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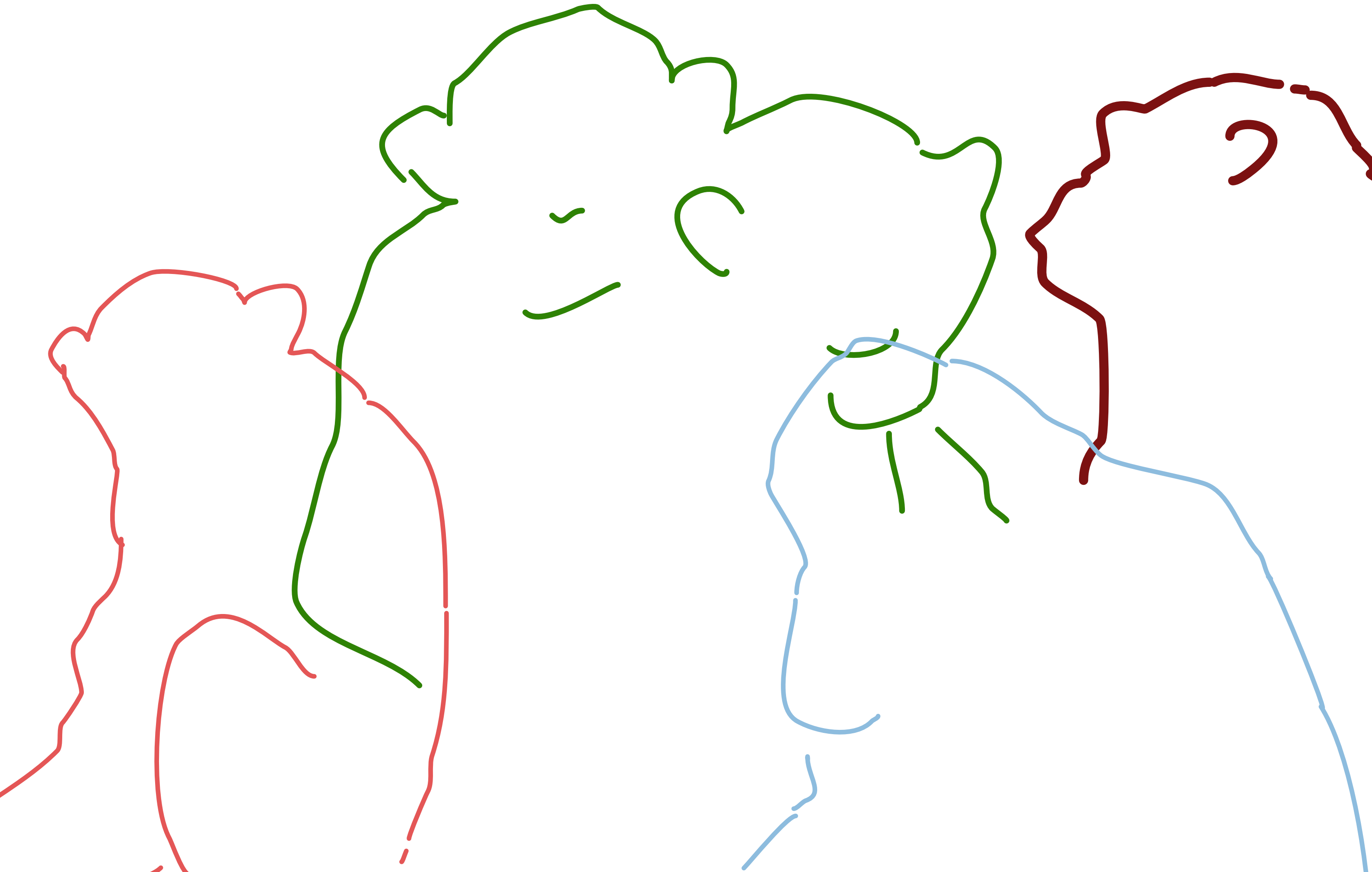

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Group dynamics and decision-making in habitual route use in Taï chimpanzees (*Pan troglodytes verus)*

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My interest in the interaction between man and environment, as a main drive to start this master was through the writing of this thesis brought to a much deeper level than expected. Especially in the current years, in which we are to deal with a world-wide pandemic, and in which a lot of questions about our relation to the environment were raised, learning in this way about the origins of cognition and behavior and the plasticity of the brain was of great value and all I learned will be of great guidance for me in the future ahead.

I therefore sincerely thank Karline Janmaat, for giving me the opportunity of working on this project and for introducing me into the field of evolutionary psychology and behavioural ecology. Her guidance and patience throughout all parts of the process of which most was all new to me, made me persevere and finally finish this project.

I gratefully acknowledge Leila Porter for letting me use her habitual route use data. Without, I wouldn't have been able to do this particular study. I also thank Emiel van Loon and Miguel de Guinea for helping out with programming issues that I encountered during the data preparation of this research. Of course, I must thank Roger Mundry, for providing the guiding materials on statistical modelling and for having me on his course. It was by far one of the most intriguing courses of my studies.

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Abstract

Habitual routes are assumed to be travel paths that are, due to familiarity, energetically relatively less costly to travel on. This study derives from the idea that according to energy maximizing strategies, cognitively demanding situations possibly evoke more habitual route use. In this study I attempt to explore this assumption by linking ecological and behavioural attributes to movements as observed in primates. It compares and analyzes three years of ranging data of wild chimpanzees to learn about underlying mechanisms involved in decision-making processes concerning travel on habitual routes. I explored the chimpanzee's travel strategies by testing the influence of group size, group composition, seasonal variation, weather conditions, time of day, and human-made research trails on the probability that the chimpanzees will use habitual routes. The results of this study suggest that the probability of habitual route use increases when the chimpanzee travels alone or in a small group and thus substantiates the assumption that larger groups might take on more extensive cognitive challenges.

Keywords: Decision-making, habitual route use, group foraging size, travel behaviour.

Group dynamics and decision-making in habitual route use in Tai chimpanzees (*Pan troglodytes verus)*

When travelling to out-of-sight goals, we naturally try to compose the most efficient route. Due to our evolutionary drive to optimize fitness at all times, we have developed cognitive abilities to integrate and compute relevant information in the travel decisions we make so that we will not be exploiting unnecessary energy. But when travelling the same grounds over and over, is the least-costly route still the most attractive route? And when travelling in a group, will or will you not deviate from your developed habits?

Amongst many other factors, the decision for an individual to move over habitual grounds is assumed to be dependent on the trade-off of movement flexibility on the one hand and the saving of energetic costs on the other hand. Energetic costs here imply physical as well as cognitive demands as our brain functioning requires about 20 percent of our body's energy (Herculano-Houzel, 2012). Posing a high demand on working memory when processing information during navigating, increases the cognitive load and thus affects the energy balance. As habit formation reduces the resources needed to navigate properly, it is expected that cognitively demanding situations elicit more habitual behaviour.

This thesis will therefore study the implications of this trade-off by studying indicators of cognitive load and comparing these conditions and their executions on- and off repetitively used path trajectories of wild chimpanzees (*Pan troglodytes verus)* in Taï National Park, Côte d'Ivoire. Learning about this trade-off in primates can help us understand the origins of how and why habits are formed in human behavior and can generate insights in which situations we stick to habitual behaviour or in which we don't.

Intelligence hypotheses

To learn about the evolutionary drivers of cognitive evolution, comparative evolutionary psychology studies animal cognition by measuring and comparing brain sizes and abilities and its relation to potential influences from the environment in the shaping of cognition. Primates possess relatively larger brain-to-body sizes and greater cognitive abilities than other species do (Jerison, 1955). These advanced cognitive abilities are assumed to have evolved from the challenging ecological and social systems they face (Milton, 1981; Barton, 2000; Reader & Laland, 2002).

High biodiversity, low visibility, and widely distributed food sources in rainforests create a challenging environment that requires specific foraging techniques to be developed in order to survive. To integrate information on what to find where and when, effective foraging in these environments calls for skills in spatial awareness, spatial memory, and mental mapping (Poucet, 1993). Besides ecological pressures, social complexity is thought to be another force that drove primates' brain-to-body size to exceed those of other species (Dunbar, 1992). Interacting with others in a community with high fission-fusion dynamics as some primates do, calls for refined social skills to be developed. Studying the way in which is coped with these challenges helps us to understand the evolutionary function of cognition.

Exploring primate cognition by observing travel patterns

Where cognitive laboratories will never be able to recreate the conditions of socioecological variables as these occur in the natural environment, studying primates in their natural habitat is the only way to really learn about the influence of such a complex environment on the development of the brain as well as the adaptive value of cognitive traits (Janmaat, 2019). It is however a tough challenge to control for estimates of cognitive skills in these non-experimental settings. Yet, as movement unfolds from the interaction of physical abilities, ecological features and cognition, travel patterns of wild primates are an interesting source of information that can be used to infer cognitive processes, that cannot be studied in large-scale space in captivity. Assuming that 1) path development emerges from decision-making processes, and the anticipation and integration of foraging strategies, and that 2) the most optimal foraging strategies are those that are energetically the least costly; studying these paths might reveal the underlying mechanisms involved in decision-making.

How primates decide on travel routes in natural environments

Field studies have found primates to show anticipatory strategies involving the use and intergration of spatial, temporal and social cues while monitoring and foraging on resources (Janson, 2000). Primates have shown to be equipped to integrate spatial-temporal, as well as phenological information of food availability in foraging strategies (Janson, 2007; Janmaat et al., 2016; Noser & Byrne 2014, de Guinea et al., 2019). Efficient travel is achieved by integrating extensive knowledge of the environment as well as spatial and temporal memory about the fruiting states/food availability of available resources (Janmaat et al. 2013). In their foraging behaviour primates are thought to be able to compute 'least-cost routes to out-of-sight goals' (Green et al., 2020). Several primate species including Taï chimpanzees have been shown to reuse travel routes (Di Fiore et Suarez, 2007; Presotto & Izar, 2010; Porter et al, 2020). As chimpanzees have also shown to be able to compute novel routes based on spatial mapping (Normand & Boesch, 2009; Garber & Dolins, 2014) the question is raised why and when they decide to travel habitual or novel paths.

Route-based travel and its cognitive benefits

Optimal foraging theory assumes that foraging effort is at all times minimized to maximize foraging success and therefore survival (Pyke, 1984; Hopkins, 2016**)**. Foraging success, or achieving the most optimal food intake per energy unit used, requires balancing out the costs and benefits of energy spent on foraging on the one hand and the nutritious value gained through it on the other hand. This energy spent comprises physical as well as cognitive energy, therefore, the shortest route is not necessarily the least costly as less information needs to be stored when restricting movements to a finite number of travel paths that are repeatedly travelled.

Considering this, the cognitive benefits of route-based travel are manifolded; such travel is effective and efficient as only minimal understanding and memory of general spatial relationships is required (Milton, 2000; Poucet, 1993; Byrne, 2000). Consequently, the absence of active ‘mental processing’ while moving through familiar routes saves up cognitive capacity that can be distributed to other resources. This is consistent with observations of Noser and Byrne (2010) who reported that wild baboons travelled with higher speed and increased route linearity on repeatedly used paths and by Jang et al. (2019) who reported the same findings in human foragers.

Furthermore, travelling previously used routes supports efficient locomotion and diminishes energy expenditure as vegetation and other geographical factors on often travelled paths might be less hindering locomotion, especially in hilly and dense landscapes (Green et al., 2020). Besides physical and cognitive benefits, travelling repetitively used routes can also be beneficial for foraging strategies in the sense that it allows frequent monitoring of fruit ripeness and availability (De Guinea et al., 2019).

Lastly does route-based travel too ensure that the chimpanzees stay within home range boundaries and are therefore less susceptible to distress of coming across neighboring groups and predators (Kavaliers & Choleris, 2001; Porter, 2020). Concurrently, one could argue that predators are more likely to be found on these routes as they predictably can find prey there. However, this higher risk might be outweighed by the familiarity with possible escape routes on more often travelled paths.

Trade-offs in decision-making

As outlined above, the cognitive advantages of travelling habitual routes are multivarious. However in decision-making processes they are likely to be susceptible to several trade-offs. Habitual paths are, for example, restricting spatial flexibility in navigation. In other words, re-using the same paths can restrict the primate's ability to properly assess the environment and potentially discover novel sources of food. Another factor that might interfere with the re-occurrence of travel patterns, might be foraging party size. This was observed in a comparative study by Porter et al (2020) in which small cohesive groups of tamarins performed more route-based travel than sympatric primates living in larger groups.

Chimpanzees live in *fission-fusion* societies; these show dynamics of uniting and splitting of party members throughout the day depending on the activity, as well as the availability and distribution of resources (Aureli et al., 2008). Not much is known about the influence of group size and composition on the decision-making process of travelling habitual routes. However, there are speculations about how different forces might affect the way in which group dynamics influence foraging cognition and the usage of habitual routes.

According to Simons (2004) group movement and therefore access to increased spatial knowledge of the number of other individuals in the group, constitutes the "many wrongs principle"; the advantageous effect of large group size on navigational accuracy by the suppression of the individual error by group cohesion. Travelling in groups makes it possible to benefit from the presence and orientational abilities of others and distributes the cognitive load needed to navigate. This assumption was tested in the previously mentioned comparative study on linearity in human foragers and chimpanzees by Jang et al. (2019). In this study human foragers were observed to increase linearity when travelling in a larger group. Chimpanzees however, showed the opposite pattern. This might imply that group travel might also hinder goal-directed movement; speed and linearity might be lower because of perceived safety in larger groups, or because it is more complex to achieve navigational consensus among a larger group of individuals. Hence, live in socially bonded groups such as most primates can also be challenging and taxing on cognitive abilities, which is in line with the social brain hypothesis (Dunbar, 1992).

The implications of this hypothesis were found in a study by Janmaat (2013) which showed that moving in a party can possibly constrain monitoring behaviour, as more goal-directed behaviour was detected when chimpanzees foraged solely . The sociality of moving in a group might thus distract from goal-directed monitoring behaviour, as well as evoke free-riding on the skills of the others.

Furthermore, because of within-group competition, larger groups are required to travel further to find sufficient food and will thus spent more energy travelling (Chapman et al., 1995). On the other hand, this energy might be outweighed by reduced cognitive distress and load due to the perceived safety against predation when travelling in a larger group. That this trade-off configures towards an optimal group size was shown in wild baboons by Markham et al. (2015) who found that intermediate sized groups showed the lowest glucocorticoid (stress hormones) as well as the most optimal space-use strategies.

Besides group size, group composition is also important for the group dynamics that determine decision-making. As sexual differences manifest different motivations and ranging patterns, the composition of a group is likely to determine which strategy is used (Bates & Byrne, 2009).

All of these findings raise the question of how group size and composition influence the decision-making process of travelling habitual routes. It is therefore that, inspired by the the findings by Jang et al. (2019), Markham et al. (2015) and the comparative study by Porter (2020) I intent to explore the influence of group size and composition on the usage of habitual routes in wild Taï chimpanzees. Hereby I try to gain insights in the group dynamics determining decision-making processes in the execution of habitual behaviour, specifically.

Given the idea that using habitual routes can be a successful strategy to diminish energy with regards to the above-mentioned reasons, these assumptions are expected to be reflected in long-term observational primate ranging data. In order to disentangle the importance of social and ecological information in the decision-making process of travelling habitual routes in wild primates, in this study long-term observations will be entered into statistical models testing various predictors to gain insights into mechanisms driving decision-making.

Hypothesis

Cognitive load is expected to be lower when travelling in larger groups, as the load can be distributed among more individuals, therefore travelling in larger groups hypothetically could allow for more explorative behaviour (Ward & Zahavi, 1973). Hence, I hypothesize that the probability for Taï chimpanzees to travel over habitual routes decreases as group size increases. At the same time navigating familiar paths is assumed to be cognitively less demanding and therefore expected more evident for smaller groups. An additional support for this hypothesis could be that travelling in small groups enlarges the risk for negative outcomes of inter-group encounters and predation. Hence, movement by habitual routes is likely to be a safer travel decision as well (Boinski & Garber, 2000; Jang et al., 2019).

I also hypothesize that group composition has an effect on the probability of habitual path use. As sex differences have shown significant differences in observed movement patterns, these differences are also expected to be reflected in the usage of habitual routes (Bates & Byrne, 2009). Female travelling patterns are found to be influenced by the reproductive state a female is in at the moment of observation. As is expected from optimal foraging strategy, and considering the high metabolic costs of lactation, studies have shown lactating females to exhibit shorter travel distances and more food-directed travel behaviour than males (Bates & Byrne, 2009; Gilby & Wrangham, 2007). Lactating females for this same reason have shown smaller ranging areas and therefore more re-visits (Bates & Byrne, 2009). Opposingly they were found to show more out of range movements because of following around males when sexually receptive (Goodall, 1986). In contrast, males are generally found to show longer travel distances and more risk-taking behaviour in their movements (Bates & Byrne, 2009). Possibly underlying these patterns could be the male's involvement with territorial defence and thus the exhibition of boundary patrols. As for chimpanzees, male dominance is likely to overrule female travel patterns (a distinction between lactating and sexually receptive females has not been made in this study) and thus with a higher male ratio, a more male-oriented travel pattern is expected. This will imply fewer habitual routes with an increasing male ratio, due to their generally more explorative movement patterns.

Furthermore, I predict food availability to have an effect on habitual route use as previous research with capuchin monkeys has shown an increase in habitual routes during times when high-quality food was scarce (Presotto & Izar, 2010).

I further predict that the probability to use habitual routes will be influenced by the openness of vegetation since these routes are likely to be reused, because they are generally perceived as physically less costly and thus efficient travel paths. For this I used human- vs non-human-made trail as a proxy for openness of vegetation. By this, I try to replicate findings by Green et al. (2020), who found that for chimpanzees in Rwanda, the most intensely used routes occurred on human-made trails.

In addition, I expect the chimpanzee individuals to take predation risk into account when travelling and that this anticipated risk of predation would be reflected in habitual route use. As the risk of encounters with predators is generally higher during early- and sunset hours, and as habitual routes are generally travelled by predators too, I expected habitual routes to be avoided during these hours (Kouakou et al., 2011; Janmaat et al., 2014).

Lastly, did I expect rainy days to stimulate goal-directed movement due to the desire to take shelter (Janmaat et al., 2014). Therefore, I predicted rainy days to show a higher probability of habitual route use. As I expected both threats to be integrated in decision-making I also test for an interactive effect of rain and the time of day.

Relevance

Current technological developments allow for tracking and mapping of long-term structural patterns of mobility behaviour as observed by experimenters over time, opening up relevant new possibilities in the field of behavioural ecology and comparative wild primate studies (Janmaat, 2021).

While these possibilities keep increasing, at the same time the population densities and the habitat of this species is, due to threats of deforestation, rapidly decreasing. Because of the spatial and ecological conditions required for this kind of studies, it is of high importance to study primates in their natural context. It is therefore extremely urgent that cognition of primates in their natural habitat is being studied as intensively as possible while we still can (Janmaat, 2019).

Using insights from cognitive science, evolutionary psychology and behavioural ecology, this current study aims to learn about the underlying mechanisms of decision-making processes associated with travelling habitual paths. By determining the route network of Taï chimpanzees and studying respective differences in behaviour and environment on- and off repetitively used path trajectories I attempt to investigate the cognitive benefits of route-use. By exploring the influence of group size and dynamics on particular paths travelled, cognitive attributes that might be involved in this decision-making process are tried to be inferred. Ultimately this can help us better understand in which way ecology shapes cognition and how cognition has evolved. This helps us increase our understanding of the origin of human behaviour and the function of habit formation.

Methods

Design

To infer cognitive processes involved in spatial decisions of non-captive primates, insights from the field of cognitive behaviour ecology are converted in predictions and compared to the behaviour of primates as observed in their natural habitat (Janson & Byrne, 2007). In this respect, this study is using observational and spatial data of wild chimpanzees to test the interactive effect of several predictor variables on the probability of the chimpanzees travelling on habitual routes. To estimate the effects several Generalized Linear Models (GLM's) with binomial error structure and logit link function are designed (Baayen, 2008).

Study site and subjects

The data used for this study was collected in the years 2009-2011. In periods of 4 to 8 consecutive weeks, with a total of 275 full days in fruit scarce periods (May-August), Karline Janmaat and Simone Ban have followed five habituated adult chimpanzee females (*Pan troglodytes verus)* in the Taï National Park, Côte d'Ivoire, West Africa (5°50'20'' N, 7°19'16'' W). The Taï chimpanzees live in a community with a size of about 20-40 individuals and their home range covers about 38.65 km² (MCP 100, Jang et al, 2019).

Each female was followed from the point of waking until the construction of a sleeping nest. All significant changes in foraging-related behaviour were observed and relevant locations were marked and tracked. Simultaneously GPS locations were recorded. The observational periods were planned during the short dry season, a period of general fruit scarcity in which the chimpanzees are expected to perform more efficient foraging behaviour.

For this study, only data of two individuals, Isha and Julia, was used because of the lack of availability of habitual route use data of the others.

Measures

Habitual paths

GIS Analyses. To determine travel trajectories, first location data of the chimpanzees as collected with a handheld G.P.S (Garmin 60 CSx) were cleaned (Janmaat et al., 2013). The habitual path segments derived from this data were determined by Leila L. Porter (2020) according to methods proposed by Porter & Garber (2013) and Di Fiore & Suarez (2007). First daily paths, a cumulative set of sequential GPS points visited on a given day were derived. The average amount of paths per day per study period varied between 25 and 50 (Porter et al., 2020). These daily paths were then compared over the days per study period and paths that ran parallel to one another (~30 m) for a distance of minimum 75 meters, for more than two days were considered to be a 'route'. The number of routes per study period varied from 29 (Julia 2009: 25 days) to 149 (Isha 2011: 50 days) and showed hardly any overlap over the years (Porter, 2020). Coordinates of these routes were derived with 1-meter intervals in GIS software.

Habitual paths. To align these segments with the behavioural data, at first, the cleaned GPS data was aligned with the behavioural data (Appendix 1a). An R code, kindly provided by Emiel van Loon was then used to determine whether each datapoint from the behavioural data was on or off a habitual route segment (Appendix 1b). To do so, the coordinates as determined by Leila Porter were compared with the coordinates of all travel paths. As the habitual route segments were derived with a 60m wide polygon, buffers were to be applied in this reversed check as well. To test for the accuracy of imposing different buffers, a visual sensitivity analysis was performed for 2 different buffers (15 and 30 meters). By plotting and visualizing both resulting datasets next to each other, it was checked which buffer resulted in the most accurate, corresponding data (see Appendix 2). It was decided to continue the analyses with the 30meter buffer.

Group size & Formation Group size was derived by counting the number of independent individuals, those that walk independently, at each moment of observation. As the data was gathered by two observers Karline Janmaat and Simone Ban, an interobserver reliability test was performed on the data. This showed a reliable correlation coefficient for party size for follows of 1173-2086 sampling minutes (r_S=0.82-0.99) (Janmaat, 2013).

To measure the influence of the composition of the group on the probability that chimpanzees walked on habitual routes, a male ratio was generated by dividing the number of males older than 9 years in the group over the total of males and females older than 9 years, for each separate observation. Individuals older than 9 years were assumed to be able to make independent travel decisions as they did not always follow the mother anymore. A male ratio of 1 represents an all-male group a value of 0 an all-female group. As at all times a female focal was followed the male ratio varied between 0-0.83.

Seasonal variation and weather conditions The influence of seasonal variation in food availability was tested for by counting the number of unique trees the chimpanzees visited per day. Fewer food trees thus indicate a lower distribution and availability of food sources. The summary statistics of this variable can be found in the Appendix 3.

Weather conditions were inserted as whether or not it was raining at the moment of observation. As I expected there to be an effect of avoidance of habitual routes in sunset and sunrise hours because of predation, for this condition a quadratic interaction with time of day was modelled. I predicted the probability to increase after sunrise and before sunset as during these hours, routes are likely to be avoided due to the risk of encounters with predators. Time of day was measured in seconds after midnight (range:19412s – 68342s).

Openness of vegetation Lastly I tested for the effect of 'openness of vegetation' as a characteristic of the type of travel paths. For this test the variable 'human research trail' was used to test an effect of human-made research trails on habitual route use, where I expected that human-made trails and habitual routes would often overlap. For this variable as well as for the variable of rain the data was found to be unbalanced (Appendix 6).

Procedure

Data preparation The data was cleaned on typos and the missing values that could be generated were filled using OpenRefine software. There was quite some data missing for the variables 'rain/no rain' and 'on/off track' (see Appendix 4), since not all observers collected this data. Rows of the test data that included missing values were removed (Appendix 1c). The samples for the models comprised a total of 16651 datapoints for Isha of which 7662 (46%) were on habitual routes and a total of 7334 for Julia of which 1943 (26%) were on habitual routes. (See Table 1).

Table 1

Data specifics after data cleaning

Ind	Year	Date	Total Days	Datapoints.	On HR	Mean groupsize ± sd	Mean Male Ratio ± sd
Isha	2009	25/07- 14/08	12 days	2143	22%	4.4 ± 3.2	0.46 ± 0.16
	2010	25/06- 13/08	19 days	4935	60%	4.9 ± 3.5	0.30 ± 0.27
	2011	10/07- 30/08	30 days	9574	56%	3.0 ± 2.7	0.19 ± 0.26
Julia	2009	13/06- 20/07	9 days	1882	26%	2.7 ± 1.4	0.18 ± 0.26
	2010	11/05- 06/07	20 days	5452	27%	9.1 ± 4.9	0.41 ± 0.22

As the subjects were followed and repeatedly observed and as consecutive observations are expected to be related, the datapoints were highly correlated in time and space. To control for this autocorrelation two approaches were used: firstly, lagged predictor variables were inserted in the models to control for the temporal correlation *(*Keele & Kelly, 2006). The lag structure used was decided upon by inspecting the residuals and using the autocorrelation function (ACF)- and the partial autocorrelation function (PACF) plots as guiding in the construction and comparing of different structures by Akaike Information Criterion (AIC) (Appendix 5). The ACF provides coefficient values of auto-correlation between observations at time *t* and the observations at previous times. The PACF then finds the correlation of the residuals to identify the order of the lag predictors.

As the time difference and correlation between the observations is not consequent and as it is debated on whether lag predictors might suppress the explanatory power of the other predictors (Dormann et al., 2007) another smaller subset of the data was tested in which only the changepoints on which habitual paths were entered and left were used to make subsequent data points less dependent on each others. This subset was filtered on all changepoints on which a habitual route was entered or left; resulting in a smaller and balanced response distribution (Table 2). Appendix 6 shows the frequency distribution of the predictor- and response variables of the data used in fitting the three separate models.

Table 2

Data specifics subset data, changepoints

Ind	**Year**	**Date**	**Total Days**	**Datapoints**	**on HR**	**Mean groupsize ± sd**	**Mean Male Ratio ± sd**
Isha	2009	25/07- 10/08	9 days	64	48%	3.9 ± 3.2	0.49 ± 0.13
	2010	25/06- 13/08	21 days	170	50%	5.0 ± 4.1	0.33 ± 0.26
	2011	10/07- 30/08	45 days	353	50%	3.1 ± 2.8	0.18 ± 0.25
Julia	2009	13/06- 20/07	8 days	41	46%	2.4 ± 0.8	0.16 ± 0.25
	2010	11/05- 06/07	23 days	165	50%	8.7 ± 4.8	0.41 ± 0.23

* *Note that the mean group sizes and male ratios barely deviate. However, because only the changepoints were considered, the distribution between on and off habitual routes is balanced in this set.*

Statistical Analyses

To investigate the effect of the above mentioned predictors on the usage of habitual paths I designed several Generalized Linear Models (GLM's) with binomial error structure and logit link function, in R (v 4. 0. 2.) using the function glm (R packages; Bates et al., 2015).

Since there was habitual route data for only two chimpanzees there were not enough levels to include individual as a random effect in a mixed model; therefore, it was decided to make separate Generalized Linear Models for Isha and Julia and one combined model with ‘individual’ as a separate fixed effect (Table 3).

To facilitate interpretation of the estimates, before fitting the models all categorical predictors were centered and all quantitative predictors were z-transformed to a mean of zero and standard deviation of one. Model stability was assessed by comparing the estimates obtained from the model with estimates excluding one observation at the time using Dfbeta. This showed no apparent influential cases. Variance Inflation Factors were determined to rule out collinearity among the predictors (Field, 2005) using the function ‘vif’ of the package ‘car’ (Fox & Weisberg, 2011). For this analysis the model was simplified, leaving out the interaction and revealing a maximum VIF of 1.87 for Mratio for Isha and a maximum VIF of 1.85 for number of independent individuals for Julia.

To test for the overall effect of the fixed effects and simultaneously protect from multiple testing errors, I compared the full models with the null models with just the lag and control predictors, using a likelihood ratio test, function ‘anova’ (Dobson, 2002). When the likelihood test revealed significance the significance of individual predictors was assessed using another likelihood ratio test using the function ‘drop1’ ($p<0.05$).

I predicted that the probability of habitual route use decreases as the number of independent individuals in the group increases. At the same time, I expected that with an increase in male ratio the probability of habitual route use also decreases.

I expect an increasing number of trees fed on per day, as indicator of fruit availability and seasonal variation, to have an negative effect on habitual route use as well. I also predicted more habitual route use on rainy days and I expected this to interact with the time of day as habitual routes might be avoided in the early mornings and late afternoons because of the risk encountering predators (Kouakou et al., 2011; Janmaat et al., 2014).

Lastly, I expect to see an effect of human-made research trails on habitual route use because these paths are likely to be used repeatedly as such due to their openness of vegetation. As I test the same prediction on different datasets, I expect to find similar results for both separate chimpanzee models (Model 1 & Model 2) as well as for the different sample sizes (Model 3).

Table 3

Model Formulations

Ind	**Model**	**Response**	**Predictor**	**Lags**
Isha	1.	on HR~	Number of independent individuals	Lag(onHR,1)
			Male Ratio	Lag(onHR,3)
			Number of trees per month	Lag(onHR,6)
			Rain* I (Time^2)	
			On or off trail	
Julia	2.	on HR~	Number of independent individuals	Lag(onHR,1)
			Male Ratio	Lag(onHR,2)
			Number of trees per month	Lag(onHR,3)
			Rain * I (Time^2)	Lag(onHR,5)
			On or off trail	
Isha & Julia	3.	on HR~	Number of independent individuals	-
			Male Ratio	
			Number of trees per month	
			Rain * I (Time^2)	
			On or off trail	
			Individual	

Results

Model 1: Isha

Conducting a full- versus null model comparison with a likelihood ratio test revealed a significant overall effect of the predictor variables on the usage of habitual routes in the model of Isha (χ^2=45.5, df= 7, $p < 0.001$; n= 16.651) (Table 4). Specifically, was there a higher probability for Isha to travel on a habitual route when she travelled in a smaller group or alone compared to when she was travelling in a larger group (estimate: -0.17, SE: 0.079, $p = 0.008$) (Fig 1a). In addition, I found an effect of the usage of human-made research trails on the probability of habitual route use. This effect was in the opposite direction of my predictions; the probability for Isha to travel on a habitual route was lower on the human-made research trails (estimate: -1.096, SE: 0.402, $p = 0.006$).

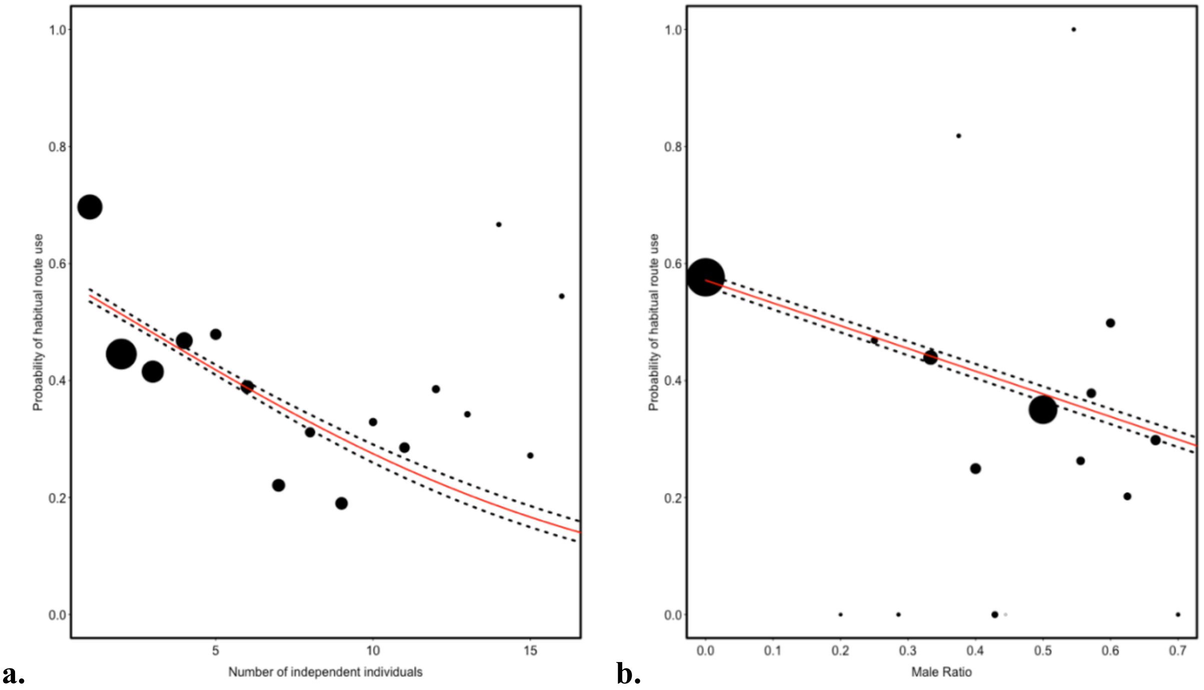
The interaction of time of day and rain did not show to have a significant effect of habitual route use probability. When fitting a reduced model without the interaction, and with rain and time included as separate variables, time did show a significant effect (Table 5). Instead of the expected quadratic relationship in which habitual routes would be avoided during sunrise and sunset, the probability of habitual route use decreased over daytime (as seconds after midnight increased) (estimate: -0.099, SE: 0.043, $p = 0.020$), (Table 5), (Fig 3). This reduced model, without the interactive effect, turned out to slightly better fit the data than the initial model (AIC: Full: 4998.6, Reduced: 4993.6)

The male ratio also revealed a trend effect in the predicted direction, with the probability of habitual route use increasing when group composition involved relatively fewer males (estimate: -0.09, SE: 0.063). The non-significance of this effect was likely caused by the high correlation of the predictors of male ratio and number of independent individuals, as for larger group sizes, there are likely to be more males in the group (r (16649) = 0.67, $p < 0.001$) and a possible collinearity problem. Testing the same model without the number of independent individuals did reveal a significant effect of male ratio, indicating that the probability of habitual route use to decrease as male ratio increases (estimate: -0.21, SE: 0.043, $p < 0.001$) (Fig 1b).

Fig 1.

The (separate) probability of Isha showing habitual route use for the number of independent individuals (a.) and male ratio (b.) in the group.

The probability for each group size is represented by the black dots varying in size according to the number of observations. The significant predicted probability and confidence intervals are represented by the red and dotted lines.



a. **b.**

Table 4

Model Isha: Factors influencing the probability that Isha travels habitual routes.

Predictor	**Est.**	**SE**	**Lower CI**	**Higher CI**	χ^2	***p***	**min**	**max**
(Intercept)	-3.586	0.079	-3.745	-3.433				
No_indep[1] [3]	**-0.171**	**0.064**	**-0.297**	**0.046**	**-2.672**	**0.008 ***	**-0.176**	**-0.167**
Mratio[1]	-0.097	0.063	-0.221	0.026	-1.543	0.122	-0.101	-0.093
Trees per day[1]	0.029	0.045	-0.058	0.117	0.655	0.512	0.027	0.032
Rain[2]	0.193	0.268	-0.333	0.715	0.718	0.620	0.160	0.232
Time[1] [o]	0.071	0.046	-0.019	0.161	1.555	0.106	0.068	0.074
On/offtrail (on trail)[2]	**-1.096**	**0.402**	**-1.853**	**-0.290**	**-2.729**	**0.006 ***	**-1.213**	**-1.036**
Rain*time[2] [o]	-0.031	0.177	-0.378	0.314	-0.178	0.859	-0.054	-0.004

[1] Z-transformed to mean of 0 and SD of 1

[2] Centered

[3] Log transformed

[o] I(z.time^2)

Note: The Lag predictors (Lag 1, Lag 3, Lag 6) are not shown in the results

Table 5

Reduced model Isha: Factors influencing the probability that Isha travels habitual routes.

Predictor	**Est.**	**SE**	**Lower CI**	**Higher CI**	χ^2	***p***	**min**	**max**
(Intercept)	-3.513	0.079	-3.641	-3.390				
No_indep[1] [3]	**-0.147**	**0.064**	**-0.272**	**-0.021**	**-2.293**	**0.022 ***	**-0.151**	**-0.143**
Mratio[1]	-0.108	0.063	-0.231	0.016	-1.711	0.086	-0.111	-0.104
Trees per day[1]	0.026	0.045	-0.062	0.113	0.574	0.566	0.023	0.028
Rain[2]	0.177	0.182	-0.179	0.532	0.974	0.330	0.163	0.198
Time[1]	**-0.099**	**0.043**	**-0.182**	**0.015**	**-2.318**	**0.020**	**-0.101**	**0.096**
On/offtrail (on trail)[2]	**-1.111**	**0.406**	**-1.873**	**-0.290**	**-2.736**	**0.008 ***	**-1.230**	**-1.052**

[1] Z-transformed to mean of 0 and SD of 1

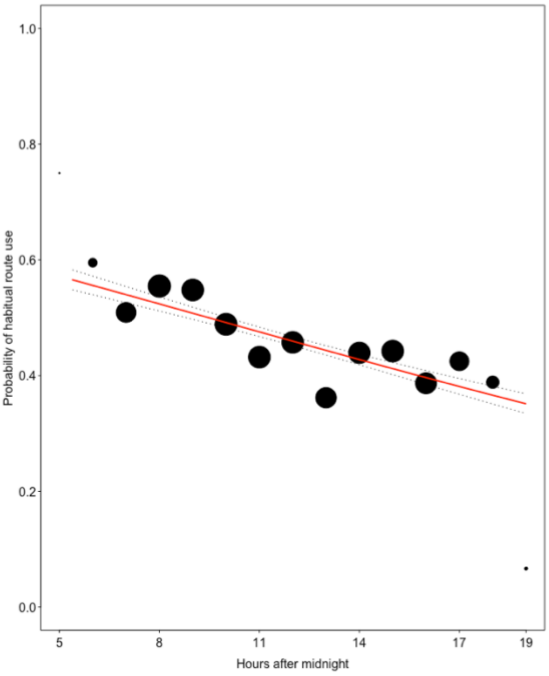
[2] Centered

[3] Log transformed

Note: The Lag predictors (Lag 1, Lag 3, Lag 6) are not shown in the results.

Fig 3.

The (separate) probability of Isha of showing habitual route use predicted by time of day.



Model 2: Julia

For Julia's model the full versus null comparison likewise showed overall significance (likelihood ratio test: χ^2= 14.15, df= 7, p = 0.049, n=7333). However, when testing for the individual predictors, only the predictor on/off trail showed a significant effect (estimate: -1.99, SE: 0.762, p = 0.009) (Table 6). Also for Julia, due to unbalanced data this effect was not substantial when plotted. In addition, the quadratic effect of time showed a trend effect.

As for Isha, for Julia a reduced model was fit, excluding the non-significant interactive effect of time*rain and adding them as separate predictors (Table 7). For Julia however, this only revealed a positive trend for rain but did not reveal other significant effects, such as an effect of on/off trail nor a better fit overall (AIC: Full: 1859.4 Reduced: 1861.1). Also testing for male ratio without the predictor of number of independent individuals did not reveal a significant effect of the number of males in the group on the probability of habitual route use.

Table 6

Model Julia: Factors influencing the probability that Julia travels habitual routes.

Predictor	Est.	SE	Lower CI	Higher CI	χ^2	*p*	min	max
(Intercept)	-4.166	0.134	-4.437	-3.911				
No_indep[1] [3]	-0.146	0.106	-0.353	0.062	-1.374	0.169	-0.154	-0.136
MRatio[1]	0.133	0.106	-0.074	0.340	1.254	0.210	0.122	0.144
Trees per day[1]	-0.058	0.071	-0.196	0.081	-0.816	0.414	-0.063	-0.050
Rain[2]	-0.042	0.914	-1.957	1.558	-0.046	0.963	-0.310	0.188
Time[1] [º]	0.152	0.080	-0.005	0.310	1.894	0.058	0.142	0.160
On/offtrail (on trail)[2]	**-1.993**	**0.762**	**-3.400**	**-0.376**	**-2.616**	**0.009 ***	**-2.451**	**-1.750**
Rain*time[2] [º]	0.276	0.415	-0.503	1.106	0.664	0.507	0.186	0.437

[1] Z-transformed to mean of 0 and SD of 1

[2] Centered

[º] I(z.time^2)

Note: The Lag predictors (Lag 1, Lag 2, Lag 3, Lag 5) are not shown in the results

Table 7

Reduced model Julia: Factors influencing the probability that Julia travels habitual routes.

Predictor	Est.	SE	Lower CI	Higher CI	χ^2	*p*	min	max
(Intercept)	-4.003	0.101	-4.208	-3.81				
No_indep[1] [3]	-0.143	0.106	-0.351	-0.66	-1.343	0.179	-0.153	-0.132
MRatio[1]	0.157	0.107	-0.053	0.366	1.467	0.143	-0.146	0.170
Trees per day[1]	-0.060	0.070	-0.198	0.078	-0.858	0.390	-0.066	-0.053
Rain[2]	0.590	0.352	-0.117	1.256	1.673	0.094	0.516	0.661
Time[1]	0.039	0.071	-0.100	0.179	0.552	0.581	0.032	0.047
On/offtrail (on trail)[2]	**-1.849**	**0.754**	**-3.245**	**-0.259**	**-2.451**	**0.014 ***	**-2.297**	**-1.579**

[1] Z-transformed to mean of 0 and SD of 1

[2] Centered

[3] Log transformed

Model 3: Subsample

In the smaller subsample in which only the data of the changepoints was considered (n= 793), and in which the data of Isha and Julia was merged, no significant effects were found. (Likelihood ratio test: χ^2= 3.54, df= 7, p = 0.831, n=793) Some of the estimates were going in the same direction; the number of independent individuals, and on/off trail both showed negative estimates as for all the other models (Table 8). Testing for male ratio separately, without including the number of independent individuals, did not reveal a significant effect on habitual route use probability. Fitting the reduced model, did not show any significant changes of effects compared to the full model except a slightly better fit. (AIC: Full: 1113.8, Reduced: 1112.7)

Table 8

Model subsample Isha + Julia

Factors influencing the probability that Isha & Julia travel habitual routes.

Predictor	**Est.**	**SE**	**CI** lower	**CI** higher	χ^2	**p**	**min**	**max**
(Intercept)	-0.074	0.115	-0.299	0.150				
No_indep$^{1\ 3}$	-0.094	0.115	-0.319	0.131	-0.815	0.415	-0.104	-0.080
MRatio^1	0.042	0.106	-0.165	0.250	0.400	0.690	0.030	0.054
Number of trees^1	0.005	0.076	-0.144	0.155	0.072	0.943	-0.003	0.014
Rain/no rain (rain)^2	-0.095	0.537	-1.162	0.966	-0.177	0.859	-0.246	0.069
Time$^{1\ o}$	0.059	0.080	-0.098	0.217	0.732	0.464	0.048	0.069
On/off-trail (on trail)^2	-0.908	0.703	-2.462	0.398	-1.292	0.196	-1.183	-0.519
Rain^2 *time$^{1\ o}$	0.188	0.304	-0.406	0.799	0.064	0.537	0.110	0.297
Individual	0.012	0.182	-0.345	0.368	0.617	0.949	-0.008	0.029

^{1} Z-transformed to mean of 0 and SD of 1

^{2} Centered

^{3} Log transformed

^{o} I(z.time^2)

Discussion

The aim of this study was to gain insights into cognitive and ecological attributes involved in decision-making processes in wild chimpanzees by studying their observed travel patterns. I mainly focused on the assumed influence of foraging party size and group composition on the decision to travel habitual routes. Ultimately my aim was to contribute data on social dynamics to the existing work that has been done on individual decision-making processes concerning route-based travel.

Group size

Based on the idea that habitual paths would yield cognitive savings, and assuming that travelling alone or in small groups is cognitively more demanding as the information load cannot be distributed as much as in large groups, I predicted an increasing group size to negatively affect the probability of using habitual routes. Besides cognitive skills required for navigating, it is expected that the safety of these habitual paths might also play a role in this decision. Smaller groups that are more susceptible to predators are assumed to travel less far and show less explorative behavior (Chapman et al., 1995). Even though predators more predictably know where to find their prey on these routes, they are relatively safe routes as familiarity with the area makes it easier for the chimpanzees to find ways to escape by quickly climbing trees.

For Isha’s trajectories I found that indeed the probability of travelling over habitual routes decreased as the number of independent individuals in the group increased suggesting larger groups to show more explorative behaviour or travel more novel paths. It’s hard to disentangle which underlying motives play a role in the decision to travel habitual paths. As there is accounted for the anticipated risk of predation through the quadratic interaction of time of day, and as this effect was smaller compared to the effect of group size, one could argue that the reduced cognitive load of travelling together with more individuals might play a larger role.

Group composition

In the first instance, only in Isha's reduced model, a trend was found for an increase of habitual route use with a decreasing male ratio. This trend was consistent with my expectations and could be an indication that females generally perform more risk aversive behavior or goal-directed movement (Byrnes et al., 1999). As male ratio was slightly correlated with the number of independent individuals there was also tested for male ratio separately, without the number of independent individuals. This indeed showed a significant effect. However, this was only the case for Isha's model, not for Julia nor the combined model. Yet after testing for each variable separately, and comparing AIC values, the combination of both predictors turned out to best predict the data.

Seasonal variation in food availability

As a proxy for seasonal variation, the model also tested for the effect of the number of food trees fed per day. Although it was expected that the number of food trees as an indicator for food scarcity would influence the paths travelled, no effect of this on the probability of habitual route use was found. It was expected that fewer trees fed on per day would imply more scarcity, more revisits to similar fruit trees, and therefore, according to findings by Presotto & Izar (2010) more habitual route use. However, it could be that fewer trees fed on also means there was less travelling in general, hence fewer chances to move over habitual routes. On the other hand, habitual routes are generally paths that pass by more food trees (Porter, 2020). Therefore, it is hard to disentangle the cognitive benefits of travelling on habitual routes from the monitoring and foraging benefits of walking on these particular paths. In future research the type of behavior executed on the routes should be added, as to distinguish the particular function of the habitual routes in the executed travel patterns. Secondly, it must be noted that as an indicator of seasonal variability and food scarcity, 'trees per day' is not the most complete proxy of food availability. Therefore, to learn more about this relationship it is important to, in future instances, also include information about the location of the trees and the nutritional intake values in the analyses as well as control for the overall distances travelled.

Lastly, even though food availability appeared to fluctuate between years, data gathering took place in periods of food scarcity therefore this study was unable to make a proper comparison of food scarce versus non-scarce periods. However, as there was quite some variation in the number of trees visited per day *(*Appendix 6*)*, it is surprising that no effect was found. This might imply that the chimpanzees are able to approach the same tree from different directions. Nonetheless, long-term monitoring of route use, as well as the phenology and location of fruiting trees, would allow for more precise analyses of how seasonal variation influences habitual route use.

Human-made research trails

A contradictory effect was found for the predictor of human-made research trails, as a proxy for the openness of vegetation. In line with findings by Green (2020), this was assumed to be a characteristic that would enhance the efficiency of movement and therefore possibly increase the probability that such a trail would be used as a habitual route. Isha's model showed an overall decrease rather than an increase in the chances of habitual path use when moving on human-made research trails. Also, testing for a correlation and plotting the two variables did not reveal substantial overlap between the research trails and the habitual route segments. Reasons for this could be that research trails are avoided as habitual routes due to the chances of coming across researchers, illegal poachers, or predators. Personal communication with Janmaat revealed that leopards were often spotted on camera traps placed on research trails. This could be tested in the future by testing for an interactive effect of group size and research trail use. If indeed, this effect is caused by risk avoidance of encountering predators, I would expect that this is especially true when the number of males in the group is low, as chimpanzee males have been observed to chase predators (Janmaat et al., 2014).

Alternatively, since these trails are located for research purposes specifically it might also be that the locations of these trails are not convenient for foraging. The trails might not pass enough feeding resources or might not configure as travel bouts in between important feeding areas. This could explain why they might not be incorporated as habitual routes in travel strategies. More information about the location of these routes in combination with feeding data could substantiate these findings.

Weather conditions

One trend effect for weather conditions of rain was found in Julia’s reduced model, suggesting habitual route use to increase during rainy days. As was expected this might mean that rain could motivate goal-directed movement, and possibly encourage the integration of habitual routes in energy maximizing foraging strategies. Contradicting directions of estimates were found for Isha’s models and the combined model. Because of this and because of Isha’s models being the largest and possibly most reliable models, I suggest no inference can be made here. Also, why caution for interpretation is necessary and what most likely has disturbed these results is that for all models, the distribution of the variables ‘on/ off track’ as well as ‘rain/no rain’ was very unbalanced (Appendix 6) with very few observations of the chimpanzees on track and in rain. For future studies it is recommended to collect more data on this or infer the data from other sources such as daily weather reports and mapped locations of the research trials.

Time of day

Lastly, the reduced model did show a significant effect of the predictor of time on the probability of habitual route use, showing Isha to be less likely to use habitual routes as seconds after midnight increased. It could be that this has to do with deviating motivational drivers at the end of the day, namely; the selecting- and construction of a sleeping nest. At the end of the day, chimpanzees are re-grouping and collectively looking for a place to nest. This could explain why Isha performed less habitual movement at this time. For Julia and the combined model, no significant effect of time of day was found. Also were the estimates all showing the opposite direction. However, Julia's model did show a trend for the modelled quadratic relationship. Suggesting that the risk for predation, which is higher in early morning and late afternoon, might be incorporated in her movement strategy. Nonetheless, these contradicting results suggest that further substantiation of the effect of time on habitual route use is necessary.

Difference between models

The comparison of the results of Isha's model with the model of Julia does not show substantial overlap. There are several arguments that can explain why Isha and Julia's results are deviating. Firstly, the difference could lie in the different size and distributions of the dataset. Isha's data was gathered over 3 years whereas for Julia there were only two study periods. Besides this, there was a difference in the percentage of habitual route use; Isha was walking on habitual routes in about 46% of the observed cases whereas Julia was walking on habitual routes for 26% of the time. Looking beyond the specifics of the data, what is most plausible to have played a role in the individual differences in travel patterns is that Julia was in oestrus during the study period in 2010 (Porter, 2020). This is likely to have influenced her ranging pattern in a way in which she was more dependent on the ranging behaviour of the males (Goodall, 1986).

Limitations

This study started with the incentives to study the relationship between cognitive load, decision-making and habit formation. In the end it was limited to solely study the effect of group size, group composition and some ecological variables as predictors of travelling habitual paths. In the first place, the exact costs and benefits of group travel for cognitive energy were hard to grasp. Where on the one hand group travel is expected to save cognitive energy due to shared knowledge, sociality of moving in a group can be cognitively demanding as well. In this type of research these influences are hard to isolate and it is therefore important to stay cautious. Secondly, can one argue that speculating about habitual behaviour by considering a route a habitual route after two passings might too simplistic.

There are many ways however, in which this type of research can be enriched in order to learn more about the trade-offs at stake, that were beyond the scope of this project. As proposed by Garber & Boinski (2000) a trade-off that might involve group size, daily path length, home range area, and resource monitoring is likely to play a role in the forthcoming of foraging strategies of wild chimpanzees (Garber & Boinski, 2000). In this direction, Presotto et al. (2019) in elephant navigation studies found, navigational strategies to be adjusted to the familiarity of the environment. Border and home range area is considered to be an influential factor in the emergence of movement patterns, in particular the increase of the usage of habitual routes outside of home range and core areas (Presotto et al., 2019). This study was limited to behavioural datapoints only because processing detailed information about the daily path lengths, home range area and familiarity with the surroundings was beyond my capabilities for this study. Future studies are highly encouraged to also incorporate information such as path length, home range area and motivational aspects in order to learn more about the dynamics and implications of this trade-off.

Furthermore, as group behavior and the observed communal spatial choices, is proposed to be the result of consensus between individual interests (Janson, 2007). It is extremely challenging to unravel the individual processes and influences that are at play in the emergence of cooperative travel decisions. It should also be mentioned that because at all times a female focal was followed, an all-male group (male ratio = 1) was never part of the observational data and could thus not be tested for, reducing the overall variation in this predictor variable. To extend knowledge on the different dynamics involved in group decision-making processes a closer look at group specifics should be aimed for.

Group specifics can be extended, in terms of age, reproductive status, and rank of dominance. As knowledge and spatial skills increase over the years it is expected that the decision for Taï chimpanzees to incorporate habitual routes in their travel strategies might also be dependent on the average age of the members in the group. Secondly, considering that group decisions are joint consensus highly influenced by the degree of dominance within the hierarchical structure of the group, rank should also be accounted for in future models (Murray et al., 2006; Murray et al., 2007). As rank was found to strongly influence (female) chimpanzee space use, this influence should be controlled for in the observation of travel patterns.

Secondly, more thorough information on phenology and seasonal changes in food sources, or observations in both food rich and scarce periods, can show insights on how path development emerges when food is scarce and the incentive to maximize net energy and decrease cognitive load is stronger.

Besides the theoretical limitations, other shortcomings of this study can be identified in the data preparation as well as in the analyses itself. For the analyses part, I experienced difficulties with implementing an autocorrelation term in my models. I, therefore, decided to use a lag predictor structure. However, this might not cover the autocorrelation as accurately as a calculated term would do. For future studies, it is recommended to firstly aggregate towards a single data point per travel bout and to then implement an autocorrelation term, as to double-control for this.

Future research

Nowadays algorithms are available that can inspect bulks of GPS data on repeatedly used trajectories, in a more efficient way than was done for this study. Currently, software can identify these habitual route segments much faster and easier; for example, Habitual Route Analysis Methods (HRAM) could be used to determine route networks on a larger scale (Janmaat et al., 2021). In this way, the refersed buffer check is not needed anymore, and accuracy will be improved. This could potentially elevate this type of research a lot in the near future.

Once these habitual route segments are derived, they should then ideally be identified and labeled on a more detailed level than was done in this study, including more information about motivational-, familiarity- and phenological aspects. Once a clear impression of the behavior that takes place on- and off these routes is achieved, more solid comparisons can be made to learn about the effects of habitual route use on cognitive load.

Besides an array of other potential influencing factors, there are also opportunities in the already available data as collected by Karline Janmaat, namely the inclusion of the other three followed chimpanzees could be added to the analyses once habitual route segments for these chimpanzees are determined. This can show more insights into individual differences, as well as allow for more complex and integrated (mixed) modelling.

Significance

Our behaviour is often guided by habits. Habit formation evolved because of the limited capacity of our working memory. When performing habitual behaviour cognitive load is reduced and the resources in working memory can be allocated to other attributes. Assuming that individuals might make decisions about where to travel next based on their estimate of which travel route will yield them the largest net pay-off, it is expected that the decision to travel habitual grounds can be linked to attributes that pose a high cognitive load.

Expecting that group movement increases spatial knowledge available, and therefore decreases the cognitive load posed on travelling, this study tested the effect of group size on the usage of habitual path segments. The results suggested there to be a lower probability of habitual route-use when chimpanzees were travelling in larger groups. In other words showing less explorative behaviour or novel paths when travelling alone or in a small group.

Conclusion

This study tried to gain insights into when and why chimpanzees decide to travel over habitual routes. Considering that habitual routes are generally energetically less costly, these routes were expected to be travelled upon more often in the generally more cognitively demanding situations. Ranging data of two wild chimpanzees and the respective habitual routes were investigated in general linear models testing several predicting factors. The results suggested a selection of attributes that were more likely to occur on- or off habitual routes. Group sizes were found to be generally smaller on habitual route segments, male ratio was generally lower, and also the time of day was found to determine whether or not the chimpanzees used habitual routes. To further substantiate these findings further research is encouraged. Nonetheless, the results of this study suggest that it may indeed be that larger groups take on more risks and larger cognitive challenges thereby substantiating the social intelligence hypothesis or, social complexity as a driver of cognitive evolution.

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Appendix 1

R scripts provided

a. Chimp tracks

b. Habitual Route check

c. Data preparation

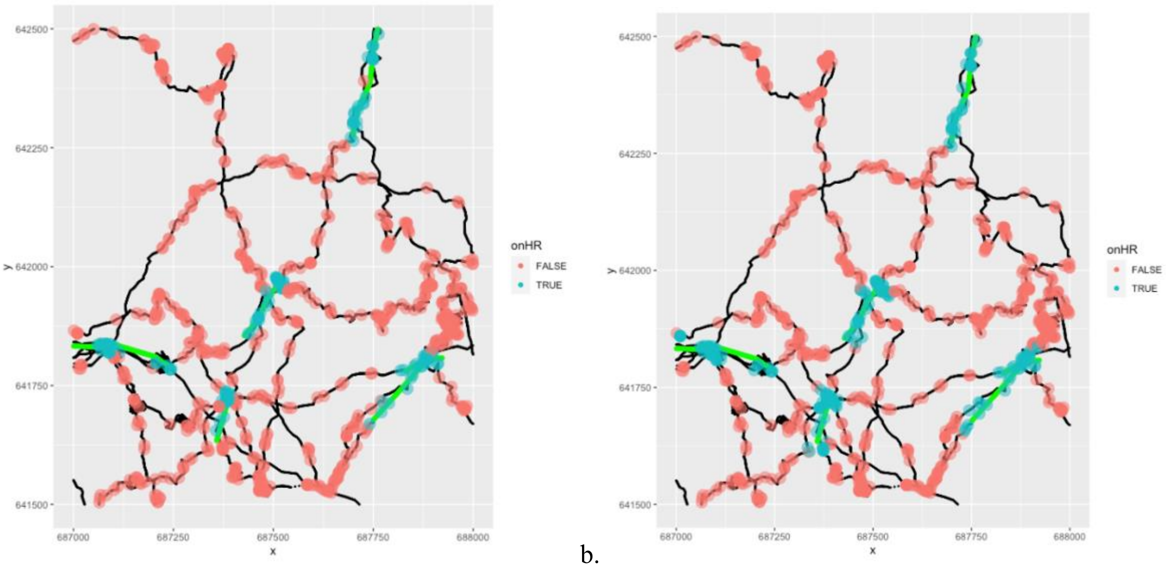
d. Statistical analyses I & II

Appendix 2

Figure 1. Determination of applied buffer

Plotting the results of two different buffers; 15 (1a.) and 30 (1b.) Green lines are habitual route segments.

Datapoints (dots, blue=onHR, red= offHR) and travel paths (black lines).



a. b.

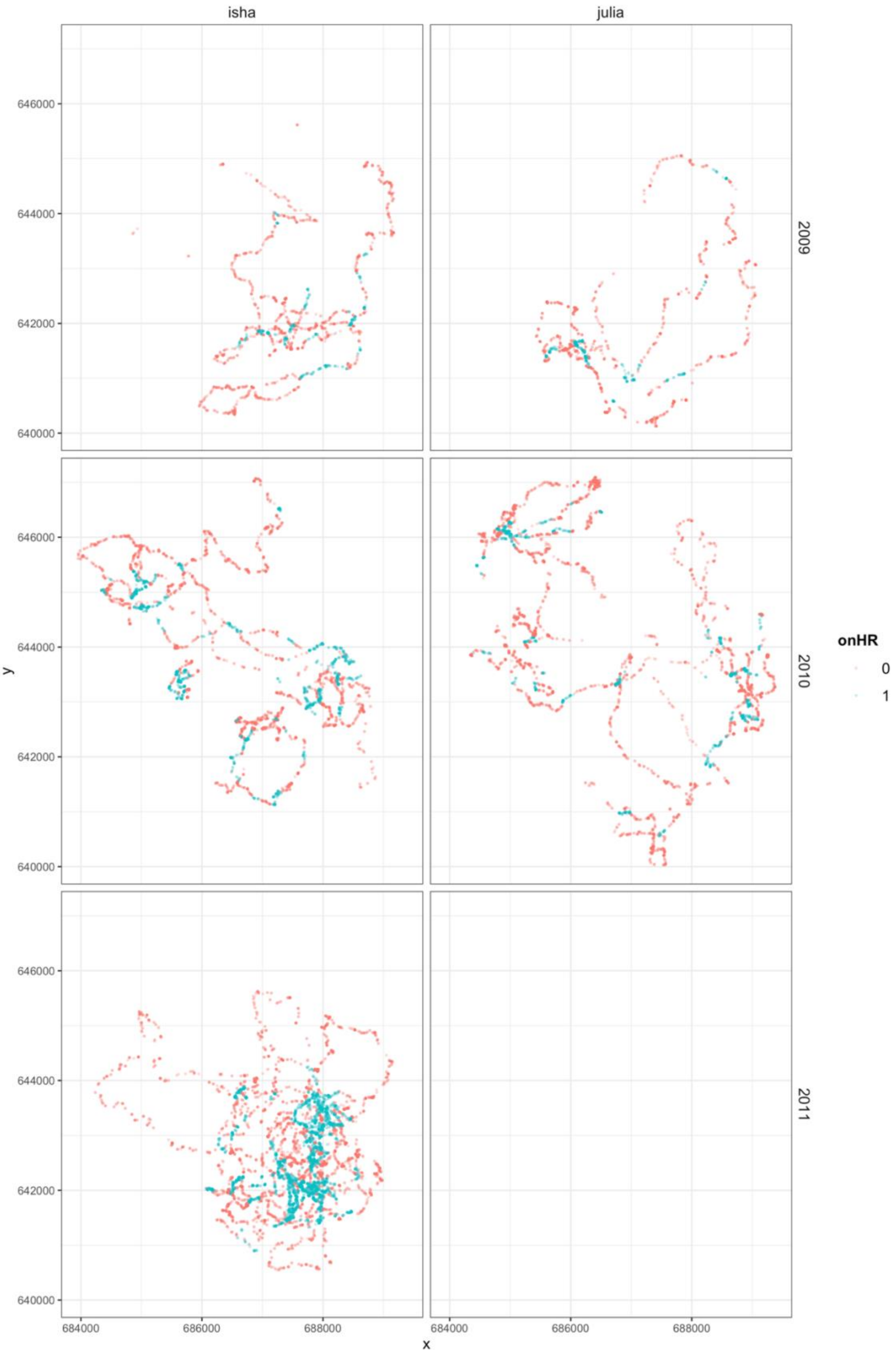
Table 1

Accuracy and probability of different buffers.

Ind	**Year**	**Date**	**Total Days**	**Datapoints**	***on HR*** *buffer=15*	**on HR** *buffer=30*
Isha	2009	25/07- 14/08	12 days	2143	*15%*	22%
	2010	25/06- 13/08	19 days	4935	*27%*	60%
	2011	10/07- 30/08	30 days	9574	*45%*	56%
Julia	2009	13/06- 20/07	9 days	1882	*21%*	26%
	2010	11/05- 06/07	20 days	5452	*19%*	27%

Fig 2. Overview habitual route use Isha & Julia

The blue dots indicate habitual routes



Appendix 3

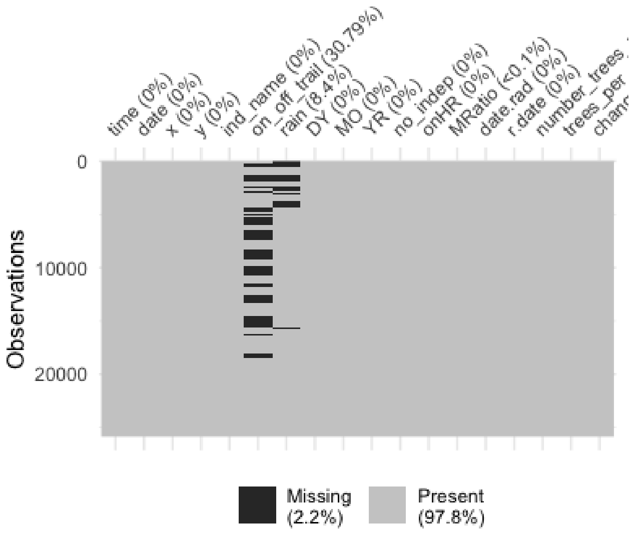
Table 1.

Average number of unique trees fed on per day.

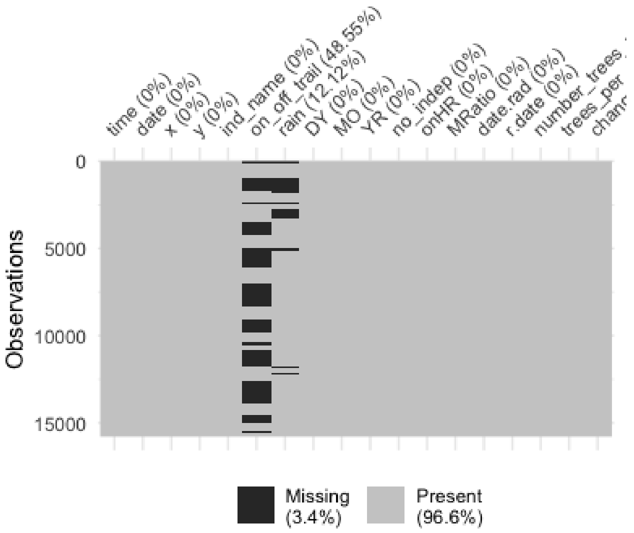
Ind	**Year**	**Month**	**Average number of trees fed on per day**	
			Individual model	Subset
Isha	2009	07	18.6	16.8
		08	12.2	11.4
	2010	06	16.4	16.4
		07	12.5	12.2
		08	25.8	24.8
	2011	07	15.5	14.8
		08	19.5	18.6
Julia	2009	06	14.0	12.1
		07	13.9	12.0
	2010	05	12.7	11.9
		06	13.9	13.2
		07	12.2	12.7

Appendix 4

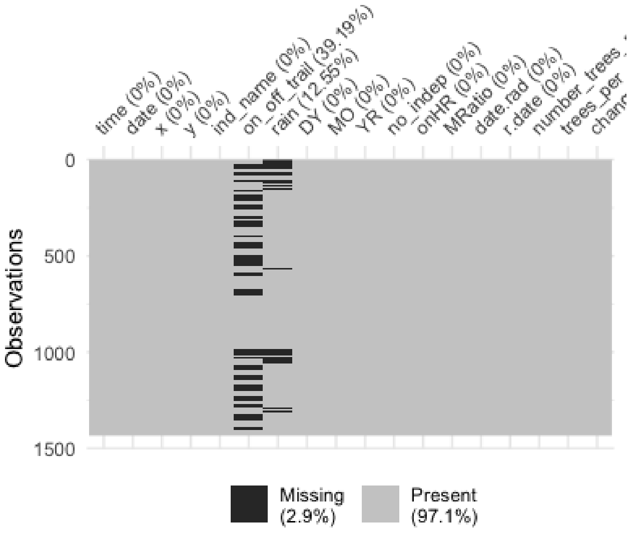
Fig 1. Missing data Isha (a.), Julia (b.), and combined (c.)



a.



b.



c.

Appendix 5

Figure 1a. ACF and PACF plots lag structure Isha

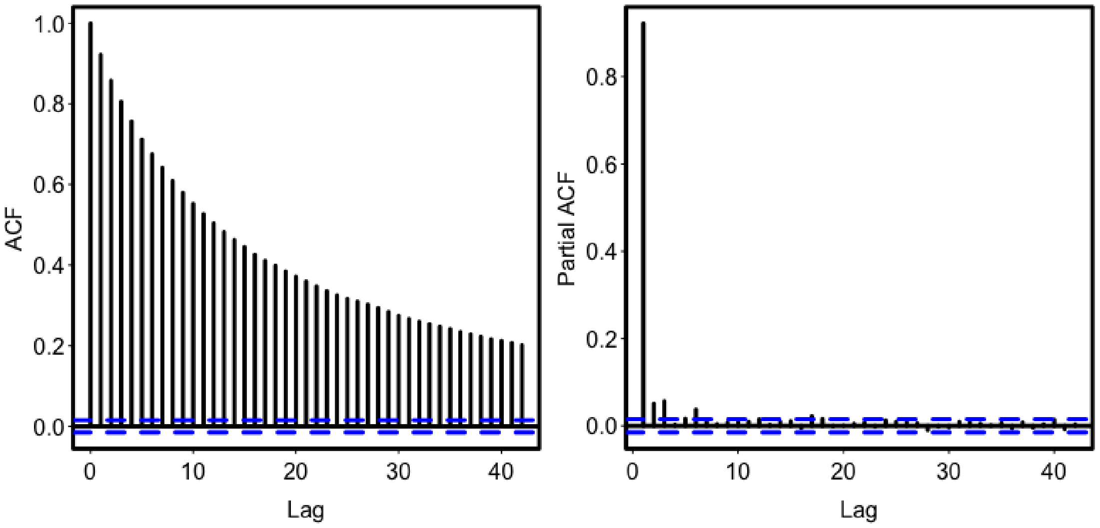
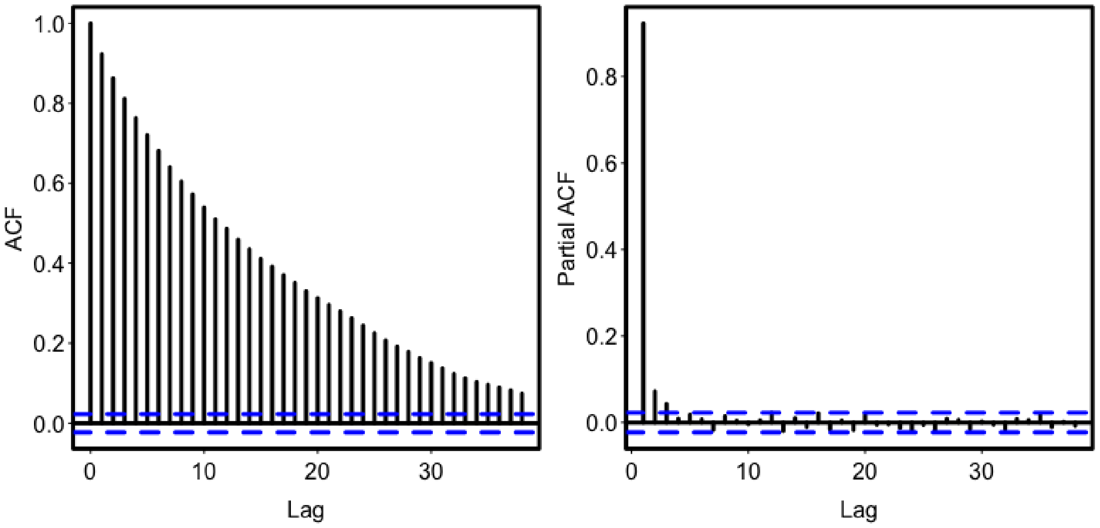


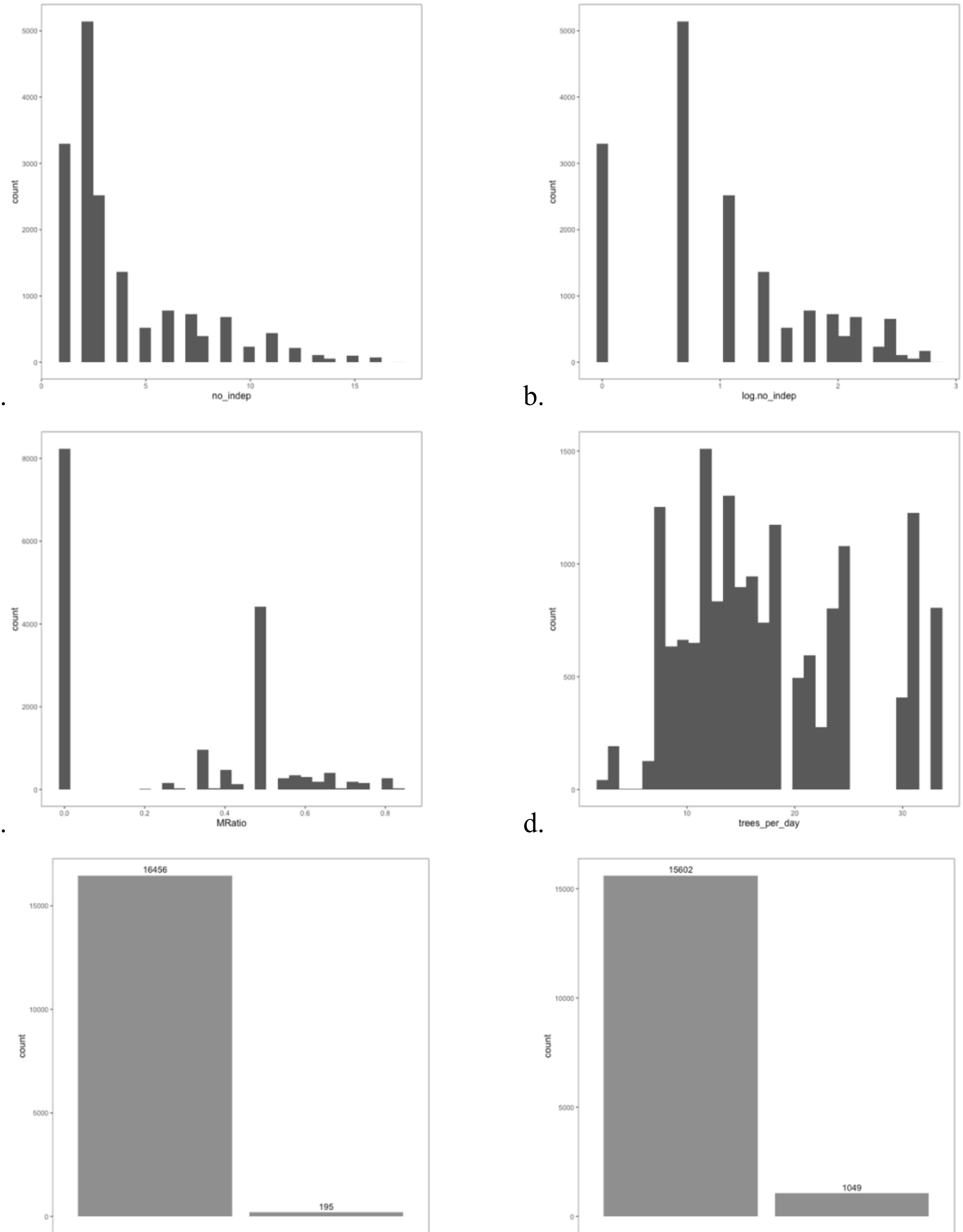
Figure 1b. ACF and PACF plots lag structure Julia



Appendix 6

Fig 1. The frequency distribution histograms for the predictor variables of the model of Isha

for a) The number of independent individuals in the group. b) Log-transformed number of independent individuals. c) Male Ratio. d) Number of trees fed on per day. e) On/off-trail. f) Rain/no rain.



a.

b.

c.

d.

e.

f.

Fig 2. The frequency distribution histograms for the predictor variables of the model of Julia

for a) The number of independent individuals in the group. b) Male Ratio. c) Number of trees fed on per day. d) On/off-trail. e) Rain/no rain.

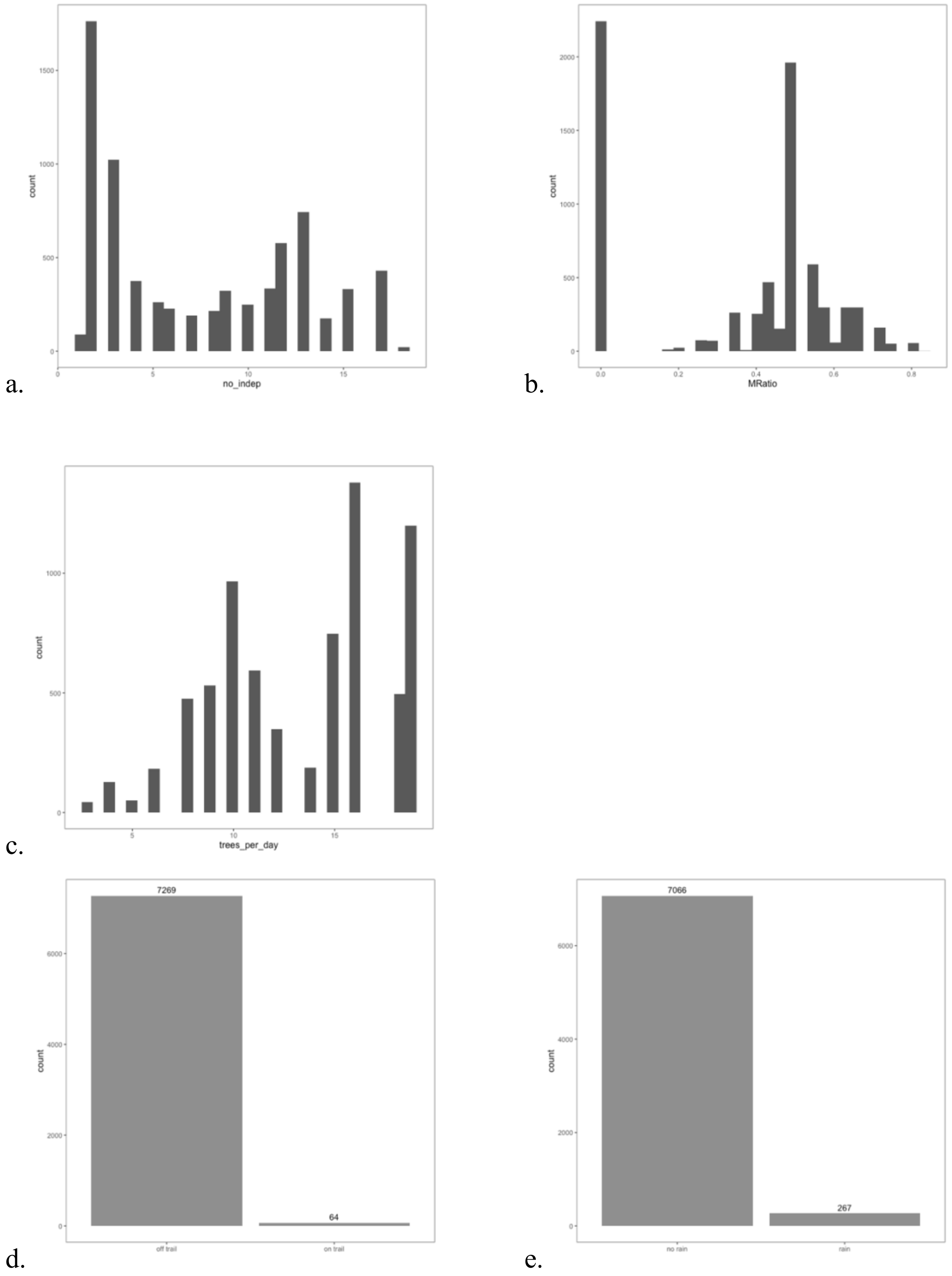


Fig 3. The frequency distribution histograms for the predictor variables of the subsetted model of Isha & Julia

for a) The number of independent individuals in the group. b) Log-transformed number of independent individuals. c) Male Ratio. d) Number of trees fed on per day