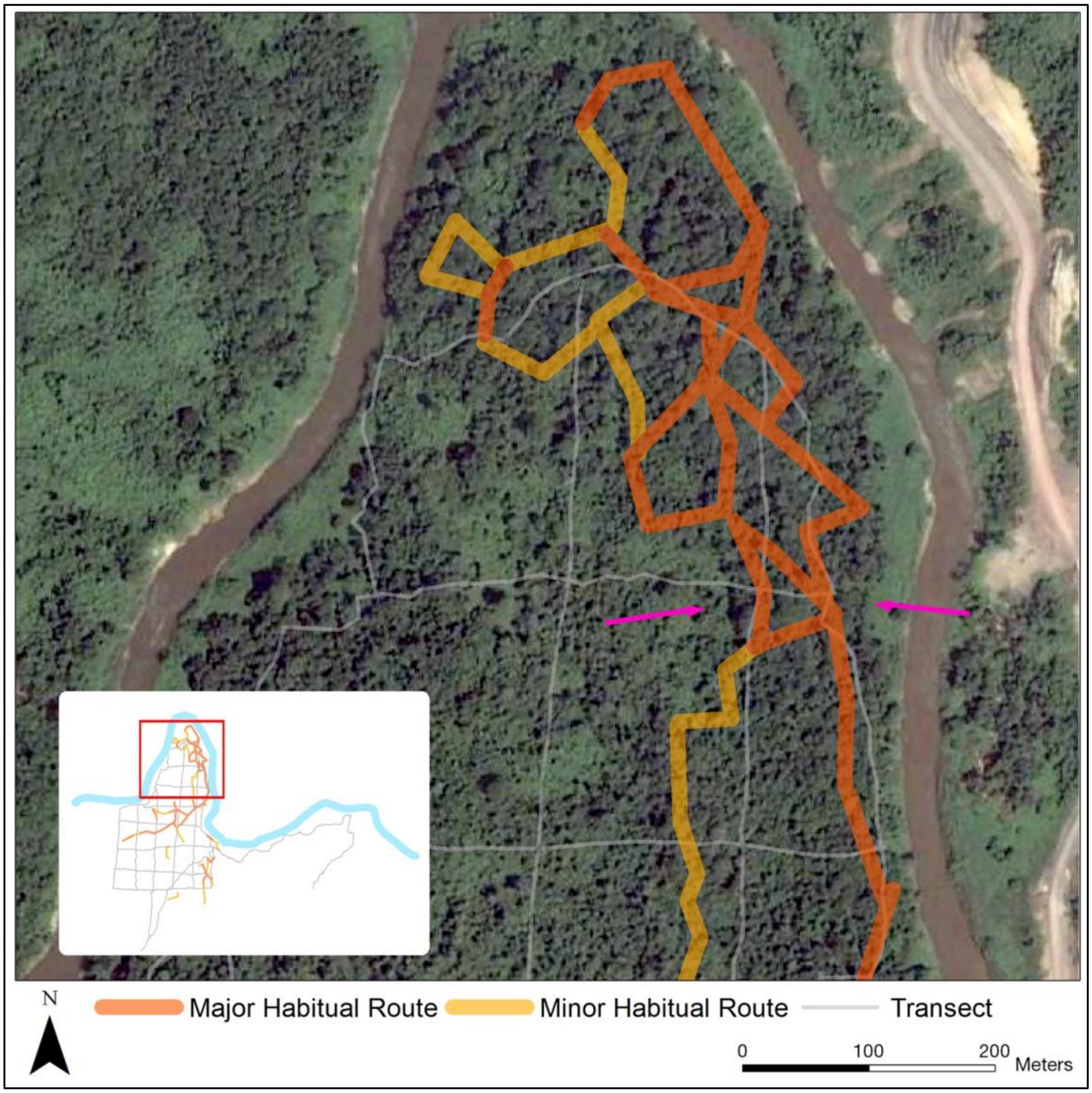

Figure 2.7: Habitual route network overlaid on satellite imagery of Kutai National Park, Indonesia showing possible arboreal bottlenecks (pink arrows) through strips of denser forest between forest clearings. Larger trees appear as darker green areas with more shadows whereas clearings are brighter green with fewer shadows. Images © Google Earth and DigitalGlobe 2018.

Our results imply that habitual routes may in part result from repeated travel along routes that pass through the sequences of interconnecting large trees also with more large resource trees. This is consistent with the arboreal habitual travel routes reported in mantled howler monkeys (*Alouatta palliata*), which passed through areas with high canopy connectivity and resource availability (Hopkins, 2010).

Study 1 found that large trees of key species helped explain the locations of nodes in the network. Overall, Study 2 found evidence that he spatial configuration of the habitual route network was also explained in part by orangutans selecting travel routes through areas of high resource density and good canopy cover, while avoiding alternate more resource-poor routes and forest clearings.

General Discussion

Together, our results from these two studies provide information about the features that contribute to shaping the spatial configuration of these orangutans' habitual route network. Nodes were often located at large individual trees of preferred food and/or nest resources and orangutans travelled between these nodes on routes that maintained arboreal access to a greater number of large trees and resources compared to alternative routes nearby. These results are consistent with those for other highly frugivorous and arboreal primate species that target important patchily distributed resources while maintaining access to less preferred resources during travel (Asensio et al., 2011; Shaffer, 2014).

The presence of habitual route networks has been used as evidence for primates using route-based cognitive maps (Di Fiore & Suarez, 2007; Porter & Garber, 2012). Our results are consistent such findings and further suggest that ecological factors contribute to the spatial configuration of habitual route networks. Such results are also consistent with those published on several other mammals including bison (*Bison bison*), elephants (*Loxodonta Africana*), and lynx (*Lynx canadensis*), for which ecological constraints contribute to the spatial configuration of habitual routes (Bruggeman, Garrott, White, Watson, & Wallen, 2007; Douglas-Hamilton, Krink, & Vollrath, 2005; Squires et al., 2013).

Since local ecology may influence the configuration of primates' local habitual route networks, the routes of different populations of a given species may appear very different as a function of local ecological conditions despite their using similar foraging strategies (Presotto & Izar, 2010). Similarly, species that have similar travel patterns may appear to be using the same foraging strategies, when in reality, their travel patterns could be shaped by similar ecological factors yet using different foraging strategies.

Our results are also consistent with orangutan arboreal travel being partially constrained by arboreal bottlenecking, since arboreal travel routes passing through areas with many large trees would likely have better canopy connectivity than areas with few large trees. In our study area, orangutans, especially flanged adult males, have been observed to travel on the ground, and the *P. p. morio* subspecies is known to travel terrestrially more than other subspecies (Ancrenaz et al., 2014; Thorpe & Crompton, 2009). Such terrestrial travel may reduce the effects of arboreal bottlenecking in this population, since alternate terrestrial travel paths are possible through areas with poor canopy connectivity. Although an interesting possibility, we were unable to analyze terrestrial travel since we had insufficient data on terrestrial travel. Our lack of data owed in part to orangutans' increased speed of travel and increased agitation when they descended to the ground, probably because this brought them closer to human observers to whom they were not fully habituated and aimed to avoid. As the orangutans in this population become more habituated, we hope to collect more data on terrestrial travel to examine how it relates to the use of arboreal route networks.

Despite a small number of orangutans in this study, our data also suggest possible differences between age/sex classes in orangutan travel route selection. In contrast to all other studied orangutans, the two young male orangutans (one juvenile, one unflanged) chose travel routes that passed by fewer resources than alternate nearby routes. Rather than selecting travel routes for foraging efficiency, these routes could reflect travel for different priorities (e.g. social reasons, such as avoiding encounters with residents or flanged males). This difference could provide an interesting avenue of future research with a larger and longer term orangutan sample.

Habitual route networks also have implications for assessing coordinate-based cognitive maps. Many previous studies have considered circuitous routes - those lacking direct linear travel towards resources and a lack of novel travel routes - as evidence against primates using coordinate-based cognitive representations (Bezanson, Garber, Murphy, & Premo, 2008; Janson & Byrne, 2007; Normand & Boesch, 2009; Poucet, 1993). Such conclusions may not be appropriate for orangutans and other species where circuitous travel may be preferred or more efficient than straight-line travel due to local ecological conditions that constrain their travel or affect the distribution of travel targets. Individuals may use coordinate-based spatial representations of resource locations yet travel circuitously to reach them due to ecological affordances and constraints and/or maintaining access to additional resources during travel. This may suggest that linear travel is not necessarily an efficient foraging strategy in some species and/or in some areas of habitat, especially habitat areas which present highly variable travel conditions (Garber, 2016; Hopper, 2010). If so, orangutans may also use coordinate based cognitive maps (or a combination of both), yet choose to follow efficient habitual routes.

Further research on important temporal factors could yield additional insights into how primates use habitual route networks. Many primate resources are only available for part of the year (including the key taxa examined in Study 1) and for orangutans the timing of their availability can be irregular, and travel associated with such resources changes accordingly (Morrogh-Bernard et al., 2009). Therefore, we predict that primates' usage of habitual route networks is sensitive to the availability of temporally variable resources (e.g. ripe fruit). Primates capable of monitoring and predicting the availability of such ephemeral resources would be able target particular areas of their networks only when resources were likely to be present thereby improving foraging success. To assess this possibility, Suarez et al. (2014) compared field observations of spider monkeys (*Ateles belzebuth*) to computer-simulated models that travelled randomly along the same habitual route networks. Even when simulated travel was constrained to the route network and controlled for resource detection range, the primates found resources more efficiently than the simulations, suggesting they used a more complex foraging strategy than random travel along the networks. How primates detect timing cues is of course a major question.

Although temporal variation in resource availability likely affects travel decisions, the majority of orangutan resources (including fruit trees) appear at consistent locations spanning several years. Additionally, such locations may remain important orangutan travel targets when not producing fruit for other reasons (i.e. bark, leaves, flowers, nesting, social meeting, etc.). This could be especially important for the *P. p.* morio orangutan subspecies (studied here)¸ who appear to eat more plant parts/species than other orangutan taxa (Russon et al. 2009). Visiting important resource locations when they are not productive could also facilitate monitoring and updating knowledge about the phenological status of the resources they provide (Di Fiore & Suarez, 2007; Garber & Porter, 2014; Janmaat, Ban, & Boesch, 2013; Milton, 1981), and orangutans have been reported to do this. Results of this study are consistent with the habitual route network enabling a monitoring strategy since it connected large key resource trees at nodes by passing through areas relatively rich in large tree resources. This possibly enabled the orangutans to monitor the status of both preferred and other resources during travel to destinations that currently provide resources.

Di Fiore and Suarez (2007) hypothesized that habitual route networks may contribute to the construction of primates’ ecological niches. Repeated seed dispersal along habitual routes over long time frames could increase resources along these routes compared to other areas. Our results are consistent this hypothesis. However, applying our findings to niche construction may be problematic since our study site was relatively new, so some orangutan resources likely remained unidentified, leading us to underestimate the total number of resource trees relative to all large trees. Furthermore, recent droughts, winds, and heavy rains, from El Niño Southern Oscillation events and earlier forest fires (Russon et al., 2015) may also have disrupted niche construction and/or forced orangutans to change their ranging patterns in the study area in the recent past.

Overall, the spatial configuration of the orangutans' habitual route network in our study area was well explained by current ecological conditions. This is likely the case for many other large-bodied arboreal primate species in which habitual travel route networks have been found. Primate habitual route networks are likely the product of how primates cognitively encode spatial information, combined with current/recent ecological considerations in their habitat. Our results highlight the importance of including ecological factors in future studies examining primate travel patterns for evidence of primate spatial cognition.

Chapter 3: Research Paper 2: Behavioral changes leading up to escapes from researchers in wild orangutans (*Pongo pygmaeus morio*).

Adam O. Bebko, Anne E. Russon, Jin Kang

Abstract

Primate travel routes can be disrupted by humans, especially in populations with little human contact. Primatologists typically treat these disruptions as a nuisance, yet they may be useful to examine strategies primates use to avoid threats. This study examined changes in behavior and travel prior to wild orangutans escaping from human observers for evidence of whether they may plan such escapes in advance. We predicted that wild orangutans would alter aspects of their activity budget and space use. We collected ranging and other behavioral data from wild orangutans (*Pongo pygmaeus morio*) in Kutai National Park, East Kalimantan, Indonesia. Using mixed multilevel regression models and mapping software, we examined travel routes and behavior on days when orangutans escaped from our observation team and compared them to days when they did not escape. Consistent with predictions, orangutans significantly altered their behavior leading up to escapes. Orangutans increased their time spent travelling and travel speed, while decreasing their time spent feeding on escape days compared to normal days, and this difference became greater leading up to an escape. Orangutans also targeted travel towards areas of habitat they typically avoided. Overall, our results suggest that these wild orangutans altered their behavior several hours in advance of successfully escaping human observers. Although preliminary, our results are consistent with orangutans deliberately attempting escapes by prioritizing traveling over feeding and by targeting travel away from their normal travel routes.

Keywords: Travel, Orangutan, Spatial Cognition, Habituation, Ecology

Behavioral changes leading up to escapes from researchers in wild orangutans

Primatologists observe primates' travel patterns to assess how they encode and use spatial information cognitively. However, human presence can disrupt their normal travel patterns, especially in populations with little human contact. Typically, primatologists treat these disruptions as a nuisance to data collection. Yet they may be useful in themselves to examine human-influenced changes in behavior, and primates' strategies for hiding, fleeing or otherwise responding to potential predators and threats. Increased understanding of such escape and avoidance strategies could be essential for effective management of threatened primate populations in increasingly human-impacted habitat. This study examined changes in behavior and travel prior to wild orangutans escaping from human observers for evidence that suggest they plan such escapes in advance.

Many animal species alter their behavior to avoid threats, especially to reduce the risk of predation (Lima & Dill, 1990). Anti-predator behavioral strategies can involve changes in how animals travel, forage, and rest (Barnier et al., 2014; Christianson & Creel, 2010; Creel & Christianson, 2008; Lima, 1998; Lima & Dill, 1990; Nelson, Matthews, & Rosenheim, 2004). Most wild animals tend to perceive human activities as threatening, often triggering behavioral changes similar to anti-predator responses even in the absence of direct predation (Frid & Dill, 2002). Such human-induced changes include increased travel time, speed, and changed travel direction (e.g. bottlenose dolphins - *Tursiops aduncus*, elk - *Cervus elaphus*, southern right whales - *Eubalaena* *australis*, moose - *Alces alces*), interrupted resting and reduced foraging success due to increased vigilance (e.g. elk - *Cervus elaphus,* caribou - *Rangifer tarandus caribou*, red-crowned cranes - *Grus japonensis,* harbor seals - *Phoca vitulina*), and choosing safer but less rewarding habitats (e.g. chough - *Pyrrhocorax pyrrhocorax*, elk - *Cervus elaphus,* grizzly bears - *Ursus arctos*) (Ciuti et al., 2012; Constantine, Brunton, & Dennis, 2004; Cristescu, Stenhouse, & Boyce, 2013; Duchesne, Côté, & Barrette, 2000; Henry & Hammill., 2001; Kerbiriou et al., 2009; Lemon, Lynch, Cato, & Harcourt, 2006; Z. Li, Wang, & Ge, 2013; Naylor, Wisdom, & Anthony, 2009; Neumann, Ericsson, & Dettki, 2010; Rumble, Benkobi, & Gamo, 2005; Steckenreuter, Möller, & Harcourt, 2012; Vermeulen, Cammareri, & Holsbeek, 2012). As with anti-predator behavior, these human-induced behavioral changes carry energetic costs and the associated negative consequences (Amo, López, & Martín, 2006; Brown, 1999; Kerbiriou et al., 2009; Lima, 1998; Neumann et al., 2010).

Similar to other wild animals, wild primates generally perceive humans as a threat. However, individual primates' reactions can vary greatly depending on their past exposure and experiences with humans. Populations with little human contact typically react to humans as predators, often with fear and aggression (Cipolletta, 2003). Some primate populations may have developed human-specialized behavioral responses to avoid direct predation by humans (Bshary, 2001; Dooley & Judge, 2015; Doran-Sheehy, Derby, Greer, & Mongo, 2007). Such responses can include threat/alarm vocalizations with a decrease in other vocalizations, increased travel distance and time, changes in social behavior, and learning about human behavior to develop specific strategies to escape and evade them (Bshary, 2001; Cipolletta, 2003; de la Torre, Snowdon, & Bejarano, 2000; Dooley & Judge, 2015; Jack et al., 2008; Masi et al., 2009). In this context, escaping means that primates successfully left the presence of humans and could not be relocated after searching. Human-specific escape strategies include (but are not limited to) immediately fleeing, using distraction or decoys, learning to discriminate human from natural threats (Bshary, 2001), changes in vocalization rates and types, and changes in ranging patterns (Bshary, 2001; de la Torre et al., 2000; Dooley & Judge, 2015). Some primates attempt to escape from humans even after being observed over long-duration neutral encounters. For example, gorillas have attempted escape from human observers even after observation sessions lasting several days, commonly by scattering their group and fleeing (Cipolletta, 2003; Doran-Sheehy et al., 2007).

After many repeated neutral encounters with humans, primates' reactions typically change gradually from fear and aggression to curiosity or ignoring humans they recognize (Cipolletta, 2003). This change over time is called habituation (Fedigan, 2010). Habituation can take several years, and may occur on an individual and/or group basis (Doran-Sheehy et al., 2007). When habituated, primates do not appear to significantly alter their behavioral patterns in response to humans, maintaining similar travel distance, speed, and resting time as measured using automated radiotelemetry (Crofoot, Lambert, Kays, & Wikelski, 2010).

Although researchers do not typically represent direct threats to primates, they typically disturb primates’ behavior and ranging in unhabituated populations. Few studies have examined the nature of such disturbances, and the few that have typically focused on quantifying primates’ progression towards habituation over long time intervals on the order of years. Such studies have examined gradual changes in broad travel patterns such as daily travel distance and frequencies of fear reactions but have not examined changes in space use and changes in behavior on timescales smaller than years or months. Human-primate encounters create challenges that may provide a unique window into how primates alter their behavior to avoid or mitigate novel and stressful situations. To our knowledge, no studies have examined primates’ strategies and use of knowledge about their habitat to evade observers.

Scientific study of orangutan habituation and responses to humans, including human-specific escape strategies, is very limited: the most recent published reports we found were Mackinnon (1974) and Rijksen (1978). Orangutans’ intelligence and flexible behavioral repertoire make them ideal candidates for examining escape strategies including advance planning of escapes. Adult orangutans experience very low natural predation and humans represent their greatest threat through hunting for food, sale in the illegal pet trade, or conflict over human crops (Spehar et al. 2018). Orangutans typically react to humans by initially hiding until certain they are detected; once detected, they make fear/aggression displays, then typically attempt to move away (Mackinnon, 1974; Rijksen, 1978). During these fear/aggression displays, they frequently vocalize, performing “kiss squeaks” and other low-frequency vocalizations including “lorks”, “gorkums”, and “grumphs”, and shake or throw branches at the humans (Hardus et al., 2013; Mackinnon, 1974; Rijksen, 1978). After initial reactions, they may remain stationary and quiet for several hours, sometimes building or returning to nests. Among adults, male orangutans usually react less fearfully to humans than females, and males occasionally descend to the ground to chase humans away (Mackinnon, 1974; Rijksen, 1978).

After several consecutive days of observation, orangutans partially habituate to humans, but on re-encountering the same individuals at a later date, they can revert to fear/aggression responses (Mackinnon, 1974; Russon et al., 2015). It can take many repeated observations (sometimes spanning several years) for orangutans to fully ignore the presence of humans and unfamiliar humans can still evoke fear/aggression responses in wild orangutans who are habituated to familiar humans (pers. obs.). Even after days of continual observation with few/no fear/aggression responses, wild orangutans often attempt to flee from humans by moving away quickly, sometimes taking advantage of diversions (i.e. noisy monkeys or fast-moving gibbons nearby) or waiting until humans are distracted (i.e. looking at notes, taking photos) to attempt escape (Mackinnon, 1974).

Even with experienced observers, orangutans can disappear, and even when their direction of escape is known, it can be difficult to relocate them (pers. obs.). Their skill in escaping also suggests that they alter their behavior in some way prior to and during escapes to increase their chance of success. After 1-2 yrs. experience following/observing orangutans in Kutai National Park, East Kalimantan Indonesia, our observation teams reported being able to predict that an orangutan would try to escape up to several hours in advance of their actually doing so. Evidence of behavior changes in advance of escaping observers would be consistent with their using some form of prior planning. Wild orangutans have demonstrated some behavioral evidence of advance planning of travel direction. Adult “flanged” male orangutans announced their future travel directions up to 24 hours in advance through long-distance vocalizations (long calls) aimed in the direction in which they actually traveled (up to 24 h in advance), and re-emitted long calls when changing directions (van Schaik, Damerius, & Isler, 2013).

If orangutans plan their escapes ahead of their actual attempt, we would expect that they would systematically change their behavior in the hours leading up to an escape. We hypothesized that wild orangutans would display behavioral changes leading up to successfully escaping from observers. Specifically, we predicted the orangutans would alter aspects of their activity budget including changes in time spent feeding, travelling, resting, threat vocalizations, and defecation. We included defecation since local experts claimed that orangutans defecate more when stressed. We would also expect them to change their space use including their location, speed, and direction of travel, to access habitat suitable for escapes over habitat suitable for foraging and other normal activities. Therefore, we also hypothesized that before an escape, orangutans would alter their ranging patterns. Specifically, we predicted that they would increase travel speed, and deviate from their typical travel routes and target areas of habitat they normally avoided.

Method

Subjects and Setting

We observed wild orangutans (*Pongo pygmaeus morio*) in Kutai National Park, East Kalimantan, Indonesia. The study area spans 4-5 km^2 along ~8 km of the south bank of the Sangatta River, accessed by a 200 m grid transect system covering approximately half the area plus several old local trails. The forest has evidence of small-scale illegal logging and hunting in the recent past (pers. obs.). Habitat in the study area was highly disturbed by Borneo-wide forest fires in 1982/83 and again in 1997/98 that heavily damaged the forests in the majority of Kutai N.P. (Setiawan, Nugroho, & Pudyatmoko, 2009), although some small patches of primary forest remain. Burned forest in the study area has been regenerating, and now consists of a mix of primary and secondary lowland riverine and hill forest. The original rainforest in this area was a mixture of riparian and upland mixed dipterocarp forest which experiences masting (Ashton, Givnish, & Appanah, 1988; Leighton, 1993).

Project facilities are ca 1km downriver of Mentoko, the orangutan study site used previously by Rodman, Leighton, Mitani, and Campbell from 1970 through the mid 1980s and near study areas used by Suzuki from 1983 through 2014. The presence of previous research sites suggest that some older orangutans could have had contact with researchers. However, because the population in our study area consisted of many immature/young adult orangutans and few older adults, previous contact with researchers likely had minimal impact on this study. The area's orangutans may also have had recent contact with humans from encounters with Kutai National Park staff and local people. Our research team found evidence of small-scale use of this part of the national park by local people (hunting traps, logging, fishing) and surveys conducted by nearby industries. Our early contacts with local orangutans sometimes elicited threat/aggression displays; some continued for several hours and recurred intermittently for several days. On the other hand, several other orangutans reacted very little to early encounters with our research team; reasons may involve unusually good feeding conditions in the first year of our project relating to El Niño Southern Oscillation events (Russon et al. 2015, pers communication).

Sampling

We found orangutans by searching the study area on foot. Once found, we recorded the orangutan's behavior (feed, travel, rest, social, other) during full-day focal individual follows using a continuous event sampling procedure. We considered a full day observation to be observation spanning an orangutan's entire active period - from the time an orangutan arose from its nest in the morning until resting in its evening nest (Morrogh-Bernard et al., 2009)

We attempted to follow orangutans continuously, to a maximum of 10 days to limit stress. When we lost an orangutan during a follow, we noted the time and any relevant details.

Data Collection

Data collection for this study spanned January 2010 to December 2012. During that period, we observed more than 30 orangutans, of which 18 were observed repeatedly, identified, and named. We recorded behavioral data on the orangutan's activity (feed, rest, travel, social, other), height in the trees, type of locomotion, foods eaten, and any defecation, vocalization, or nesting.

We collected orangutan travel data by creating GPS waypoints every 15 minutes as close as possible to the trunk of the tree that the orangutan occupied using Garmin 60cs and 60csx handheld units. We made an accompanying record of the orangutan's behavior at each data point to facilitate combining behavioral and GPS data and improve detection of data collection errors. In rare cases, behavioral observation sheets and GPS data sheets were lost or damaged and some observer errors were detected; we excluded these observation days from analysis.

To estimate GPS error, we collected waypoints from stationary locations over 3 months using the method described in Bebko (2017).

Measures

Orangutan escape

An orangutan escape was any instance when observers lost contact with an orangutan they were following for at least one hour. Days on which orangutans escaped and were found again were also coded as escape days. We considered an escape day to be any day on which an orangutan escaped. A non-escape day was considered a "normal day".

Orangutan behavior and activity budgets

We recorded orangutan behavior in four standard categories: rest, feed, travel, and other (Morrogh-Bernard et al. 2002). Rest consisted of orangutans remaining stationary in one location without performing other actions (usually sleeping or sitting on a branch). Feed consisted of orangutans consuming any item. A feeding bout ended when we recorded a pause in food consumption longer than 5 minutes. Travel consisted of the orangutan changing location, either arboreally or on the ground, including travel within the same tree. “Other” activity consisted of any behavior that could not be classified as rest, eat, or travel (e.g. social behavior, nesting).

As a basis for assessing behavioral change within a day, we calculated hourly orangutan activity budgets, including the total time spent on feeding, eating, and travelling during 60 min periods. We excluded “Other” behavior from these analyses because it was rare, which made comparisons between days impossible. Orangutans frequently performed two activities at once (e.g. eating while travelling) so activity categories were not mutually exclusive; therefore, total activity time within a one-hour period could be greater than 60 min.

Travel routes

Orangutan travel routes were estimated by connecting the sequence of GPS waypoints marking the focal orangutan’s locations over the course of a day. Full day travel routes spanned an orangutan’s entire active period.

Orangutan Travel Speed

For GPS data, small travel segments are indistinguishable from GPS error (Mason & Knight, 2001). Therefore, to calculate orangutan travel speed we first noise cleaned all orangutan travel routes. Noise cleaning involved collapsing consecutive GPS points falling within the estimated error of the GPS device into their centroid (Bebko, 2017). Since we could not measure smaller movements than the GPS error, orangutans were considered stationary at such centroids. We calculated the orangutan's travel speed for every noise-cleaned travel segment by dividing the distance travelled by the duration of the travel. Since we were interested in the speed of travel *when an orangutan was travelling* (excluding stops), we calculated travel speed only for travel segments which did not include stops longer than 15 minutes (i.e., at least two consecutive GPS points).

Direction of travel at the end of a travel route

Calculating travel direction directly from the last segment of the travel route was problematic since GPS error could lead to large deviations from the actual travel direction. Therefore, we estimated an orangutan's final travel direction by averaging over the final four GPS waypoints (i.e., final 45 min) of their route. We drew vectors connecting each of these final waypoints to the last point of the route. For example, if the final waypoint is labeled point A, and each preceding waypoint labeled B, C, D, we drew vectors BA, CA, DA then averaged the three vectors. This method estimated the orangutan's "average" travel direction leading up to the final point; note that it could not detect last-minute changes in direction.

Analyses

GPS Error Estimation

We calculated GPS error to account for inaccuracies during analyses. Using the methodology from Bebko (2017), we calculated the estimated 95% error circles for all GPS error data collection sessions and determined the mean radius of such circles. (Department of Natural Resources WA., 2004). This represented a 95% confidence limit on the distance a recorded GPS point may have deviated from its true location.

Changes in behavior before an escape

To examine behavioral changes prior to escape, we compared each orangutan’s behavior in the hours leading up to an escape with their behavior during the same time period on a normal day. For all escape days, we calculated the orangutan’s hourly activity budget in the four hours leading up to their escape (henceforth, the “pre-escape interval”). To assess other behaviors possibly related to escaping, we also counted the hourly frequency of defecations and kiss-squeaks over the same 4-hour time interval. In cases where there was insufficient pre-escape observation time for a complete pre-escape interval, or where the 4-hour interval extended into the orangutan’s overnight sleep period, we used as much time as possible without including any sleeping. For a matched comparison to these 4-hour pre-escape intervals, we randomly selected normal days from the same orangutan. To control for time of day, we selected the same time interval at the same time of day as the pre-escape interval from the selected normal day. We omitted from analyses all individuals with too few observation days to yield a matched interval.

Since there were many observations from each orangutan, and since many observations were recorded on the same observation day, our data violate the assumption of independence required for many statistical tests. Therefore, to account for this nesting of data into days of observation and individuals, we used multilevel regression models. We created separate models for each activity (feed, rest, etc.) to examine whether being an escape day and/or the number of hours before an escape predicted the hourly time spent for each activity (Model 2a - Model 2e). Since we predicted hourly behavioral changes on escape days but not on normal days, we included an interaction term in each model between hour and escape day. We allowed random intercepts in the model, but the models assume the same relationship between variables based on orangutan and observation day (non-random slopes). In other words, for the example of feeding time, we allowed the model to account for the fact that some orangutans might spend more time feeding than others, and that orangutans feed more on some days than on others, but the model “averaged” any observed ***changes*** in behavior across individuals and days.

Model 2 (a-e)
R-Statistics code for the multilevel regression models of orangutan activities predicted by time before escape or comparison time and escape day (random intercepts only).

```
Activity ~ Hour + Escape Day + (Hour * Escape Day)
          + (1 | Orangutan) + (1 | Date)
```

Where *Activity* was one of the orangutan activities (1a: Travel, 1b: Feed, 1c: Rest, 1d: Defecation freq., 1e: Kiss squeak frequency), *Hour* was the time in hours before the escape or comparison point, *Escape Day* was a dummy coded variable contrasting escape days vs. normal days, and *Hours * Escape Day* was the interaction term. *Orangutan* was the identity of the orangutan, and *Date* was the date of observation.

Changes in orangutan travel speed leading up to an escape.

To examine whether orangutans changed their travel speed on escape days vs. normal days, we calculated orangutan travel speed for all travel segments from escape day and normal day travel routes. To compare escape days and normal days, and to examine whether speed changed over the course of a day, we then created a random slopes multilevel model (accounting for nesting within an individual orangutan and day of observation as above) of travel speed predicted by the time of day and whether it was an escape day (Model 3).

Model 3
R-Statistics code for the multilevel regression model of orangutan travel speed predicted by time of day and escape day (random intercepts and slopes).

```
Travel Speed ~ Time + Escape Day + (Time * Escape Day)
            + (1 | Orangutan) + (1 | Date)
```

Where *Travel Speed* was orangutan travel speed for one travel segment, *Time* was the time of day, *Escape Day* was a dummy coded variable contrasting escape days vs. normal days, and *Time * Escape Day* was the interaction term. *Orangutan* was the identity of the orangutan, and *Date* was the date of observation.

Spatial distribution and direction of orangutan escapes

To examine the spatial distribution of orangutan escapes we mapped all escape points along with the final points of the matched time period on normal days using ESRI ArcGIS 10. To examine if orangutans were altering their travel routes during escapes compared to their typical travel routes, we mapped the locations of escape with respect to the orangutans' habitual route network previously identified in orangutans ranging in the central part of our study area (Bebko, 2012, 2017). The habitual route network represents travel routes that were frequently reused, shared by multiple individuals. Using a multilevel regression model with random intercepts (Model 4), we compared closest distance to the habitual route network between escape locations and normal day "control" locations.

Model 4
R-Statistics code for the multilevel regression model of closest distance to habitual route network predicted by escape location vs. "control" location (random intercepts only).

```
   Distance ~ Escape Location
+ (1 | Orangutan) + (1 | Date)
```

Where *Distance* was the distance in meters from nearest habitual route, and *Escape Location* was a dummy coded variable contrasting escape location vs. "control" location. *Orangutan* was the identity of the orangutan, and *Date* was the date of observation.

We also mapped the direction of travel at the end of the travel routes for all escape days and matched normal days relative to the habitual route network. To calculate direction of travel, we averaged the direction vector from the final 3 waypoints to the final waypoint. We then projected this direction vector forward by 50 m to examine whether the travel direction was related to the habitual route network. We classified these travel directions according to the criteria described in Table 3.1, then assessed whether travel direction changed on escape days vs. normal days with a chi-squared test for independence.

Table 3.1
Coding system for travel direction relative to habitual route network.

Category	Criteria
Moving along network	Both location and end of the direction vector within habitual route network.
Moving towards network	Location outside network and end of direction vector within network.
Moving away from network	Location within network, end of direction vector outside network.
Far from network	Both location and end of direction vector outside network.

Results

We used a total of 85 observation days from 12 orangutans for the analysis of behavioral changes before an escape on 42 escape days, and 45 normal days. Note: These numbers are not equal since some days had observations from multiple orangutans and some days had multiple escapes.

GPS error estimation

The average radius of 95% GPS error circles calculated from stationary locations was 20.34 m (sd = 9.97, range = 6.37 - 45.20), therefore we estimated the GPS error to be 20 m, instead of the error estimate reported by the devices themselves, which usually ranged between 5-14 m (pers. obs.).

Changes in Orangutan Activity before escape

Regression analysis for changes in orangutan activity on escape vs. non-escape days are summarized in Table 2.

Table 3.2
Regression coefficients for orangutan activities

Random Effects		Fixed Effects				
	S. D.	Predictor	Est.	*S. E.*	*t*	*p*
Model 1a: Travel						
Date	5.75	(Intercept)	8.40	2.34	3.59	0.0003***
Orangutan	4.40	Hour	0.48	0.65	0.73	0.4653
Residual	8.89	Escape Day	14.26	2.73	5.23	< 0.0001***
		Hour*Escape Day	3.89	0.94	4.15	< 0.0001***
Model 1b: Feed						
Date	13.12	(Intercept)	27.05	4.32	6.26	< 0.0001***
Orangutan	8.33	Hour	-0.10	1.09	-0.09	0.9278
Residual	14.83	Escape Day	-12.88	4.95	-2.60	0.0093**
		Hour*Escape Day	-4.10	1.58	-2.60	0.0094**
Model 1c: Rest						
Date	15.20	(Intercept)	22.69	4.56	4.98	< 0.0001***
Orangutan	8.55	Hour	-0.65	1.11	-0.58	0.5625
Residual	15.06	Escape Day	-3.39	5.28	-0.64	0.5206
		Hour*Escape Day	0.37	1.61	0.23	0.8163
Model 1d: Defecation						
Date	0.20	(Intercept)	0.10	0.08	1.30	0.1948
Orangutan	0.00	Hour	-0.02	0.03	-0.68	0.4956
Residual	0.38	Escape Day	0.07	0.11	0.61	0.5415
		Hour*Escape Day	0.03	0.04	0.74	0.4569
Model 1e: Kiss Squeak						
Date	6.13	(Intercept)	0.72	1.71	0.42	0.6740
Orangutan	3.82	Hour	-0.18	0.32	-0.56	0.5728
Residual	4.28	Escape Day	2.46	1.77	1.39	0.1652
		Hour*Escape Day	-0.16	0.46	-0.34	0.7321

Note: *** Significant at $p < 0.001$, ** Significant at $p < 0.01$, S.D.: Standard deviation, S. E.: Standard error of the mean

Changes in travel

Consistent with predictions, we found significant results from the regression model for travel (Table 3.2). The *hour* term was not statistically significant. Probing the model for normal days indicated that on normal days, orangutans' time spent on travel did not change during the 4-hour pre-escape periods. The *escape day* term and *hour*escape day* interaction terms were statistically significant and positive. Probing the model for escape days indicated that on escape days, the total average time of travel was higher than on normal days and travel time increased during the 4-hour pre-escape period.

Changes in feeding

Consistent with predictions, we found significant results from the regression model for feeding (Table 3.2). After probing the model, the interpretation of the results was similar to travel although feeding decreased rather than increased on escape days. On normal days, orangutans' time spent on feeding did not change over the 4-hour pre-escape period (*hour* term not statistically significant). On escape days, the total average time spent of feeding was lower than on normal days (*escape day* term statistically significant and negative), and feeding time decreased through the 4-hour pre-escape period (*hour*escape day* interaction term statistically significant and negative).

Changes in rest, defecation, and kiss squeak

Contrary to predictions, regression models for changes in rest, defecation, and kiss squeaks were not statistically significant (Table 3.2), indicating that rates of these activities did not differ reliably between escape and normal days, and that there were no detectable changes in these activities over the 4-hour time period between escape and normal days.

Summary of changes in orangutan activity

Together, the results of the models on orangutan activity show that on normal (non-escape) days, all the activities measured remained consistent over the 4-hour pre-escape period. However, in the four hours culminating in an escape, orangutans spent increasingly more time travelling and less time feeding than they did on normal days (Figure 3.1). Resting, kiss squeaks, and defecation did not differ significantly on escape days vs. normal days and did not change over the 4-hour interval. Orangutans also travelled terrestrially during the four-hour pre-escape interval (73%) more often than on normal days (11%) (t (298) = 11.82, $p < 0.0001$).

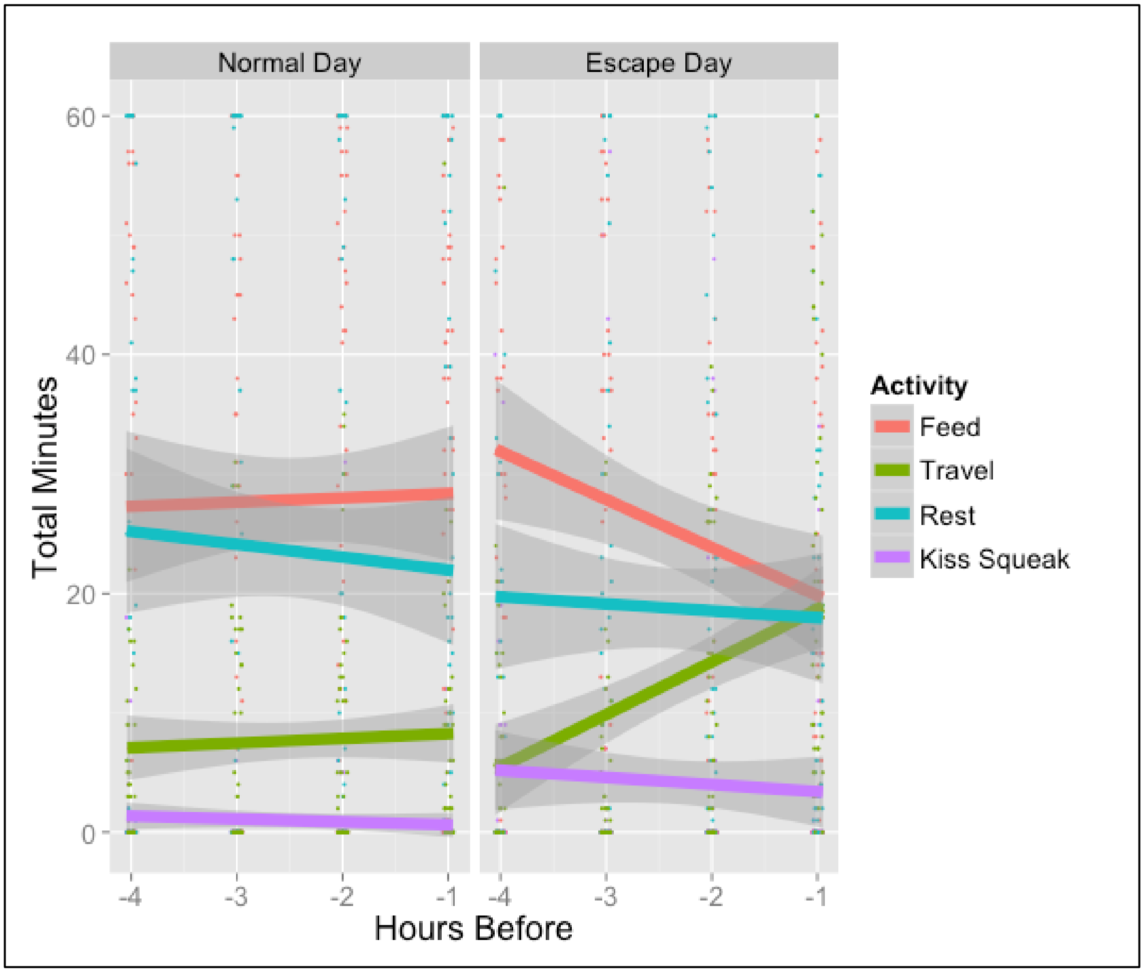

Figure 3.1: Changes in hourly orangutan activity budget over 4 hours either before an escape or on a normal day in Kutai National Park, Indonesia. Thick lines show the regression line for time spent on each activity during each hour, and small dots show the individual data points. Shaded grey areas represent 95% confidence intervals on the regression lines. Frequency of defecation not included on graph.

Changes in orangutan travel speed

Consistent with predictions, the regression model for orangutan travel speed was significant (Table 3.3). There was no average change in travel speed over the course of a normal day (time term not significant). Similarly, there was no average difference in travel speed between escape days and normal days (escape day term not significant). However, on escape days, the average travel speed increased over the course of the day, whereas on normal days, travel speed did not increase (interaction term significant and positive) (Figure 3.2).

Table 3.3
Regression coefficients for orangutan travel speed.

Model 2: Orangutan Travel Speed

Random Effects			Fixed Effects				
		S. D.	Predictor	Est.	S. E.	*t*	*p*
Obs. day	(Intercept)	2.19	(Intercept)	3.32	0.65	5.10	< 0.0001***
	(Slope)	0.15	Time	-0.02	0.05	-0.48	0.6411
Orangutan	(Intercept)	0.33	Escape Day	-1.50	0.89	-1.69	0.0915
	(Slope)	0.04	Time*Escape Day	0.18	0.07	2.55	0.0109*

Note: *** Significant at $p < 0.001$, * Significant at $p < 0.05$.

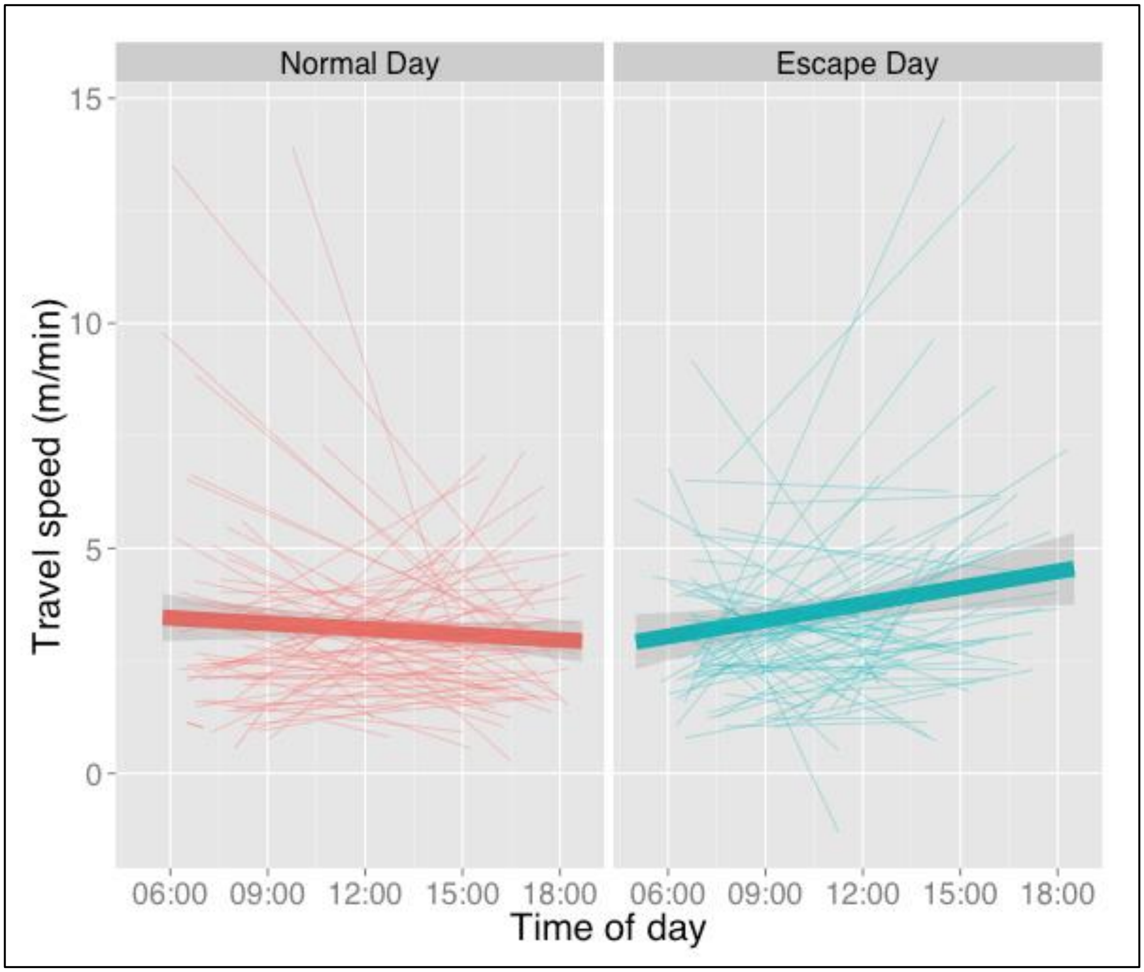

Figure 3.2: Changes in travel speed on escape days vs. normal days. Thin lines represent individual observation days, large thick line represents regression line for estimated speed over the course of a day. Shaded grey area is the 95% confidence limit for this regression line.

Changes in habitat use

Escape locations were significantly farther from the orangutans' habitual route network compared to the last location from selected normal days (Table 3.4). The model indicated that escape locations were 62.06 m farther from the habitual route network than normal day "control" locations (Figure 3.3).

Table 3.4
Regression coefficients distance to habitual route network of escape locations.

Model 3: Orangutan Travel Speed

Random Effects			Fixed Effects				
		S. D.	Predictor	Est.	S. E.	*t*	*p*
Orangutan	(Intercept)	582.4	(Intercept)	453.80	136.99	3.31	0.0009***
Date	(Intercept)	0.0	Escape Location	62.06	29.46	2.11	0.0352*

Note: *** Significant at $p < 0.001$, * Significant at $p < 0.05$.

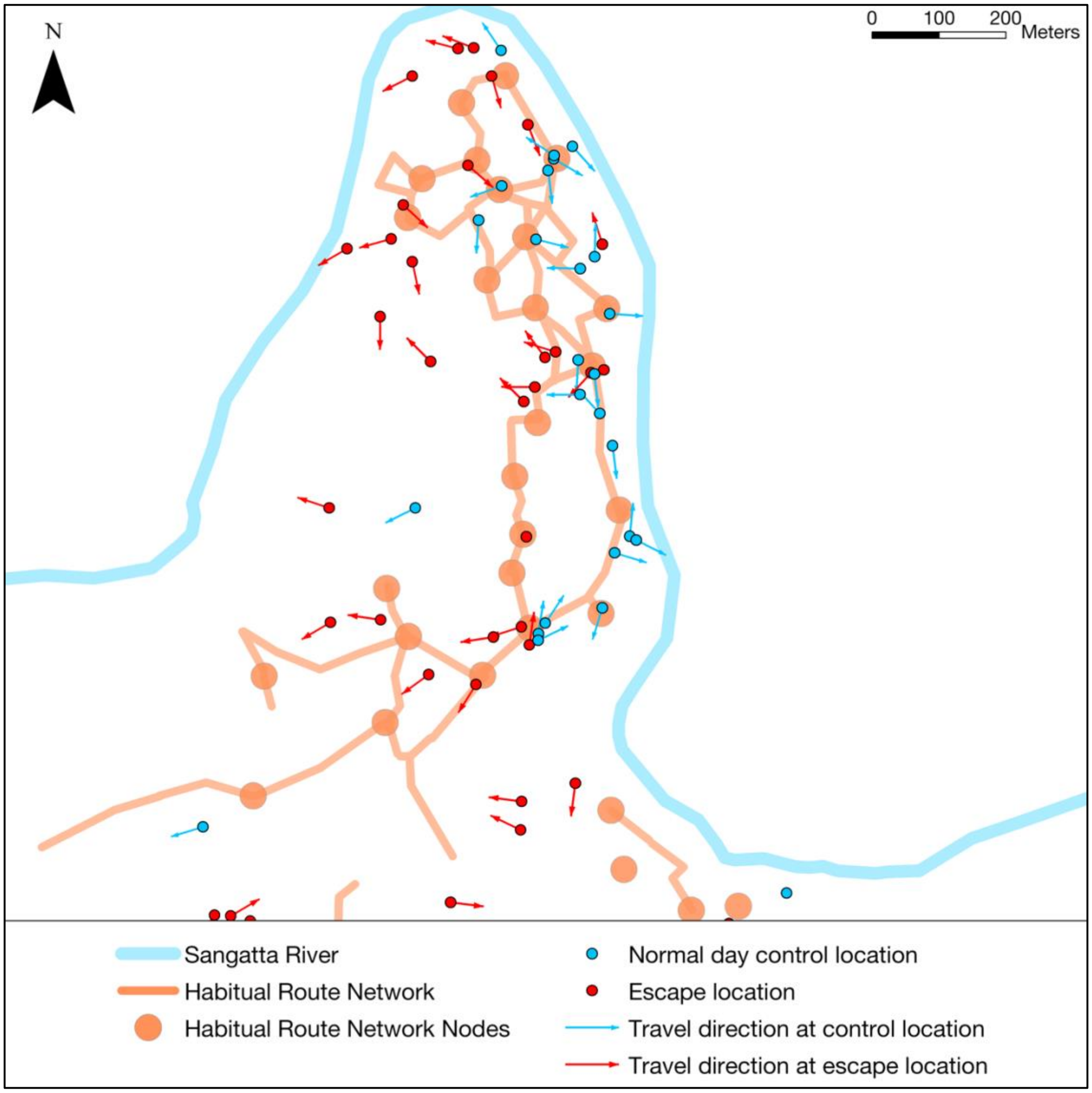

Figure 3.3: Location and travel direction where orangutans escaped our observation team (red) mapped with respect to the final locations of matched "normal" day control locations (blue) in Kutai National Park, Indonesia. Data are overlaid on the orangutans' habitual route network (orange).

Orangutans' travel direction leading up to their escape was more likely to be far from the habitual network, whereas the travel direction at the same time of day on randomly selected normal days was more likely to be along the routes in the habitual network, but escape days and normal days did not differ in the proportion of routes travelling away from or towards the network (χ^2 (3) = 8.37, *p* = 0.039) (Figure 3.3-4). Field observers reported that orangutans typically travelled towards clearings and areas with little canopy cover during escapes, but we were unable to test this statistically.

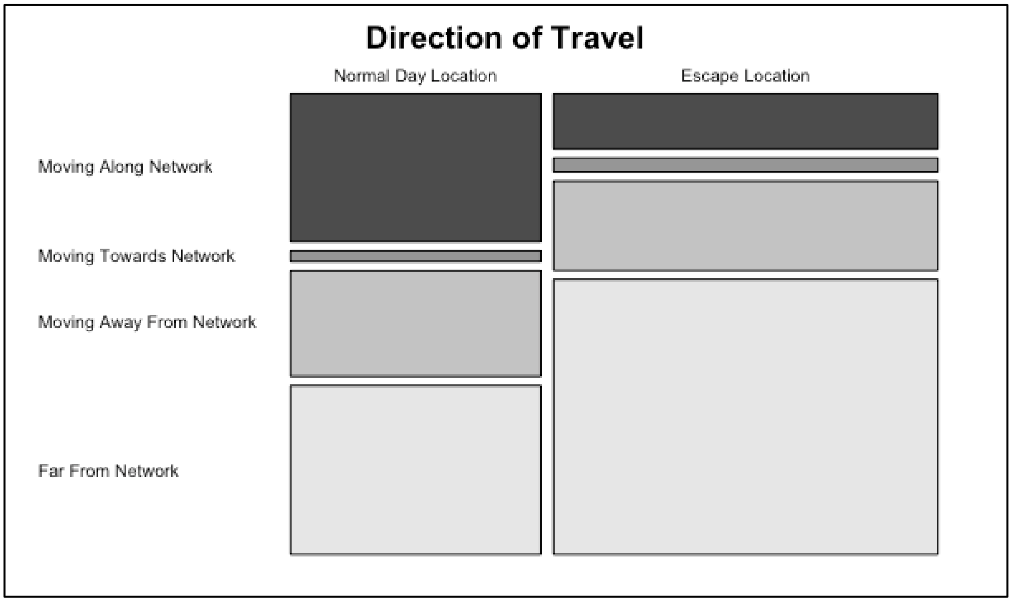

Figure 3.4: Mosaic plot of the orangutans' travel direction at normal day "control" locations vs. escape locations. Mosaic plots show contingency tables with the heights of the boxes matching between columns if data matches the expected cell counts. The area of each cell represents its frequency. Data collected in Kutai National Park, Indonesia.

Discussion

Similar to previous reports on orangutans (Mackinnon, 1974), this study found orangutans to be adept at escaping human observers and did so frequently. Consistent with predictions, these orangutans significantly altered their behavior leading up to escapes. Their activity budget changed at least four hours before an escape compared to that of a normal day. In particular, they spent more time traveling and less time feeding on escape days compared to normal days. This is consistent with findings from many other animals that prioritize threat avoidance over foraging success and travel longer distances when threatened (Ciuti et al., 2012; Constantine et al., 2004; Cristescu et al., 2013; Duchesne et al., 2000; Henry & Hammill., 2001; Kerbiriou et al., 2009; Lemon et al., 2006; Z. Li et al., 2013; Naylor et al., 2009; Neumann et al., 2010; Rumble et al., 2005; Steckenreuter et al., 2012; Vermeulen et al., 2012). Travelling increased and feeding decreased every hour leading up to an escape, whereas activity budgets remained stable over the same time period on normal days. On escape but not normal days, orangutans also increased travel speed over the course of the day; on escape days, they were also more likely to travel terrestrially. Together, these results suggest that leading up to an escape, orangutans were using time that they normally spent on feeding to travel farther.

Increased terrestrial travel during escapes may suggest that the observation team had more difficulty following terrestrial orangutans. However, there were at least two re-used terrestrial routes reported by field staff, one of which was classified as a habitual route. Such routes were reported to be relatively free of dense ground vegetation and were not difficult for the observation team to follow the orangutans. This suggests that at least some terrestrial routes may be habitual, however, more data is required to assess this in our population. It follows that a portion of the escape routes could represent as-yet-undetected habitual routes (although see below for a counter-argument).

Previous studies have established that during habituation, primates tend to travel longer distances than when they become habituated. Our results suggest that escape days may contribute substantially to this change, This is consistent with Cipolletta (2003) and Doran-Sheehy et al. (2007), who suggested that gorillas' longer daily travel distance in the early stages of habituation was due to groups actively fleeing human observers. Several of the orangutans we studied were not well habituated during the time these data were collected, and we lacked remote tracking technology, so we could not assess such changes in travel distance directly.

Contrary to predictions, there were no statistically detectable differences between escape days and normal days in resting, kiss-squeaking, or defecating. Although orangutans likely felt threatened on escape days, they may have inhibited kiss-squeaking to increase stealth. The lack of increased defecation could owe to the reduced amount of time spent feeding on escape days.

Although our results are consistent with orangutans deliberately changing their behavior in advance of an escape from human observers, results could also be explained if orangutans were simply switching to an established alternative daily routine that we rarely observed. For example, during times of resource scarcity, orangutans may be less tolerant of observation. Our observation team may have been more likely to lose orangutans due to their changed routine - rather than because orangutans deliberately attempted to evade them. However, several of our results make this alternative unlikely. Prior to escapes, we found that orangutans targeted locations in areas where they do not typically travel, far from their habitual route network. If such escapes were an alternative routine, we would expect that in some instances the observation team would not lose them and observe them using this rarely visited habitat for other reasons (e.g. for rarely accessed but important resources). However, this had not yet been observed in our study area, and in the instances where the orangutans were relocated after escaping, they were typically back along their network. Additionally, although not tested statistically, field staff reported that orangutans often escaped at locations where there was little forest canopy cover and dense ground vegetation, making human travel difficult. We suggest that rather than orangutans adopting alternative routines on escape days, our results are more consistent with orangutans deliberately leaving their habitual route network and targeting such areas to evade humans.

Anticipatory behavior, increasing speed when nearing goals, and targeted movement towards specific locations have often been used as indicators of goal-directed travel and planning in other primate studies, and our results are consistent with this interpretation (Janson & Byrne, 2007; Noser & Byrne, 2007b; van Schaik et al., 2013). Based on the fact that orangutans alter their behavior and space use hours before escaping, we suggest that orangutans may encode spatial knowledge about the locations of forest clearings and use this information to escape unwelcome visitors, including human observers. In this study, due to limited manpower (and the orangutans' skill in escaping), we were usually unable to relocate the orangutans once they escaped and so could not assess their behavior afterwards. Future studies with more manpower and methods designed to better relocate orangutans after escaping might be able to examine whether orangutans target these forest clearings for other reasons than escape by examining their behavior after escapes. If orangutans return to normal activities after an escape, it would suggest they use clearings as part of an alternative daily routine. If, on the other hand, they remain irritated at the presence of humans, and attempt re-escape, it would provide support for deliberate escapes using spatial memory and planning. Longer-term observation of this orangutan population will also yield more information about whether the observed travel away from the habitual route network is a rare but normal occurrence, or only occurs during escape events.

This study was successful in showing how a situation that many researchers treat as an annoyance can be used to learn more about the organization and flexibility of orangutan behavior. Previous studies have typically focused on comparing primate behavior before and after habituation, demonstrating that individuals gradually shift from human-altered behavior to their more normal behavior (Cipolletta, 2003; Doran-Sheehy et al., 2007; Jack et al., 2008). Typically, such researchers treat data collected during habituation as less useful. In this study, we demonstrate that semi-habituated primates provide unique situations in which to examine their behavior and its determinants.

Overall, our results suggest that wild unhabituated orangutans alter their behavior several hours in advance of successfully escaping human observers. Although preliminary, our results are consistent with orangutans deliberately attempting escapes by prioritizing traveling over feeding, and by targeting travel away from their normal travel routes towards areas where humans are less able to follow them.

Chapter 4: Research Paper 3: Deep neural networks can model wild orangutan space use from satellite imagery at resolutions approaching ten meters

Adam O. Bebko

Abstract

Animals do not use their home ranges uniformly, visiting certain areas frequently while avoiding other areas entirely. Previous studies have typically examined animal space use on spatial scales that affect entire populations. Modelling animal space use on a more local scale would allow examining the areas and the proportion of a given habitat that animals actually use regularly as well as areas they tend to avoid. In this study, I applied deep machine learning to model space use in a population of wild orangutans (*Pongo pygmaeus morio*) in Kutai National Park, East Kalimantan, Indonesia. I predicted that neural networks would be able to learn patterns in satellite images to successfully model orangutan space use in our study area. I compared several architectures of deep convolutional neural networks and trained them using behavioral and ranging data paired with raw visual-wavelength satellite imagery of the area. I evaluated the effectiveness of the neural network by validating the model using a variety of machine learning diagnostics. The final model accurately predicted orangutan space use in our study area with resolutions approaching 10 m. The model used visible-wavelength satellite images alone, indicating orangutan space use must be related to local visual characteristics of their habitat. Possible factors may include different colors/brightness of local vegetation and ecological features. This study demonstrated the potential of using machine learning technology for applications in animal behavior and ecology.

Keywords: Orangutan, Habitat, Deep Neural Networks, Modelling, Ecology

Deep neural networks can model wild orangutan space use from satellite imagery at resolutions approaching ten meters

Animals do not use their home ranges evenly. Even within regions of similar habitat (e.g., rainforest), animals can visit certain areas frequently, while avoiding other areas entirely (Di Fiore & Suarez, 2007; Hopkins, 2010; Lührs et al., 2009; Noser & Byrne, 2010; Porter & Garber, 2012). Understanding and predicting areas of habitat that animals prefer has important applications for conservation and management. The ability to identify and model preferred areas of habitat would be beneficial for assessing a habitat's population carrying capacity, detecting areas of degraded habitat, and/or flagging areas important for conservation.

Previous studies that model animal space use have typically examined spatial scales that affect entire populations (i.e. 10 – 1000 km) (Hickey et al., 2013; Laundré, Hernández, & Altendorf, 2001; Palminteri et al., 2012; Squires et al., 2013). Although important, such modelling does not provide a description of local conditions at spatial scales pertaining to individual animals or small groups. Modelling animals' space use on a more local scale would allow examining the areas and the proportion of a given habitat that animals actually use regularly as well as areas they tend to avoid. This would allow for more detailed assessment of usable habitat size and quality. However, collecting the data required for such models at resolutions pertaining to individuals can be very expensive and time consuming. In-situ surveys often involve large, highly trained teams working for time spans of several months, and satellite-derived data are often low in resolution (especially in developing countries) so typically they can only be applied to larger-scale population-level applications. In the few studies that have examined more local scale data, researchers have typically focused on the animals’ preferences for broad habitat types, regional topology, and/or anthropogenic disturbance, rather than the characteristics of localized habitats within their study areas (i.e Howard et al. 2015).

Freely available data from scientific satellites are improving in resolution but lag considerably behind the resolution of commercial mapping and navigation satellites. Mapping applications such as Google Earth now provide global maps at resolutions of less than one meter (in some areas resolution approaches 10 cm). However, these commercial satellites are typically based on visible wavelengths which, compared to multi-band scientific satellites (i.e. LANDSAT), are less useful for classifying vegetation and other habitat characteristics important to animals (Xie, Sha, & Yu, 2008). Nevertheless, the field of deep machine learning has recently made great advances in computer image recognition and analysis (F. F. Li, Johnson, & Yeung, 2018; Zeiler & Fergus, 2014). Using machine learning, computers are now able to learn complex non-linear patterns within large image datasets that may be unrecognizable to humans (Ng, 2018). Despite these great advances in machine learning technology, animal researchers have been slow to adopt it in their research (Phillips, Anderson, & Schapire, 2006). The recent availability of free high-resolution satellite imagery combined with state-of-the-art free machine learning packages opens up new avenues for analysis of animal space use at smaller spatial scales.

Some researchers, especially in the field of ecology, have begun applying machine learning algorithms to habitat modelling using Maximum Entropy (MaxEnt) models (Hickey et al., 2013; Howard et al., 2015; Phillips et al., 2006). MaxEnt models outperform generalized linear models and generalized additive models in modelling animal distributions (Phillips et al., 2006). However, MaxEnt requires a suite of ecological predictor variables to input into the model and can only detect exponential relationships and interactions between predictors.

A more modern group of machine learning algorithms, called deep neural networks, could provide an alternative to MaxEnt models. Deep neural networks consist of a network of many artificial “neurons” that are linked mathematically in processing layers. No assumptions are made about the structure or relationships within the data, so the network can learn extremely complicated patterns in the data that other models, including MaxEnt, would not be able to detect. Deep neural networks can be specialized for processing image-related data (F. F. Li et al., 2018; Ng, 2018; Zeiler & Fergus, 2014) and could yield improved results with satellite imagery compared to other models. To date, very few studies have used deep neural networks in animal research (i.e. Browning et al., 2018) and I found none relating to modelling space use. However, ecologists examining continent or country-scale habitat classification have been using deep neural networks for at least a decade, albeit rarely (Xie et al., 2008).

Orangutans provide an excellent candidate species for the application of machine learning in modelling space use. Orangutans are now critically endangered, with wild populations declining rapidly throughout their range due to extensive habitat loss (IUCN, 2018). Orangutans inhabit tropical rainforest on the islands of Borneo and Sumatra and are now predominantly found in protected areas and small forest fragments disconnected from larger populations (Husson et al., 2009; Utami-Atmoko et al., 2017). Modelling orangutan habitat preferences could have important applications for managing this remaining habitat and highlighting areas important for orangutan conservation. Such modelling could also contribute to designing reforestation efforts and the creation of habitat corridors to reconnect separated populations.

Orangutan behaviors, especially travel decisions, are likely based in part on local ecological factors, similar to other arboreal primates (Di Fiore & Suarez, 2007; Hopkins, 2010; Lührs et al., 2009; Noser & Byrne, 2010; Porter & Garber, 2012). Some such ecological factors, especially the distribution of tree species that orangutans use for resources, could be among the visual characteristics detectable from satellite imagery. For example, visible-spectrum satellite images may show particular patterns of colors and shadows for trees of certain species, or particular colors for areas devoid of trees including dirt and grass. If such visual characteristics are consistently present in areas orangutans visit often and absent in areas they avoid, deep machine learning algorithms should be able to learn and correctly identify these associations after extensive training with pre-coded data.

In this study, I apply deep machine learning to model orangutan space use in a population of wild orangutans (*Pongo pygmaeus morio*) in Kutai National Park, East Kalimantan, Indonesia. Rough surveys have estimated the park's orangutan population at around 1700 individuals (Utami-Atmoko et al., 2017) with some 2000 more living outside the park boundaries per the most recent estimate (Meijaard et al., 2010). However, the extent of intact orangutan habitat within the park's boundaries is unknown, and parts of the park experience severe human damage and encroachment. The recently established Bendili orangutan study area is located along the park's northern border between areas facing major human encroachment, and areas relatively free of human presence. For this reason, it is a key location to assess habitat quality and orangutan space use to highlight areas important for orangutan conservation and areas where habitat may be degraded.

Using orangutan ranging data collected in the Bendili study area, I trained a deep neural network by combining behavioral and ranging data with raw satellite imagery of the area. I predicted that the neural network would be able to successfully learn patterns from the satellite images to model orangutan space use. I evaluated the effectiveness of the neural network by validating the model using a variety of machine learning diagnostics.

Method

Setting

Project facilities were in Kutai National Park, East Kalimantan, Indonesia ca. 1 km downriver of Mentoko, the orangutan study area used by Rodman, Leighton, Mitani, Campbell, and Suzuki from 1970 through the mid 1980s. The Bendili study spanned 4-5 km^2 along ~8 km of the south bank of the Sangatta River, accessed by a 200 m grid transect system covering approximately half the area plus several old local trails (Figure 4.1); orangutans had been studied there since the study area was established in January 2010. The forest had evidence of small-scale illegal logging and hunting in the recent past (pers. Obs.). Habitat in the study area was highly disturbed by Borneo-wide forest fires in 1982/83 and again in 1997/98 that heavily damaged the forests in the majority of Kutai N.P. (Setiawan et al., 2009), although some small patches of primary forest remained. Burned forest in the study area had been regenerating naturally, and the area consisted of a mix of primary and secondary lowland riverine and hill dipterocarp forest at the time of this study (Russon et al., 2015). The original rainforest in this area was a mixture of riparian and upland mixed dipterocarp forest (Leighton, 1993).

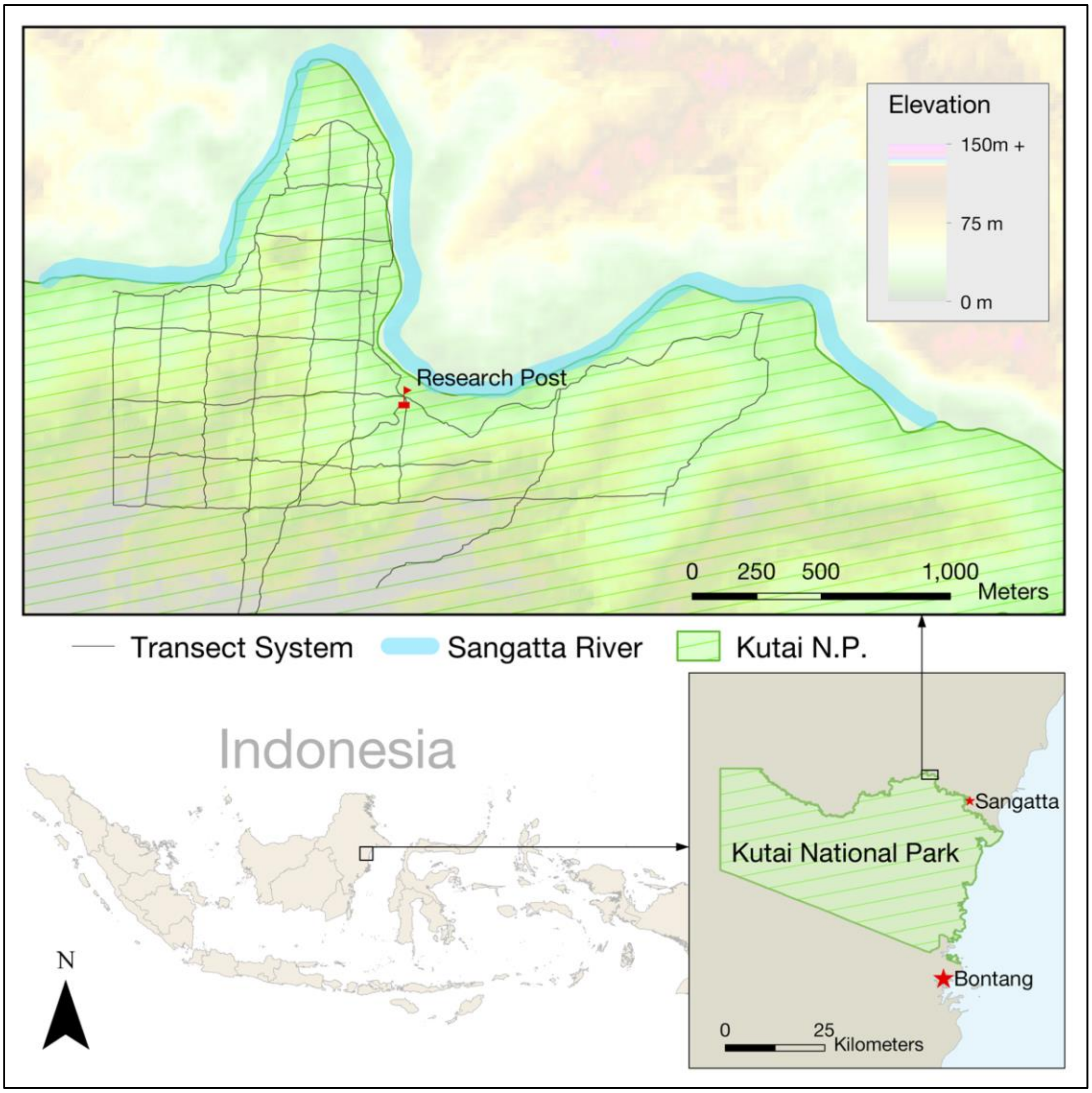

Figure 4.1: Map of Bendili study area inset on map of Kutai National Park, East Kalimantan, Indonesia.

Data Collection

Data on local orangutan habitat use used in this analysis spanned January 2010 to December 2012. We observed wild orangutans (*Pongo pygmaeus morio*) by searching the study area on foot. Once found, we recorded the orangutan's behavior during full-day focal individual follows using a continuous event sampling procedure. We attempted to follow orangutans continuously to a maximum of 10 days to limit stress. In addition to behavioral data, we collected orangutan travel data by creating GPS waypoints every 15 minutes as close as possible to the trunk of the tree that the orangutan occupied using Garmin 60cs and 60csx handheld units. To estimate GPS error, we collected waypoints from stationary locations over 3 months using the method described in Bebko (2012). During this study period, we observed more than 30 orangutans, of which 18 were observed repeatedly, identified, and named.

Measures

Travel routes

Orangutan travel routes were estimated by connecting the sequence of GPS waypoints marking the focal orangutan's locations over the course of a day. Full day travel routes were routes spanning an orangutan's entire active period. For GPS data, small travel segments are indistinguishable from GPS error (Mason & Knight, 2001). Therefore, to calculate orangutan travel speed we first noise-cleaned all orangutan travel routes. Noise-cleaning involved collapsing consecutive GPS points falling within the estimated error of the GPS device into their centroid (Bebko, 2012). Since we could not measure smaller movements than the GPS error, orangutans were considered stationary at such centroids.

GPS Error Estimation

We calculated GPS error to account for inaccuracies during analyses. Using the methodology from Bebko (2017 [in press]), we calculated the estimated 95% error circles for all GPS error data collection sessions and determined the mean radius of such circles (Department of Natural Resources WA., 2004). This represented a 95% confidence limit on the distance a recorded GPS point may have deviated from its true location.

Orangutan space use

I created a procedure for categorizing the study area into locations that orangutans revisited, did not use, or used infrequently. To determine revisited areas, I mapped all travel routes recorded during the 2010-12 study period then used an algorithm programmed in Python for ESRI ArcGIS 10 to detect overlapping travel routes while accounting for the error in GPS devices (Bebko, 2012, 2017). The result of this algorithm produces a map showing the number of times orangutans revisited locations in the study area (Figure 4.2).

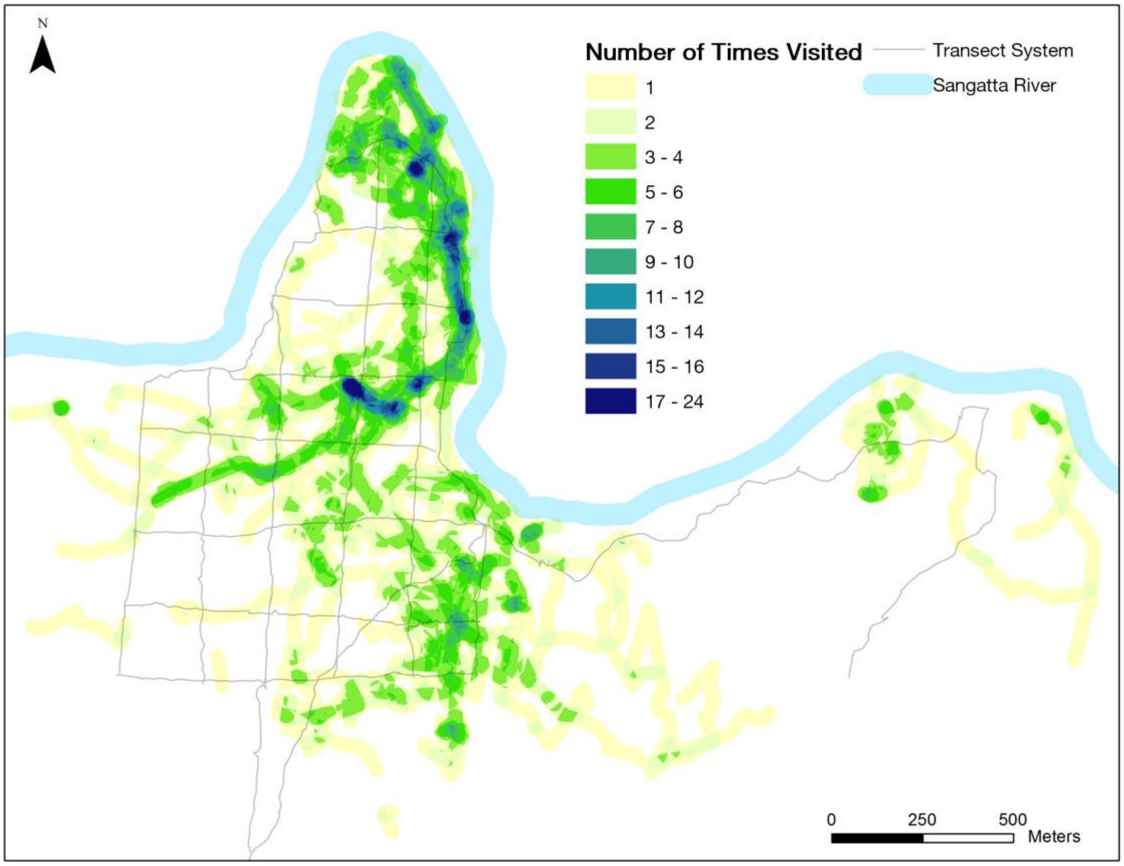

Figure 4.2: Map of number of revisits to locations in the study area. Overlapping travel routes were calculated accounting for GPS error.

To allow for analysis of these locations, I converted this map into raster data with each pixel representing a 10x10 m cell. Each cell's value was the number of times an orangutan was observed to have visited that cell (Figure 4.3). This raster data set included many areas in our study area where our team rarely searched for orangutans, and we likely targeted our searching to areas where we previously found orangutans rather than areas where we hadn't previously found orangutans. To control for this probable under-sampling of some areas, I used the raster "buffer" function, to discard all empty cells that were farther than 4 cells away from a visited cell. This means that raster cells coded with zero visits were excluded if they were far (> 40 m) from any orangutan data we collected. This process ensured that regions in the study area that the observation team did not visit were excluded from analysis.

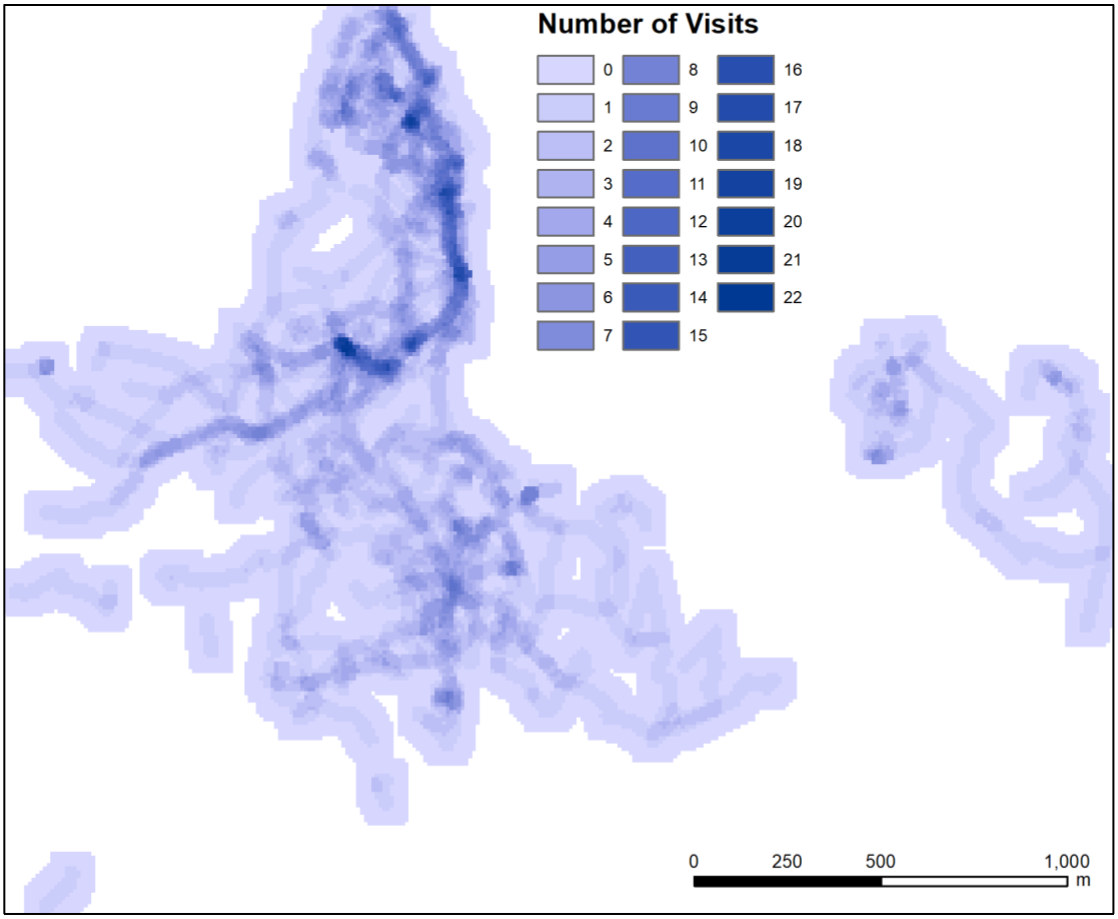

Figure 4.3: Raster image showing number of visits per cell, excluding empty cells distant from an observed orangutan travel route.

Revisited locations

To differentiate repeatedly visited areas, which are likely preferred areas for orangutan travel, from areas with zero or few visits, I binned all values in the above raster into two categories “revisited” and “less visited”. Although by definition revisited refers to two or more visits, to be conservative, and to represent areas that were revisited *frequently*, I defined revisited areas as cells with three or more visits, and not revisited areas as cells with two or fewer visits. This had the added benefit of excluding locations where only travel routes The resulting binned raster image represents orangutan space use in our study area as areas that were revisited/ not revisited.

Local Habitat

I created a high-resolution color image spanning the entire study area by collecting the highest possible resolution Google Earth Pro images (Images © 2018 DigitalGlobe and Google Earth) from all areas of our study area, then joining them together in ESRI ArcGIS to create one large GeoTIFF image of the study area (Figure 4.4). Each pixel of the resulting image represents an area of 1.40x1.41 m.

Figure 4.4: Satellite image of study area derived from a mosaic of high-resolution Google Earth Pro images (Images © 2018 DigitalGlobe and Google Earth).

To represent local habitat at each location, I created a 50x50 m moving window centered on each cell of the rasterized space use image created above. For each cell, I clipped the large Google Earth image using the moving window, resulting in a color image of the habitat around the cell. This 36x36 pixel image contains 3 data points for each pixel representing the red, green, and blue color bands.

Analysis

Deep Neural Network

Neural network models are similar to Generalized Linear Models (GLMs). Like GLMs, neural networks use many data examples to create a mathematical model that predicts a dependent variable from a set of predictors while minimizing prediction error. However, unlike GLMs, neural networks can quickly predict very complex non-linear relationships from extremely large data sets.

Neural networks use different language to describe concepts familiar to users of GLMs (Ng, 2018). Data “examples” consist of a “label” (y) and a set of “features” (x). The features and their associated labels are similar theoretically to the predictors and the dependent variable (respectively) in standard GLM regression. Neural networks are created naïve in the sense that they are initialized with no information from the dataset. To learn patterns in the data to arrive at their predictions, the network is “trained” by feeding examples into the network. The network uses the examples’ features (x) to calculate predictions ($\hat{y}$), which are then compared to the examples’ actual labels (y). The network “learns” by adjusting its internal structure to reduce the error between predictions and labels.

The internal structure of neural networks consists of “neurons” which are units that take several inputs, that are weighted and summed using functions (typically sigmoid or ReLu functions) that produce binary output (on or off). These neurons are stacked in layers. Each layer in the network can learn progressively complex patterns in the data. Data enter each layer successively up to the final layer which represents the network’s predictions. As more data are fed into the network, the network reduces error between predictions and labels by minimizing a function representing total error of all examples fed into the network. Rather than minimizing such error using least squares or other standard regression functions, neural networks use a custom function called a cost function. The appropriate cost function depends on the type of data being used, the importance of computational speed, amount of training data available, and the specifics of each use-case. Minimizing the cost function adjusts the connections between neurons in the network to reduce the network’s prediction error.

During training, the cost function is minimized using a process called gradient descent. Although it is possible to feed all data examples into a neural network at once, this is extremely demanding computationally, so researchers typically use a process called mini-batch stochastic gradient descent (SGD) (Bottou, 1998). Mini-batch SGD involves creating small batches of examples by randomly selecting subsamples (with replacement) from the data set and feeding them into the network; this ensures gradient descent is only performed on a very small number of examples at a time, greatly speeding computation time. This process balances computation time with predictive power and is currently the standard technique used in academic and industrial applications (Bottou, 1998; Google inc., 2018). This process is typically repeated thousands of times during training.

The performance of the model’s predictions can be evaluated during training by periodically calculating the accuracy of the model’s predictions. The most useful measure of accuracy is training accuracy, which refers to the percentage of examples that were correctly predicted (Ng, 2018). As the model is exposed to more batches during training, its accuracy typically improves and then stabilizes asymptotically at a maximum value. This maximum value is the model's final training accuracy. Graphing this stabilization process (accuracy over time) is called a learning curve (Ng, 2018). Learning curves are typically very noisy, so the graphs are typically smoothed to clarify overall trends. Examining learning curves allows for assessing and comparing the performance of different neural network models.

Since neural networks are trained from examples taken from one dataset, they eventually learn to predict this training data to a very high accuracy. Therefore, it is also important to assess performance of the network on data it has never seen. To accomplish this goal, a percentage of the total data set is set aside for validation of the model separate from the examples used for training. This validation dataset is never used to train the network, rather it is used to assess how the network performs on new data. Typically up to 30% of the total data is reserved for validation purposes (Ng, 2018). The percentage of correct predictions on the validation dataset is called the model's validation accuracy. Validation accuracy learning curves are typically tracked alongside training accuracy to compare the performance of different models on new data.

Data preparation for neural network training

I created one example from each cell in the raster image. For each example, its features were the RGB pixel values of the local habitat image (described above), and its label was whether the cell was revisited or not revisited. This process resulted in 24184 total examples. To validate the model's performance, I reserved 20% of the data (4836 randomly selected examples) for validation and therefore used 19348 training examples.

Neural Network Architecture

To create the neural network I used Google TensorFlow, a freely available state-of-the-art package for neural network applications in the python programming language. For this study, I used a convolutional neural network, currently the best method to analyze image data (F. F. Li et al., 2018; Zeiler & Fergus, 2014).

The first layers in the neural network were convolutional layers. Convolutional layers use filters to allow the network to learn patterns relating to subsections of images, combined with a pooling layer to ready the data for the next layers (F. F. Li et al., 2018). The first convolutional layer had 64 such filters, and each subsequent convolutional layer doubled the number of filters to allow the network to learn increasingly complex patterns on smaller portions of the images. I determined the number of convolutional layers to use by training separate networks using three or four convolutional layers then comparing the two results (Figure 4.5). Comparing these model architectures demonstrated better performance with four layers, so I used four layers in the final model.

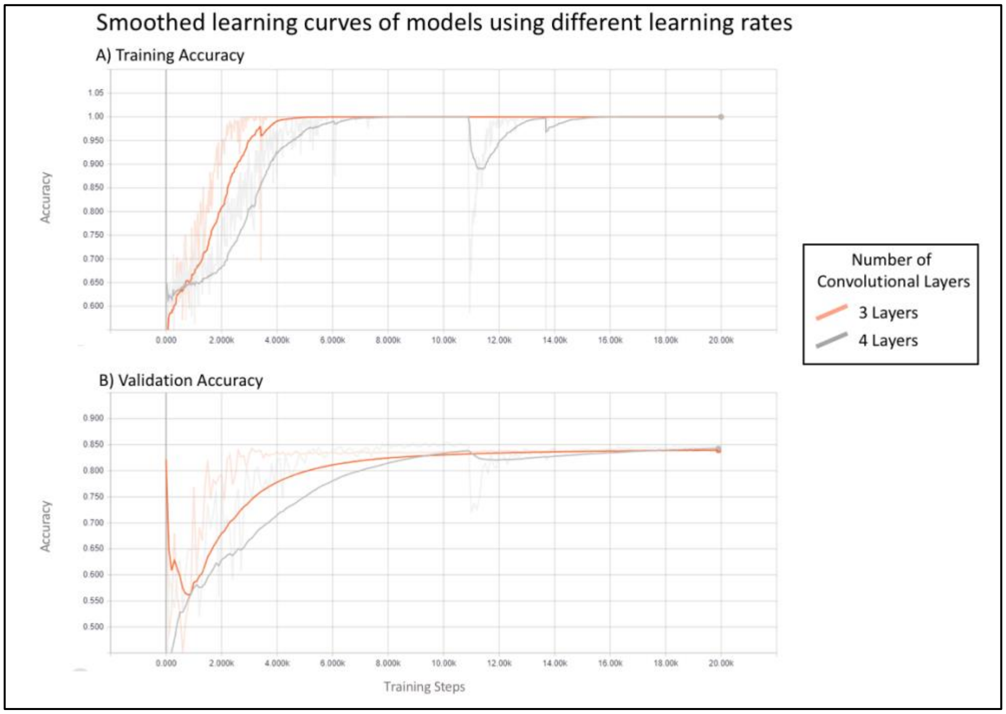

Figure 4.5: Comparison of smoothed learning curves of the most successful models on training accuracy (A) and validation accuracy (B), using three (grey) vs. four (orange) convolutional layers. Higher values are more accurate (perfect accuracy is 1.0). The network with four layers (orange, top curve) yielded the best performance. The noisier curves displayed in faded colors display the models' unsmoothed learning curves.

After the convolutional layers, data were then fed into a layer to flatten the results from the final convolutional layer back into one dimension. This flattening layer was followed by a dense layer. Dense layers, in contrast to convolutional layers consist of basic neurons with no filters or pooling applied. This dense layer finally fed into a logits layer. This logits layer stored the predicted probability of each example being labelled revisited or not revisited. These probabilities represent the model's confidence its predictions are accurate.

I calculated the model's cost function using TensorFlow's softmax cross entropy function on the logits layer of the network. The softmax cross entropy function is a logistic function that classifies the probabilities from the logits layer into distinct classes (Bishop, 2006; Zeiler & Fergus, 2014). It used values from the final logits layer to determine the most likely classification of the inputs, and the confidence in these classifications. During training, I minimized this cost function using Google TensorFlow's AdamOptimizer, which uses the ADAM algorithm (Kingma & Ba, 2015) to efficiently minimize this cost function (calculate gradient decent) on complex functions including softmax.

I visualized the final neural network model architecture using Google TensorBoard (Figure 4.6).

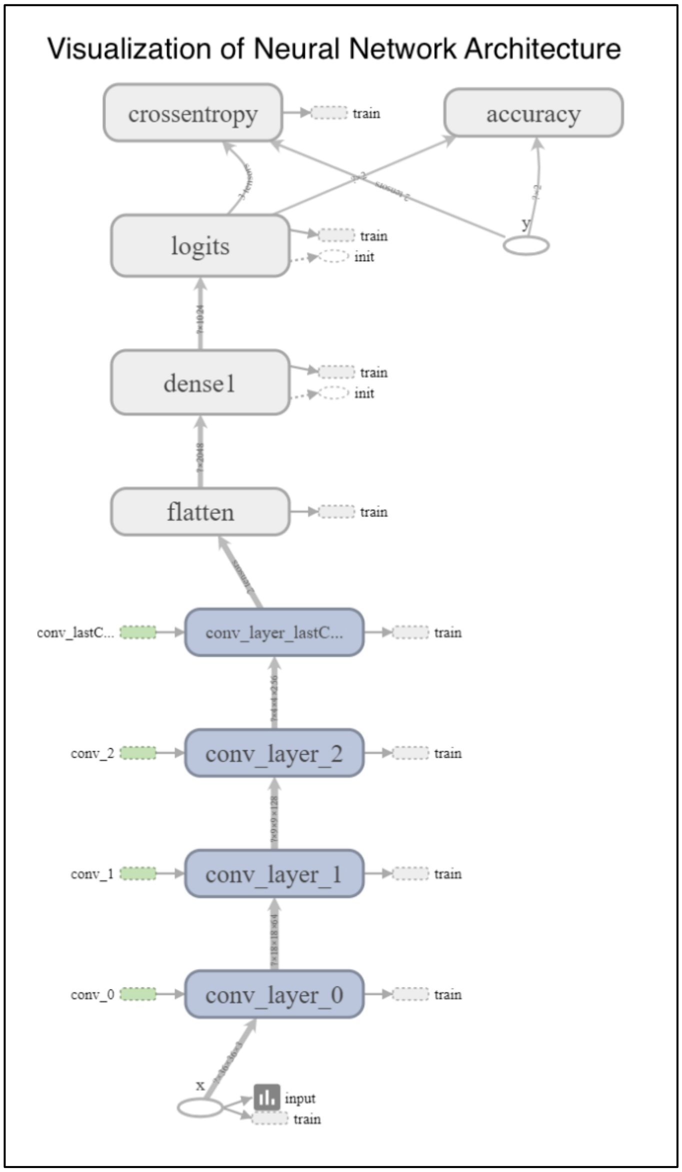

Figure 4.6: Google TensorBoard graph visualizing the selected neural network model architecture with four convolutional layers. Models using 3 convolutional layers performed worse. Inputs (x) flow from bottom to the top of the network, where accuracy is calculated by comparing predictions to observed values (y).

Network Training and Diagnostics

After selecting neural network architecture, I completed several diagnostic tests to determine the appropriate values of certain model parameters to ensure successful training. For such diagnostic tests, I trained the network over 20 000 iterations (called steps) using examples from the training dataset. I used mini-batch SGD. In each step I fed one batch into the neural network. After each step, I calculated the training accuracy on the batch and validation accuracy on the entire validation dataset. For diagnostic tests, neural network performance is evaluated using a combination of maximum training accuracy, maximum validation accuracy, and the speed at which the learning curves stabilize.

If batches contain a majority of one label the network can run into problems during training. This is because the network can achieve high accuracy by simply learning to always predict one label no matter the inputted examples (Ng, 2018). In my training dataset, batches contained mostly cells labelled “not revisited” and few (sometimes none) labelled “revisited”. Consequently, initial attempts to train the network achieved relatively high training accuracy by predicting “no revisit” no matter the inputs, since the data primarily consisted of examples labeled “no revisit”. To prevent this problem from occurring, I ensured that batches consisted of 50% positive and 50% negative examples so such “guessing” would yield an accuracy of only 50%.

The size of batches in mini-batch SGD is typically selected by training the network using several values and using the value that yields the best performance. I trained several neural networks that used different batch sizes (Figure 4.7) and selected the batch size (128) that yielded the best performance in all three performance metrics.

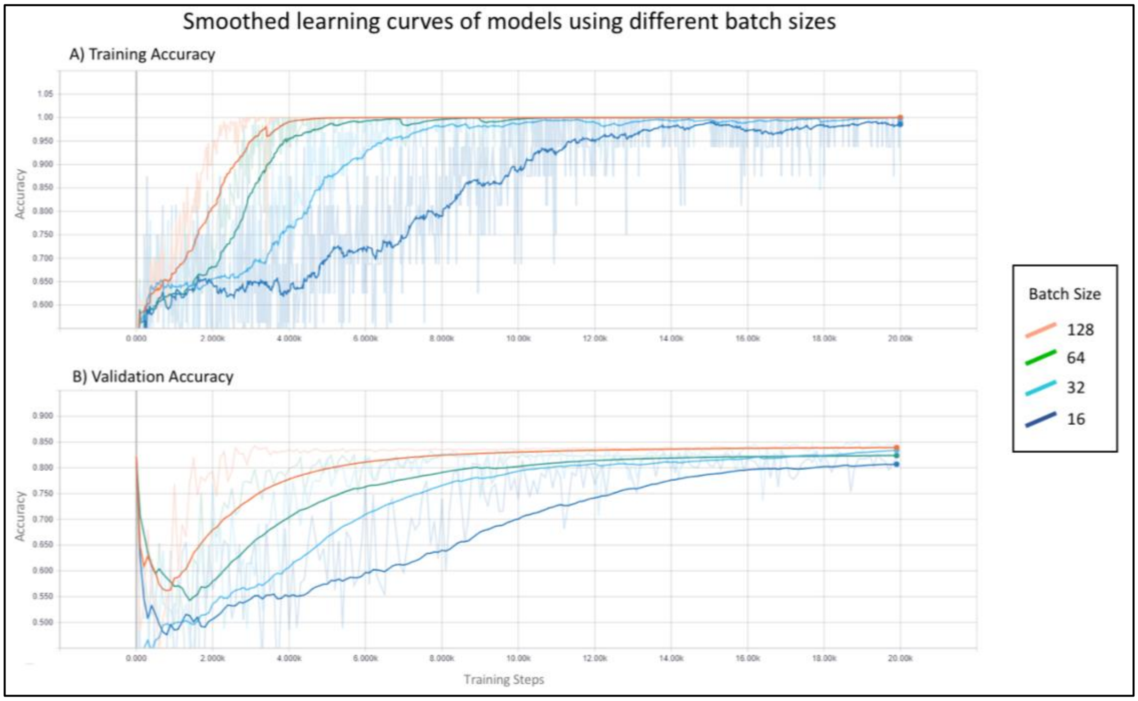

Figure 4.7: Comparison of smoothed learning curves of the models on training accuracy (A) and validation accuracy (B), using different batch sizes. Higher values are more accurate (perfect accuracy is 1.0). A batch size of 128 (orange, top curve) yielded the best performance. The noisier curves displayed in faded colors display the models' unsmoothed learning curves.

As described above, after each batch, the network's internal structure is adjusted slightly to reduce error. The speed at which the network makes such adjustments is called the learning rate. Smaller values mean that the network adjusts very slowly to new information, but higher values can result in the network over-adjusting to new information and never learning patterns from previous batches. The learning rate is typically selected by training the network using several values and using the value that yields the best performance. To determine a suitable learning rate for this network, I trained several neural network models that used different learning rates (Figure 4.8) and selected the model (learning rate of 10^{-4}) that yielded the best performance in all three performance metrics.

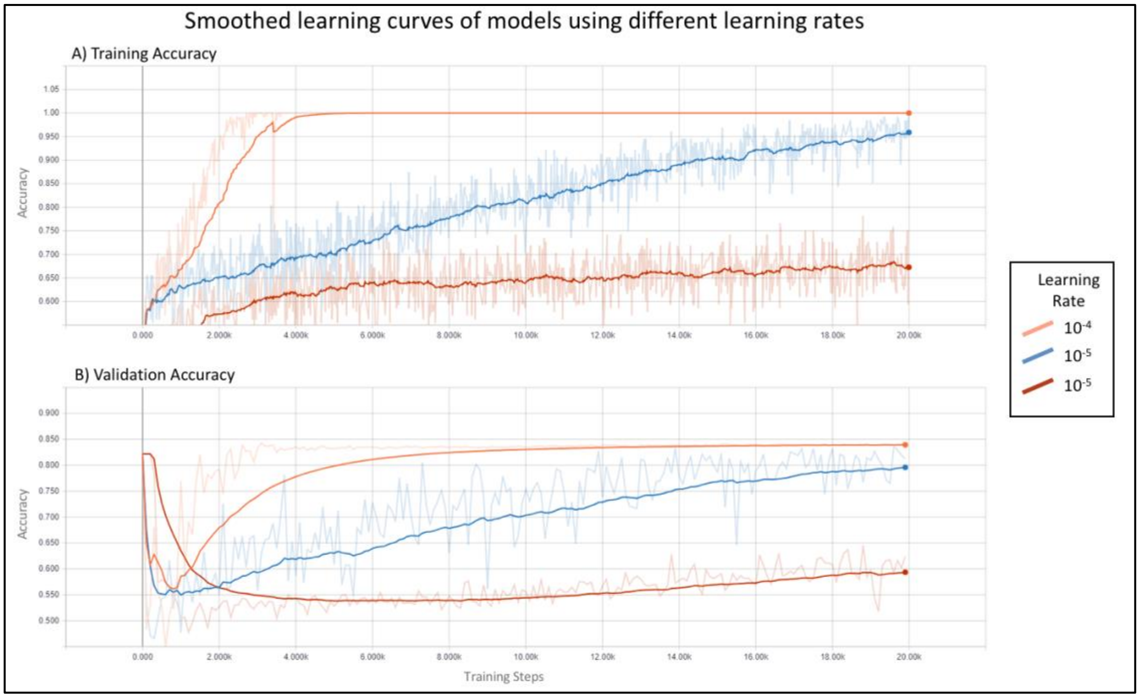

Figure 4.8: Comparison of smoothed learning curves of the models on training accuracy (A) and validation accuracy (B), using different learning rates. Higher values are more accurate (perfect accuracy is 1.0). A learning rate of 10^{-4} (light orange, top curve) yielded the best performance. The noisier curves displayed in faded colors display the models' unsmoothed learning curves.

Overall, these diagnostics took over seven days to complete on a modern personal desktop computer. Based on the above diagnostics, the final network used a batch size of 128 and a learning rate of 10^{-4}.

Results

Initially, I used several different model architectures involving "dense" (simple non-convolutional) neural networks, but these models' predictions performed no better than chance. For this reason, I selected a convolutional neural network (described above) which was successful at learning patterns in the mini-habitat images.

As predicted, the model was able to learn patterns in the Google Earth images to correctly predict orangutan space use. I trained the final network with 20 000 steps, and the network converged successfully. These iterations completed in just under 13 h on a personal desktop computer. The training accuracy of the model reached 100% after 6000 steps, meaning the model learned to correctly predict all training examples. However, at this point in training the model only achieved 77% validation accuracy.

Although the network had reached 100% training accuracy after 6000 steps, further training continued to improve its validation accuracy, and it reached an apparent asymptote at 84% validation accuracy after 16 000 batches, meaning it correctly predicted orangutan space use on 84% of examples to which it had never been exposed. Further training beyond 16 000 batches did not improve the model.

Since the model had very high training accuracy, but lower accuracy on the validation data, it is possible that the model experienced ‘overfitting’ (Ng, 2018). Overfitting occurs when neural networks are trained repeatedly on specific patterns unique to the training data, but such patterns do not apply generally to other data (e.g. validation data). However, adopting techniques to address overfitting (i.e. regularization, simplification of model, early stopping) did not improve the model’s validation accuracy. This suggests that a larger dataset allowing for more training examples or more features may be needed to improve this model’s validation accuracy beyond 84% (Ng, 2018).

Discussion

Using machine learning, this study demonstrated the utility of deep convolutional neural networks as a novel method of modelling orangutan space use on a very local scale. This method was able to accurately predict orangutan space use in our study area with resolutions approaching 10 m. Previous studies typically examined animal space use on scales on the order of kilometers (Hickey et al., 2013; Laundré et al., 2001; Palminteri et al., 2012; Squires et al., 2013), indicating that this methodology gives researchers an important new tool for an examining space use on smaller scales.

Since our deep neural network model successfully made predictions on the basis of visible-wavelength satellite images alone, orangutan space use must somehow be related to local visual characteristics of their habitat. Possible factors may include different colors of vegetation depending on the species present, shadows (darker areas) caused by larger trees, clearings (lighter colors of green) and areas with no vegetation (river or dirt). However, it is notoriously difficult to interpret which factors/patterns neural networks learn to make their predictions, especially using satellite imagery (Xie et al., 2008), so it is not currently possible to assess the visual characteristics important to this network. Nevertheless, there have been important advances in network visualization/interpretation in recent years (F. F. Li et al., 2018; Zeiler & Fergus,

2014) which may improve interpretations of neural networks in the near future, allowing for examination of potential predictive factors.

Although this neural network performed successfully based on visual imagery alone, model accuracy may improve with inclusion of data from other sources. The inclusion of data from other satellite-derived sources including elevation, slope, rainfall, forest composition, reflectance from non-visible wavelengths, etc. would likely improve predictive power of the model (Hickey et al., 2013; Phillips et al., 2006; Xie et al., 2008). Similarly, including data collected by field teams such as forest structure, canopy cover, resource distribution etc. may also improve models by providing neural networks with more features on which to base predictions. I aim to implement some of these data sources in future studies. In addition, acquiring higher-resolution aerial data from sources such as drones and aircraft, could greatly improve the model's spatial resolution (Koh & Wich, 2012). Accessing data from three-dimensional sources such as LIDAR mapping technology may allow for the assessment of space use in three dimensions, which would be especially useful for arboreal species.

Because orangutan movement data spanned several years, seasonal variation that may occur in satellite imagery is not of concern since the model examines overall features of the habitat, not small details such as small fruit, flowers or leaves. Such details may have very small impacts on the color of a pixel (i.e. browner during dry times, yellower with new leaf growth), but such changes are likely extremely minor from season to season. More major events such as fires, major droughts, etc., that cause large-scale changes to forest structure would likely reduce the accuracy of the model and may require the model to be re-trained using updated satellite imagery. Examining models on trained on seasonal data with associated seasonal satellite imagery may provide interesting predictions on where orangutans seasonal space use, however, satellite images in rural parts of Southeast Asia are updated in intervals spanning more than a year.

Because the deep neural network model was based on satellite imagery alone, it was not possible to compare it to MaxEnt Models directly. However, since the simpler non-convolutional deep neural networks failed to accurately predict the data, it is highly likely that MaxEnt models would have also failed to perform successfully. Such simpler neural networks, with enough training, should have been able to learn any relationships that MaxEnt is capable of detecting but failed to do so. Only the convolutional neural network, which was specifically tailored to image processing, was able to accurately predict the data.

This study could have important applications for extrapolating animal space use. Although the model performed well on validation data, these data were from the same area as the training data. Using a model trained from our study area, it may be possible to extrapolate outside the study area to predict areas where orangutans may be likely to range, which could help plan better focused population surveys or highlight areas that may be important for conservation. To test this possibility, I am currently developing this methodology to use as a tool for extrapolation. In theory, this method could be applied to any habitat that shares the same visual characteristics as the habitat used for training the model. Field expeditions to targets identified by the model would be important in order to ground-truth the model’s predictions and assess the success of such extrapolation. For this reason, focusing on the habitat adjacent to our study area is an important first step in validating our model for use as an extrapolation tool.

Predicting space use on a very local scale from satellite imagery could have important applications for conservation initiatives. Machine learning applications similar to those used in this study could aid in remotely estimating regions of high habitat quality quickly, without extensive field surveys. Applications might extend to local population estimates, if combined with knowledge of local species densities. Also, areas demarked for conservation may be large but useable habitat within them may be considerably smaller, so using machine learning could enable stakeholders to estimate the location(s) and proportion of suitable habitat within such areas. Machine learning could also have important applications for the management of ecotourism, by identifying where best to allow/restrict human visitors based on predictions made by neural network models and could aid in monitoring and predicting human-caused disturbance over time.

Overall this study was successful in using a deep neural network to predict orangutan space use. The neural network’s predictions were based solely on free and widely accessible data, meaning these methods can easily be tested and applied to other orangutan populations and other species. Machine learning remains a nascent field, and to date animal researchers have been slow to adopt this new technology. Although preliminary, this study demonstrates the potential of using machine learning technology for applications in animal behavior and ecology.

Chapter 5: Conclusion

Together, these studies improved understanding of the habitual travel route network of wild orangutans in Kutai National Park. Results from Chapters 2 and 4 suggest that ecological features likely shape the spatial configuration of the orangutans' habitual route network. Results from Chapter 2 demonstrated that the habitual routes connected large fruit trees of certain key species, and the routes passed through areas with more orangutan resources than alternate routes nearby. Results also implied that orangutan travel routes may in part be constrained by ecological factors including arboreal bottlenecking. Results from Chapter 4 demonstrated that a deep neural network model was able to successfully classify areas orangutans revisit and those they do not, meaning the model was able to broadly estimate locations that were likely to be part of the habitual route networks. This model used visible-spectrum satellite images, meaning that visual characteristics of local ecology were able to identify the spatial configuration of orangutan habitual route networks.

Together, these results suggest that local ecological factors may be important drivers behind the spatial configuration of the habitual route network. Though outside the scope of these studies, other ecological and cognitive factors may contribute to orangutan travel decisions. For example, elevation and slope were associated with habitual route networks in spider and wooly monkeys (Di Fiore & Suarez, 2007), and the presence of rival conspecifics altered the routes of chacma baboons (Noser & Byrne, 2007a). Further study into other ecological factors could yield important information about which types of local habitat orangutans prefer.

These findings could also have implications for studying geographic variation in orangutans. Comparing populations and assessing variation in habitual route networks and associated cognitive strategies could yield important information regarding orangutan behavioral flexibility and intelligence. Habitual route networks of different populations may have very different spatial configurations based on their local ecology. Such differences could result in orangutans using different foraging strategies (Presotto & Izar, 2010), which in turn could also drive differentiation in cognitive maps and other differences in spatial cognition between populations. Examining population differences in how ecology and habitual route networks relate to orangutan navigation strategies could shed light on this possibility.

The presence of habitual route networks has previously been used as evidence for primates using route-based cognitive maps (Di Fiore & Suarez, 2007; Porter & Garber, 2012). However, habitual route networks have also been identified in several non-primate animal species that likely rely on more limited spatial information and use heuristic navigation strategies (Bruggeman et al., 2007; Douglas-Hamilton et al., 2005; Squires et al., 2013; Wehner, Boyer, Loertscher, Sommer, & Menzi, 2006). Like the orangutans in Kutai National Park, such habitual route networks also connected important spatially-stable resources, and connecting routes were influenced by ecological variables including resource distribution and topography. Consequently, I argue that it is problematic to assume that the orangutans relied on cognitive maps that are more sophisticated than these species from the spatial configuration of habitual route networks alone.

The fact that ecological conditions are important in shaping the locations of orangutans' travel routes does not mean that cognition plays a minimal role in their navigation. Like many other behaviours, orangutans likely apply sophisticated and flexible cognitive strategies when navigating (e.g., in deciding which particular route to take through trees, which locations to target, etc.). However, based on results from the above studies, I argue that such abilities can't be determined from the spatial configuration of the routes alone. The configuration of habitual routes was consistent with route-based cognitive maps, but may also have alternate explanations. For example, some ants use habitual route networks, and their configuration shares characteristics with the orangutan's network (e.g. connecting resources, avoiding topographical obstacles, etc.) (Collett & Collett, 2009; Wehner et al., 2006). However, the ants cannot use them flexibly; small disruptions to their travel prevent them from navigating successfully (Collett & Collett, 2009; Wehner et al., 2006). Orangutans undoubtedly use more flexible and sophisticated navigation strategies compared to ants, but evidence is required to ascertain their nature. For these reasons, I argue that caution should be used when inferring that primates use more sophisticated cognitive maps compared to other animals from the presence of habitual route networks alone.

One possible avenue for exploring orangutan navigation strategies and cognitive maps may be through combining knowledge of factors affecting the spatial configuration of habitual route networks with data concerning how individuals use such networks. For example, examining behaviour that shows that an individual’s travel is based on choices, spatial information, flexible responses to disruptions, and perhaps planning could yield more insight into the information encoded in cognitive maps.

Following this reasoning, results from Chapter 3 provide support that orangutans were able to use their habitual route network flexibly when they escaped human observers. Many previous studies have considered a lack of direct linear travel towards resources and a lack of novel travel routes as evidence against primates using coordinate-based cognitive representations (Bezanson et al., 2008; Janson & Byrne, 2007; Normand & Boesch, 2009; Poucet, 1993). However, orangutan travel may be partially constrained within habitual route networks, meaning the most efficient route may not be linear. Furthermore, novel routes may occur very rarely, and are therefore difficult to observe. It is also difficult to ascertain whether a route is truly novel, or if it had been used previously without detection.

Results from Chapter 3 show preliminary evidence that orangutans may be able to plot travel routes away from their habitual route networks toward less-used areas when escaping from humans, suggesting they may encode more information than would be expected from route-based cognitive maps alone (Poucet, 1993). Orangutans typically travelled along their habitual route network, but when they escaped, they travelled “off road” leaving the network for areas that they typically avoided. Such routes were often novel[1] in that the observation team had not previously observed them, although since we do not know the entire history of the orangutans we cannot be certain. Escaping orangutans altered their behavior and space use hours before escaping from human observers and targeted areas away from their habitual route network. Orangutans prioritized traveling quickly over feeding, and targeted travel away from their normal travel routes towards areas where humans were less able to follow them. Such results are consistent with orangutans deliberately changing their behavior in advance based on spatial knowledge that includes little-used areas that may increase chances of escaping from humans. This suggests that orangutans' cognitive map may encode information that allows them to differentiate areas along their habitual route network where humans can easily follow them from areas away from the network where they can better escape and navigate to such areas using novel or little-used routes. Although preliminary, planning travel routes to out-of-sight areas that not typically accessed is consistent with orangutans using a coordinate-based cognitive map, although more research is required to confirm this possibility.

Many orangutan resources are only available at particular times of the year, especially ripe fruit. Examining how orangutans modify their use of habitual route networks in response to the availability of temporally variable resources may contribute to understanding whether they use cognitive maps to navigate. However, the majority of orangutan resources (including fruit trees) appear at

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[1] Recall that in this context, novel refers to never-before taken routes, not novel configurations of known routes

consistent locations spanning several years. Additionally, such locations may remain important orangutan travel targets when not producing fruit for other reasons (i.e. bark, leaves, flowers, nesting, social meeting, etc.). Visiting important resources when they are not productive could facilitate monitoring and updating spatial and temporal information (Di Fiore & Suarez, 2007; Garber & Porter, 2014; Janmaat et al., 2013; Milton, 1981). Examining whether orangutans revisit resources more as they near productivity could provide evidence for such monitoring behavior.

The studies presented above also contribute to developing improved methodology for modelling primate travel at a local scale. Previous studies typically examined animal space use on scales on the order of kilometers and did not account for GPS error (Hickey et al., 2013; Laundré et al., 2001; Palminteri et al., 2012; Squires et al., 2013). The new methods presented in the above studies allow for assessing orangutan space use on a very local scale with resolutions approaching 10-20 m while accounting for GPS error. Such high-resolution analysis is important for understanding local factors that may influence primate travel decisions and may play a role in cognitive maps.

Local-scale information also has important uses for conservation through improved identification of locations of high habitat quality. Such data could be applied to improved estimates of local population carrying capacity, useable habitat within conservation areas. Knowledge of locally important areas of habitat for primates could help identify locations where best to allow/restrict human disturbance and help manage human-primate conflict.

The combined results from these studies suggest that primate space use is likely the product of both ecological factors and how they encode and use spatial information. The spatial configuration of habitual route networks was well explained by local ecology, and orangutans used them flexibly with evidence consistent with advance planning, suggesting they may rely on information encoded in cognitive maps to navigate within (and when leaving) the route network. Results also show preliminary evidence consistent with orangutans using coordinate-based mental maps, although more research is required to assess this possibility in more detail. These studies demonstrate the utility of using modern mapping software and machine learning technology combined with extensive field observations for applications in primate behavior and ecology.

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