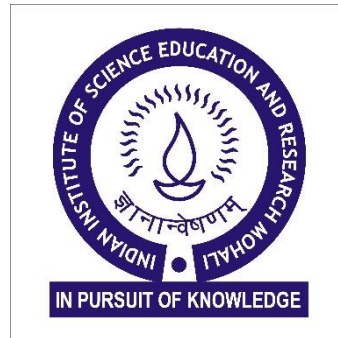# Within-Group Competition and Foraging Behaviour in Female Asian Elephants (*Elephas maximus*) in Nagarahole National Park, southern India

Awani Bapat

A dissertation submitted for the partial fulfilment of the BS-MS dual degree in Science

Indian Institute of Science Education and Research Mohali

April 2019

Certificate of Examination

This is to certify that the dissertation titled 'Within-Group Competition and Foraging Behaviour in Female Asian Elephants (*Elephas maximus*) in Nagarahole National Park, southern India' submitted by Ms. Awani Bapat (Reg. No. MS14166) for the partial fulfilment of BS-MS dual degree programme of the Institute, has been examined by the thesis committee duly appointed by the Institute. The committee finds the work done by the candidate satisfactory and recommends that the report be accepted.

Dr. N.G. Prasad   Dr. Rhitoban Raychoudhury   Dr. Manjari Jain

                                                                           (Supervisor)

                                                    Dated:

Declaration

The work in this dissertation has been carried out by me under the guidance of Dr. Manjari Jain (Supervisor) and Prof. T.N.C. Vidya (Co-supervisor) at the Indian Institute of Science Education and Research Mohali and the Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru. This work has not been submitted in part or in full for a degree, a diploma, or a fellowship to any other university or institute. Whenever contributions of others are involved, every effort is made to indicate this clearly, with due acknowledgement of collaborative research and discussions. This thesis is a bonafide record of original work done by me and all sources listed within have been detailed in the bibliography.

Awani Bapat

(Candidate)

Dated:

In my capacity as the supervisor of the candidate's project work, I certify that the above statements by the candidate are true to the best of my knowledge.

Dr. Manjari Jain

(Supervisor)

Acknowledgements

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Next, I would like to thank the Karnataka Forest Department for granting research permits for fieldwork, and the entire forest department staff for being very helpful and supportive during the fieldwork. I must express my immense gratitude to our driver, Mr. Pramod, and our tracker, Mr. Shankar, for being very accommodative and for teaching me Kannada, and the ways of the forest. I also thank Dr. Nandini Shetty and Revathe for guiding me during the fieldwork and Dopey and Whiney for being the best company anyone could have in a strange new place. I would also like to thank DST-INSPIRE for the fellowship grants, and the Indian Institute of Science Education and Research (IISER), Mohali and Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR), Bengaluru for infrastructure.

For a first research project, there were many diverse concepts and techniques to learn, which would have been a difficult task without the help and insight of the members of Animal Behaviour Lab (ABL), Evolutionary and Organismal Biology Unit (EOBU), JNCASR. I am particularly thankful to Hansraj Gautam and Dr. Nandini Shetty for sharing their data with me, and for continuously helping me with framing questions to carrying out

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Abbreviations

FSRT: Food-site residence time

FR1: Feeding rate 1

FR2: Feeding rate 2

steps_bet: Number of steps taken between two food-sites

time_bet: Time taken to move between two food-sites

ADI: Average dominance index

gp_size: Group size

no_AF: Number of adult females present in the group

ave_mean_ht_1m: Average mean grass height measured within 1-m plots

ave_cover_1m: Average grass cover of 1-m plots

ave_biomass_1m: Average biomass measured in 1-m plots

ave_cover_5m: Average grass cover of 5-m plots

ave_biomass_5m: Average biomass estimated in 5-m plots

gp_serial_no: Serial number of group feeding event

ind: Individual identity

Contents

Abstract

Within-group competition for food resources is the primary cost faced by group-living females. Asian elephant females form fission-fusion societies in which competition might be minimized by the potential for temporary group fission. However, a constraint on female group size was still found previously in the Kabini elephant population in southern India, suggesting that there might be competition for food resources. In this study, I examined the effects of age, dominance rank, group size, and feeding activity type on individual behavioural characteristics of adult females, such as food-site residence time, feeding rates and feeding costs (number of steps and time taken to move between successive feeding sites). I also examined if quantitative measures of grass distribution explained the observed behavioural measures. I found that there seemed to be a moderate level of patchiness in grass resources based on the average food site residence time and the steps moved to a new feeding site. Dominance rank (based on contest competition) had an effect on food-site residence time, with more dominant females spending more time at feeding sites. Grass abundance also affected food-site residence time positively. Feeding rates, apart from being influenced by feeding activity type, increased with increasing group size, suggesting that scramble competition was also significant. However, I did not find patch depletion (another measure of scramble competition) by groups at the temporal scale that I examined, suggesting that there were sufficient feeding sites available at that scale.

Chapter 1: General Introduction

Animals exhibit different ways of living, some being solitary throughout their lives, others aggregating in large groups, while still others forming structured groups or societies wherein individuals repeatedly interact with one another, giving rise to different kinds of relationships between them. Factors such as predation pressure, resource distribution and abundance, accessibility to mates, and infanticide avoidance may shape the social lives of species (Alexander 1974, Jarman 1974, Sterck *et al*. 1997). However, competition for resources such as food or mates is expected to pose a major cost to group-living. Thus, where there is potential for cooperation amongst individuals to harness a resource, there may also be conflict over the same resource. Depending on the strengths of the factors driving group living, and the variations in the cooperative and agonistic interactions between individuals, animals may display different types of social organisation. Since male and female mammals show vastly unequal investments in reproduction, with females facing high energetic demands owing to milk production, female reproductive success is expected to be affected primarily by the distribution of food resources, while male reproductive success is expected to depend primarily upon the accessibility of females for mating (Trivers 1972, Emlen and Oring 1977). Over the years, ecologists have come up with models to describe the different patterns of social organisations expected based on resource-risk distributions, chiefly in the context of primates, and these collectively form socioecological theory.

1.1 Socioecological Theory

Wrangham (1980) was amongst the first to suggest two main types of female social organisation: female bonded groups and non-female bonded groups. In the former case, females associate with known individuals such that the dominance relationships between them are consistent, and the majority of females stay in the same group into which they

were born. This may be explained by the cost to reproductive success due to food limitation driving female bonded groups to cooperatively defend food patches against other female groups. On the other hand, females in non-female bonded groups do not face food limitations and hence do not need to affiliate with other group members and may transfer between groups. Wrangham suggested that in the case of female bonded groups, the cost incurred due to within-group competition would be much smaller than that due to competition with other groups.

Competition may be indirect (scramble type), not involving any aggressive interactions, or it may be direct through contests, involving agonistic interactions amongst individuals that result in the winner and not the loser obtaining access to the resource being contested (Nicholson 1954). The type of competition is expected to be determined by resource characteristics, such as resource quality and dispersion. The resource may be clumped, with patches of high-density food surrounded by low-density expanses, or it may be more uniformly dispersed without much variation in food density over a relatively large area. Clumped resources which can be easily defended and monopolized by individuals are expected to give rise to contest competition if the resource is of high quality, while dispersed resources which cannot be monopolized by individuals will tend to result in scramble competition (van Schaik 1989, Isbell 1991). Scramble competition among individuals increases with the number of individuals feeding in a patch and thus constrains the group size (van Schaik *et al*. 1983, Wrangham *et al*. 1993). Contest competition, on the other hand, affects the social relationships between individuals, resulting in dominance hierarchies and kin-based associations. Thus, the differences in food abundance and distribution are expected to result in different levels of within and between-group scramble and contest competitions.

Later socioecological models (van Schaik 1989, Isbell 1991, Sterck *et al*. 1997, Isbell and Young 2002) built upon Wrangham's (1980) basic model by trying to incorporate the consequences of predation pressure, variations in population density and resource distribution affecting within and between-group competition to predict different patterns of female social organisation. If the predation pressure is low and resources do not limit female reproductive success, then females are not expected to form groups, while high predation pressure and resources limiting female reproductive success are expected to drive

females to form groups. Different combinations of these ecological factors can result in the formation of four broad types of societies:

1. High predation pressure but resources not limiting reproductive success will result in the formation of a *dispersal egalitarian* society in which within- and between-group contest is absent, and females transfer between groups.

2. When predation pressure is high, and resources limit female reproductive success but are dispersed so that individuals within a group cannot defend food patches, then a *resident egalitarian* society is expected, in which individual females do not transfer between groups, between-group contest is strong, but within-group contest is weak or absent.

3. In the case of high predation pressure, low population density, and limiting (in terms of female reproductive success) resources that is clumped such that individuals within a group can monopolize food patches, a *resident nepotistic* society is expected to form, with strong within-group contest, but low between-group contest, and individualistic, age-based or kin-based dominance hierarchies within the group.

4. Finally, if the predation pressure is low, but the population density is high, resources are limiting, and food patches can be monopolized by individuals, then strong within and between-group contest is expected. However, the within-group competition is expected to be lowered by the strong between-group competition, with dominant individuals becoming more tolerant of the less dominant individuals within the group, resulting in a *resident nepotistic tolerant* society.

1.2 Food Resource Distribution and Contest Competition

Although socioecological theory predicts the formation of social relationships between individuals or groups based on differences in food resource quality, abundance and distribution, these are are not easy to estimate in the field and can have several problems associated with estimation for the following reasons (Isbell *et al*. 1998, Isbell and Young 2002):

1. Quantitative measurements of the patchiness of food distribution strongly depend on the measurement scale used by the researchers, and on the study species. The scale at which the researcher tries to determine patchiness may not be the relevant

scale of perception by the animal. What appears to be clumped at one scale may appear to be dispersed at a larger scale for the same animal.

2. Measurement scales may also depend on the research question to be addressed. The measurement scale used for studying within-group interactions may not be appropriate for studying between-group interactions.

3. The food characteristics that the researcher may use for inferring patchiness may not necessarily be the same that the animal uses. For example, researchers may use leaf density in a tree to estimate patchiness, but the animals may be using leaf nutritional quality (Glander 1978) to make foraging choices.

These problems may be circumvented by focussing on how the animals themselves perceive the patchiness of a resource, instead of attempting to estimate it ourselves (Wiens 1976). In order to do this, a measurable behavioural aspect of the animal can be assessed. In this context, resources have been thought of in terms of *monopolizability* and *usurpability* (van Schaik 1989, Isbell 1991, Isbell and Young 2002). *Monopolizability* is the ability of an individual to hold on to a food patch, which therefore means that smaller areas can be easily monopolized by dominant individuals, irrespective of how long it takes to deplete the food in that area, whereas larger areas cannot. Thus, monopolizability is a spatial trait and is not a good measure of the patchiness of a resource because individuals may be monopolizing resources in the absence of visible behavioural interactions between them (Isbell and Young 2002). *Usurpability*, on the other hand, is a temporal trait. An area is said to be usurpable if a higher-ranking individual can take it away from a lower-ranking one. The longer the time an individual spends at a food patch, the greater the chance that a dominant individual can usurp it. Thus, the time that an individual spends at a food site or the Food-Site Residence Time (FSRT) can be used as a proxy for the usurpability of a resource (Isbell *et al*. 1998, Isbell and Young 2002, Pruetz and Isbell 2000). Individuals may have long FSRT if the food site itself is a large area or the food resource requires a long time to process prior to ingestion. However, within the same food resource, longer FSRTs may be indicative of a higher resource value (Harcourt and Stewart 2007). If there is some form of dominance hierarchy established within the group, then the lower-ranking females may have prior knowledge of the higher-ranking females and will not choose to engage in costly dominance to usurp the food sites of higher-ranking females (Koenig and Borries 2009). Thus, if the resources are clumped, dominant individuals would be able to forage at high-quality patches and would be expected to have a longer FSRT than less

dominant individuals. A second behavioural measure of the density of food resource is the distances moved between food sites by individuals (Isbell *et al*. 1998). Short distances moved between food sites are indicative of a clumped food distribution, while long distances are indicative of a more dispersed distribution.

It is important to emphasise here that a food-site is not defined as having spatial boundaries. It is the movement of animals that defines a food site and hence the scale of measurement, rather than the older, researcher-based definitions of patches. Elaborate studies on patas monkeys and vervets (Isbell *et al*. 1998, Isbell and Pruetz 1998), white-faced capuchin monkeys (Vogel and Janson 2007), grey-cheeked mangabeys (Chancellor and Isbell 2009), and mountain gorillas (Wright and Robbins 2014, Grueter *et al*. 2015) suggest that food-site residence time (FSRT) is a good measure of within-group contestability, with food-types having longer FSRT having more aggressive incidences. In all these studies, they found statistically significant support for the expectation that more dominant individuals have longer FSRT values.

1.3 Food Resource Distribution and Scramble Competition

When food resources are patchily distributed, but individual patches cannot be defended, scramble competition plays an important role in determining the species' social structure (Janson and van Schaik 1988, van Schaik 1989). Within-group scramble can occur both in the presence and absence of contest competition (van Schaik 1989). While food-site residence time is a good proxy to examine the effects of within-group contest competition at the level of individuals, it may not be useful in examining the presence of within-group scramble competition in the absence of within-group contest.

Chapman and colleagues (Champan *et al*. 1995, Snaith and Chapman 2005, 2007, Tombak *et al*. 2012) suggested the patch depletion method as an indicator of within-group scramble, irrespective of the presence or absence of any contest competition. If group size depends on the availability of food, then foraging groups can deplete patchily distributed food resources (Snaith and Chapman 2005). As food is consumed from a patch, its concentration in the patch decreases over time, requiring individuals to take more time and effort to extract more food from the same patch. This functionally depleted patch results in a reduction in the food intake rates over time (Chapman *et al*. 1995). Thus, the patch can be

inferred to be depleted if the feeding rates of individuals reduce over time (Charnov 1976, Stephens and Krebs 1986). A study by Grether *et al.* (1992) showed that food intake rate declined over the time spent in a patch. Larger groups will tend to spend less time in a patch, as they deplete patches faster, than smaller groups (Pyke 1984, Janson and van Schaik 1988, Chapman *et al.* 1995, Snaith and Chapman 2005). Studies on spider monkeys and chimpanzee (Chapman *et al.* 1995), red colobus monkeys (Snaith and Chapman 2005), and guereza (Tombak *et al.* 2012) demonstrate the usefulness of the patch depletion method to infer the presence of scramble competition by comparing feeding rates at the start and end of group feeding bouts.

1.4 Study species and area

The study species was the Asian elephant (*Elephas maximus*), one of the three extant species of Order Proboscidea (the African savannah elephant and the African forest elephant being the other two). The Asian elephant is listed as endangered by the IUCN, with only 26000 to 29000 individuals in the wild in India (Sukumar 2003). These are distributed among four main regions in India: northern, northeastern, central, and southern India, with habitats ranging from evergreen to dry thorn forests (Sukumar 2003, Vidya *et al.* 2005a). The populations in southern India are estimated to together comprise approximately 14000 individuals, of which the Nilgiris-Eastern Ghats landscape population is, by far, the largest (Baskaran *et al.* 2011). The Asian elephant population studied in this thesis is part of the Nilgiris-Eastern Ghats population, in Nagarahole National Park and Tiger Reserve (11.85304°-12.26089° N, 76.00075°-76.27996° E) and Bandipur National Park and Tiger Reserve (11.59234°-11.94884° N, 76.20850°- 76.86904° E). The Kabini Elephant Project (see Vidya *et al.* 2014) has been monitoring the elephant population centred around the Kabini river that separates Nagarahole and Bandipur and this population is referred to here as the Kabini population. Nagarahole and Bandipur National Parks primarily comprise moist and dry deciduous forests. In the dry season (approximately January to May), the backwaters of the Kabini reservoir (from the Beechanahalli Dam built over the River Kabini) recede and expose a large grassland area, which becomes an important food source for many herbivores including elephants, and enables good visibility for individual identification and behavioural observations (Vidya *et al.* 2014). As part of the Kabini Elephant Project, over 700 individuals have now been individually identified

based on various natural physical characteristics, sexed (as they are sexually dimorphic) and aged based on height and skull size comparisons with known captive elephants (see Vidya *et al*. 2014, Figure 1.1).

Asian elephant females and their offspring live in matriarchal groups, while subadult males (5-15 years) disperse and live largely solitarily thereafter (McKay 1973, Sukumar 1989, Vidya and Sukumar 2005, Nandini *et al*. 2018, Keerthipriya *et al*. 2018). The clan is the most inclusive unit of female social organisation and females belonging to different clans do not associate positively with one another (Nandini *et al*. 2018). However all adult females (>10 years old) of a clan are not found to associate with one another at all times, and the female groups seen in the field are variable in size and composition owing to fission-fusion dynamics (Nandini *et al*. 2017, 2018). Thus, the food competition faced by individual females may vary over time with changing group size and composition. This makes Asian elephants an interesting model system to examine the effects of contest and scramble competition on their feeding behaviour. On the contrary, with fission-fusion dynamics being available, within-group competition might be expected to be consistently low. However, it was found that the social structure of female elephants in the Kabini population did not change across seasons, unlike that seen in several other species that have fission-fusion dynamics in response to resource availability, suggesting that fission-fusion dynamics here might be a means of associating with different females from the clan (Nandini *et al*. 2017). Moreover, it was also found that there seemed to be a constraint on group size, suggesting high levels of competition. Therefore, it would be worth examining female elephant feeding behaviour in this population in the context of competition within groups.

Although Asian elephant diets are known to comprise of a variety of grasses, herbs, shrubs, and trees (Sukumar 1989, Baskaran *et al*. 2010), the main food source available to elephants in the Kabini backwaters is grass (Figure 1.2). During the wet season, the backwater grasslands are submerged and the elephants are mostly scattered in small groups across the surrounding forests (Vidya *et al*. 2014). Previous work showed within-group agonistic interactions in females groups (3.2 interactions per hour) in these grasslands in the dry season (Shetty 2016). Almost all agonistic interactions within groups had clear winners and older individuals tended to be the winners in 70% of the cases (Shetty 2016), suggesting that there was clear contest competition. Thus, this area is a good place to study the

relationship between the distribution of a single food source (grass in this case) and contest and scramble competition observed in this population, and in turn how it affects the feeding behaviour of individuals.
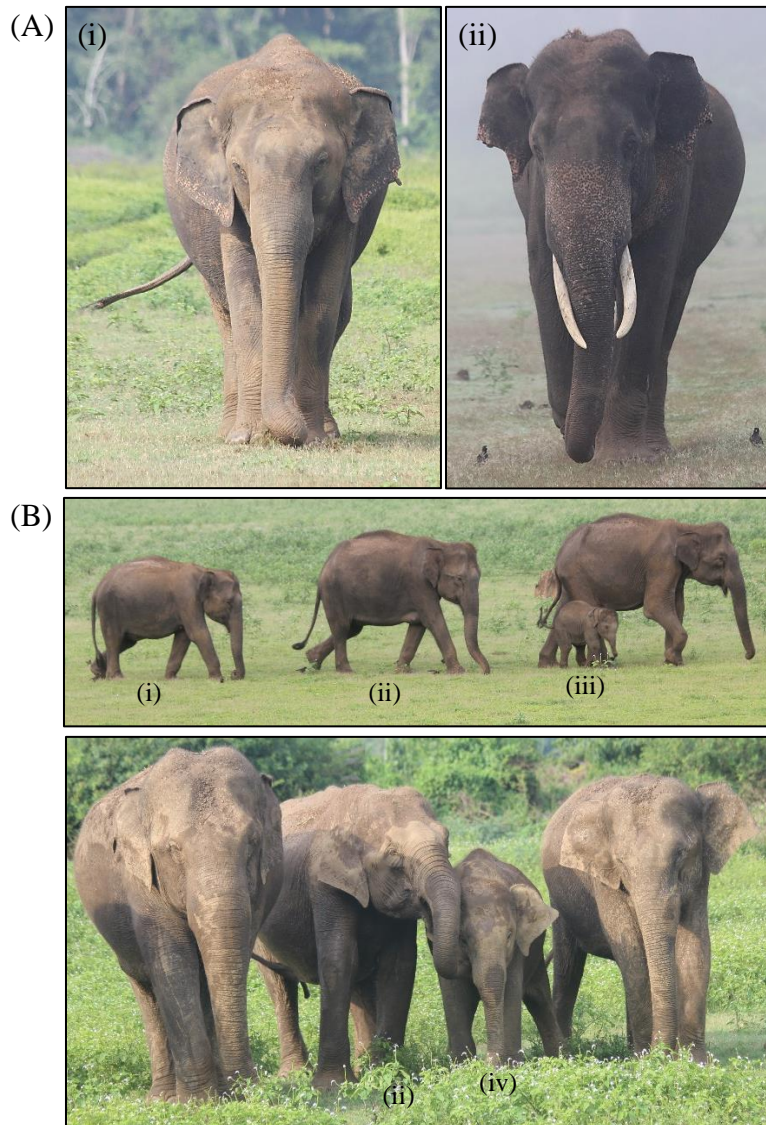
Figure 1.1: The Asian elephant (Elephas maximus).

(A) Sexual dimorphism in adult Asian elephants: (i) A typical adult female (ii) A typical adult male with tusks (males not having tusks are called makhnas, not shown here).

(B) Family groups consisting of individuals of different age classes: (i) Sub-adult female (ii) Adult female (iii) Calf (iv) Juvenile female.

Figure 1.2: Grass, the main food for Asian elephants in the Kabini backwaters.

1.5 Objectives

The objectives of my thesis were to find out whether the usurpability of food resource was related to the contesting ability of individuals, whether there was significant scramble competition based on feeding rates and patch depletion, and whether the food resource was patchy or not based on the distances moved by individuals between food-sites.

The specific objectives were the following:

1. To examine the variation in food-site residence time (FSRT), a behavioural indicator of usurpability and resource value or patchiness of food resource, with the dominance index of females and various ecological factors and determine the best predictors of the observed variation in FSRT.

   As mentioned in the introduction above, longer food-site residence time might indicate higher resource value and dominant individuals would be expected to have a longer FSRT than subordinate individuals. Therefore, I wanted to find out whether average dominance index (an indicator of dominance rank of the individual) and age (which is related to dominance amongst female elephants in Kabini) could explain FSRT. I expected more dominant or older females to show longer FSRT than less dominant or younger females. As Asian elephants do not have definite group sizes, group size was used as an additional explanatory variable. Contest competition is expected to increase with group size and thus the FSRT of females in larger groups is expected to be shorter than those of females in smaller groups. Since it was possible that total group size and group size in terms of the number of

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adult females alone could affect the competition faced by individual females, I also included the number of adult females separately as a possible explanatory variable. Since FSRT is expected to increase with increasing resource value, I also included previously estimated grass abundance variables (average mean grass height, average cover (in 1-m and 5-m plots), average biomass (of 1-m plots), and average biomass estimate (of 5-m plots)) in the model. Individuals feeding in areas with taller grass, more grass cover and biomass were expected to have longer FSRT.

2. To examine the various ecological factors affecting individual feeding rates.

   The ecological factors listed above were also used as possible explanatory variables for explaining the feeding rates of individuals. Feeding rates were measured as the number of trunkfuls delivered to the mouth per unit time. The trunkfuls of younger individuals would be smaller than those of older individuals, but they would presumably account for differences in body size. Since feeding rate is expected to be shaped by scramble competition, the most dominant individuals were not expected to have the highest feeding rates. Scramble competition increases with group size (total group size or number of adult females) and individuals in larger groups were expected to show slower feeding rates on average if there was a searching component involved but to show faster feeding rates if feeding effort was simply increased in the presence of competitors. Individuals feeding in areas with taller grass, more grass cover and biomass were expected to have higher feeding rates because of the smaller processing time required.

3. To examine the various ecological factors affecting the number of steps taken between successive food sites and time taken to move between successive food sites, both being indicators of the foraging costs incurred by individuals and the patchiness of the resource.

   As mentioned in the introduction above, the distances moved between food-sites by individuals is a behavioural measure of the density and patchiness of food resource (Isbell *et al.* 1998). The same ecological variables as mentioned above were used

as possible explanatory variables to explain the distance/time between food-sites. More dominant (or older) individuals were expected to take fewer steps and spend shorter lengths of time between food sites than less dominant (or younger) individuals, as dominant individuals are expected to feed from better quality food-sites. As competition increases with group size (or number of adult females), individuals are expected to search for food sites more, increasing the number of steps and the time taken to move between two food sites. Individuals were expected to move less / spend less time between two food sites, in areas with more abundant grass, i.e. more grass height, more grass cover and biomass.

4. To examine if there is significant within-group scramble competition using the patch depletion method.

   If the grass is distributed in patches, and this distribution of grass is assumed to constrain the group size of elephants, then foraging groups are expected to deplete patches. This depletion can be tested by comparing the feeding rates at the beginning and at the end of group feeding events. If foraging groups deplete the patches, then the feeding rates of individuals were expected to decrease with the time spent feeding in a patch.

Chapter 2: Methods

2.1 Fieldwork and Data Collection

I carried out fieldwork from 15th May to 30th June 2018 (from ~ 6 AM to ~ 7 PM) in Nagarahole National Park and Tiger Reserve (11.85304°-12.26089° N, 76.00075°-76.27996° E) and Bandipur National Park and Tiger Reserve (11.59234°-11.94884° N, 76.20850°- 76.86904° E) (Figure 2.1) to familiarise myself with elephant identification and behaviour in the study area. Whenever an elephant or a group of elephants was sighted, details such as time, GPS location, group size and composition, individual identity, etc. were noted. A female group was defined as a set of females and their dependent offspring of both sexes (sometimes also accompanied by subadult and adult males) that showed coordinated movement (especially between the forest and the backwaters or to a water source) and were usually within about 50 m of one another (see Nandini *et al*. 2018). Individuals were identified from photo or video recordings taken in the field based on various physical features such as ear shape, folds, cuts, holes, back and tail characteristics, and presence of warts or wounds (see Vidya *et al*. 2014, Figure 2.2). Females from the population had already been assigned to different clans based on social network analyses (Nandini *et al*. 2017, 2018) and the same categorisation was used.

Although I carried out some fieldwork to familiarise myself with the study system, because of the time required to both collect and analyse videos of behaviour, the videos I analysed in this study were not collected by me but by Hansraj Gautam (during his Ph.D. fieldwork) during February-June 2015 and 2016 in the Kabini backwaters area (11.888108°-11.932174° N, 76.203550°-76.230827°E) of Nagarahole National Park. Data on the group size, number of adult females, and grass abundance variables (see A.1, Appendix A)

collected by Hansraj Gautam during this period, as part of his Ph.D. work, were also available. The ages of individuals for this study were calculated from by subtracting the estimated dates of birth of individuals (maintained by the Kabini Elephant Project) from 1st February 2015, to give the ages at the start of the study period for which videos were analysed. Adult females were defined as those females who were 10 years or older on 1st February 2015. The average dominance index (ADI) calculated for each adult female based on within-group dominance interactions (see A.2, Appendix A) was used as a proxy for dominance rank. The average dominance index was based on field data from March 2009 and June 2013 and had been calculated by Nandini Shetty as part of her Ph.D. thesis (Shetty 2016).
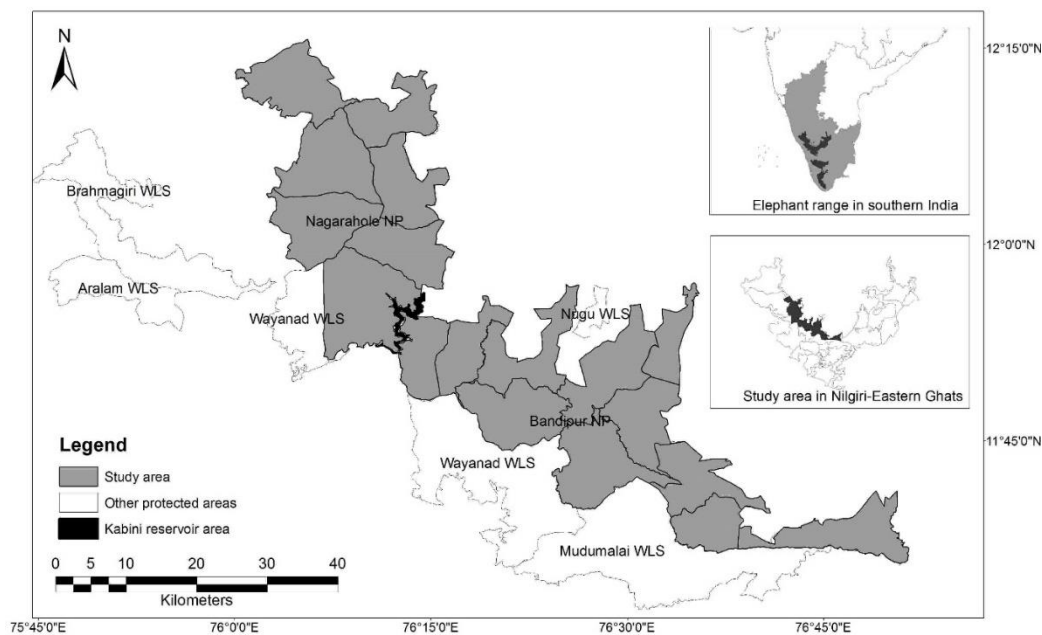
Figure 2.1: Map of Nagarahole and Bandipur National Parks and Tiger Reserves. The Kabini reservoir area is indicated in black.
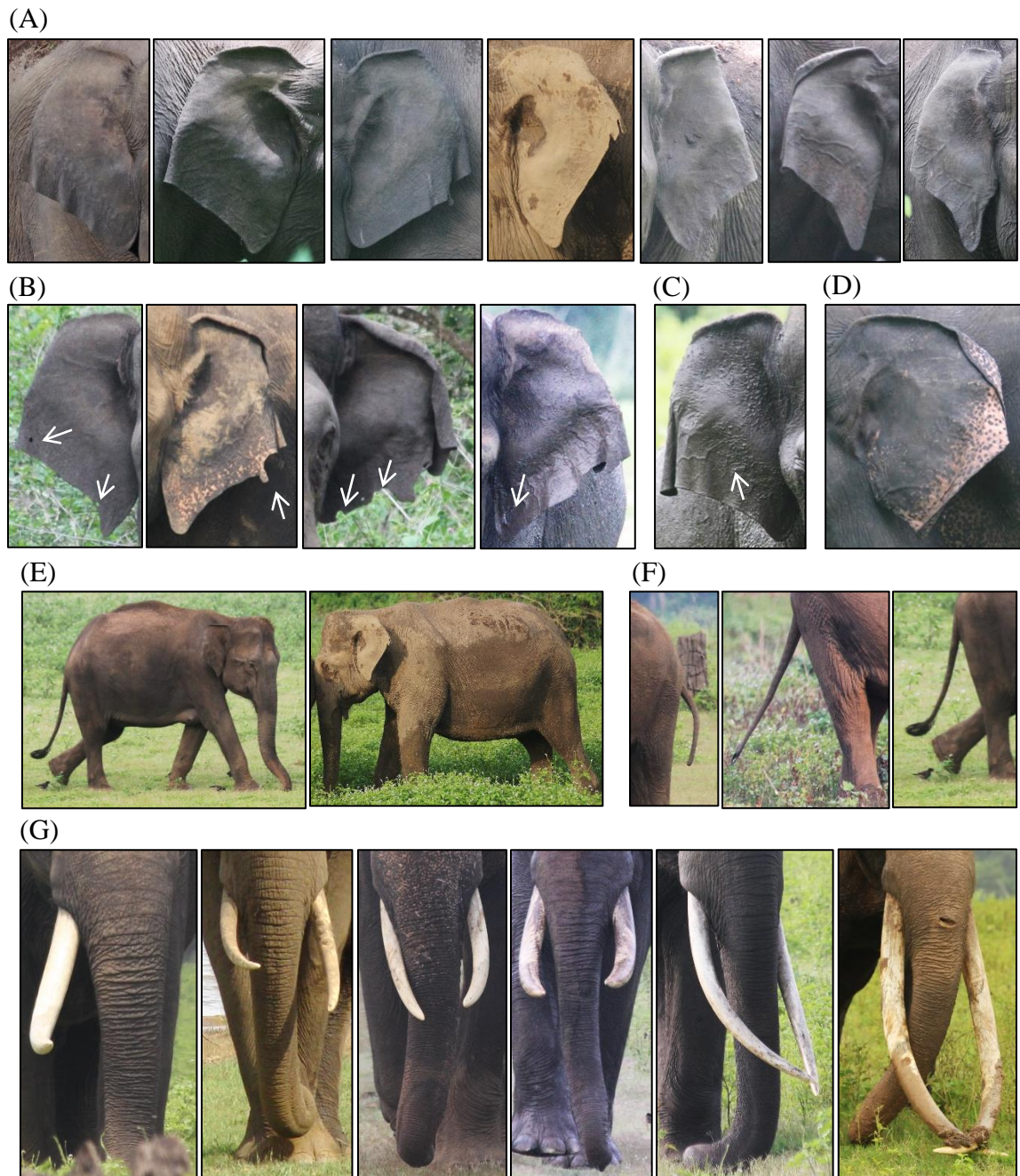
Figure 2.2: Individual identification based on physical characteristic such as, (A) Ear lobe shape and ear folds, (B) Holes, tears, nicks in the ear, (C)Veins in the ear, (D) Ear depigmentation, (E) Back shape, (F) Tail length and presence/absence of tail hair, and (G) Tusk length, shape and thickness in males.

2.2 Behavioural scoring and analysis

I carried out the behavioural scoring and analysis of videos collected by Hansraj Gautam. I used 81 focal group (Altmann 1974) video recordings of four commonly sighted clans (Kasturi, Lisa, Patricia, and Victoria) for behavioural scoring. A total of 19250.6 minutes of videos were analysed. Only videos in which the elephants were feeding on grass in the backwaters were scored. A *group feeding event* was defined as the duration in which at least one group member in the video started feeding until the last group member stopped feeding. A *food-site* was defined as any location where an individual fed. An individual was said to move to another food site if the individual walked away 4 or more steps in the same direction (as opposed to simply shuffling its feet within the food site) before feeding again. This would ensure that the individual was completely out of the immediate site where it was previously standing. The duration of each group feeding event was noted. For each adult female, the time spent at each feeding site, the total time that the female could be observed feeding, the time at which each trunkful of food was delivered to the mouth, the number of steps walked between two food sites, and the time taken to walk between two food sites were noted. The feeding activity type (Figure 2.3) - kicking or plucking grass – engaged in by the individual at each food site was also recorded. Any disruption of feeding due to disturbance from the occasional vehicle, other animals, male or female dominance, or interference by other group members, was noted. Data on feeding when there was disturbance from sources other than simply conspecific interference were not used.
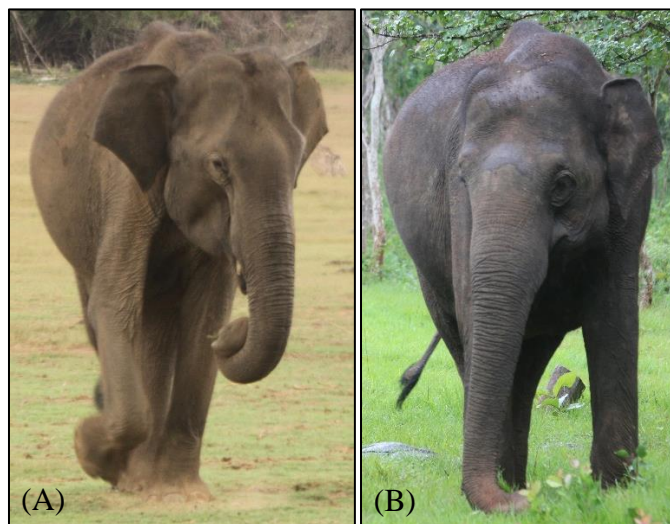
Figure 2.3: Feeding activity type may be classified as: (A) Kicking or (B) Plucking.

2.2.1 *Food-site residence time (FSRT), feeding rates and feeding costs*

The following 5 response variables were calculated from the dataset for each individual female.

1. Food-site residence time (FSRT) is the total time an individual female spent at each food site.

Feeding rates for each individual in each group feeding event for each feeding activity type were calculated in 2 ways:

2. Feeding Rate 1 (FR1) was calculated as the number of trunkfuls eaten in the total time observed feeding or walking between two food sites.

$$FR1 = \frac{Number\ of\ trunkfuls\ in\ a\ group\ feeding\ event}{Time\ observed\ feeding + Time\ observed\ walking}$$

3. Feeding Rate 2 (FR2) was calculated as the number of trunkfuls eaten in the total time observed feeding alone.

$$FR2 = \frac{Number\ of\ trunkfuls\ in\ a\ group\ feeding\ event}{Time\ observed\ feeding}$$

4. The steps taken between successive food sites (steps_bet) by each female was counted.
5. The time taken to move between successive food sites (time_bet) by each female was measured.

For each of these response variables, a linear mixed effects model was fitted with all permutations and combinations of the fixed and random variables (See Table 2.1). Feeding activity type, group size, number of adult females, age of individual (as on 1st February 2015), average dominance index (ADI) of the female, and five grass abundance variables: mean average height (1m plot), average cover (1m plot), average biomass (1m plot), average cover (5m plot), and average biomass estimate (5m plot) were used as the fixed variables. Group feeding event, clan identity, individual identity, year, and month were used as random variables. As group size and number of adult females were moderately correlated (Pearson's $R=0.71$, $P<0.05$, $R^2=0.497$) these were not included in the same model. Similarly, average biomass of 1-m plots and average biomass estimates of 5-m plots

were highly correlated (Pearson's $R=0.94, P<0.05, R^2=0.876$) and these were not included in the same models (see Table 2.2). Thus, a model could have a maximum of 6 fixed variables and 5 random variables.

The analyses were carried out using the *lmer* and *dredge* functions in R version 3.5.2 (RStudio version 1.1.463, R packages used: lme4 and MuMIn). The model with the least AICc value is considered to be the best model explaining the observed variation in each of the response variables. To determine if there were multiple best models, the models were ranked based on ΔAICc values, calculated as the smallest AICc value subtracted from the AICc value of each model. Models that had ΔAICc values smaller than 2 were considered to be equally good models. Models that had ΔAICc values greater than 2 were considered to be significantly poorer models as is the rule of thumb (Burnham and Anderson 2004).

2.2.2   *Patch depletion by foraging groups*

I used only the videos in which groups were observed feeding for 20 minutes or more to examine patch depletion. Videos shorter than 20 minutes were usually incomplete group feeding events and, therefore, not suitable to examine patch depletion. As group sizes ranged from 2 to 15 (see Appendix B) and not all the individuals could be observed feeding at the beginning and the end of a group feeding event, only the number of trunkfuls taken by the same individual in the first 5 minutes and last 5 minutes of the group feeding event were counted to obtain a measure of feeding rate. The duration between the first and last 5-minute interval was variable as the duration of group feeding events were variable. A paired t-test was carried out in Statistica 7 (StatSoft, Inc. 2004) to compare if the feeding rates in the first and last 5-minute intervals were different. As the durations between the first and last 5-minute intervals were not constant across feeding events, a Spearman's correlation was also carried out to see if the difference between the last and first interval was dependent on the duration between the two time intervals. Since it was possible that individuals might deplete patches at time intervals even shorter than 20 minutes, I also compared the feeding rates (number of trunkfuls taken in a 5-minute interval) between 10-minute intervals of the group feeding event using a paired t-test.

Table 2.1: List of response, fixed and random variables.

Response Variables	Fixed Variables	Random Variables
Food site residence time (FSRT)	Age	Group feeding event
Feeding rate 1 (FR1)	Average dominance index	Clan identity
Feeding rate 2 (FR2)	Group size	Individual identity
No. of steps taken between successive food sites	No. of adult females	Year
Time taken to move between successive food sites	Feeding activity type	Month
	Average mean grass height (1m plot)	
	Average grass cover (1m plot)	
	Average grass biomass (1m plot)	
	Average grass cover (5m plot)	
	Average grass biomass estimate (5m plot)	

Table 2.2: Correlations between some of the fixed variables.

Variable 1	Variable 2	Pearson's R	P	R²
Group size	No. of adult females	0.71	<0.05	0.497
Average cover (1m plot)	Average cover (5m plot)	0.5	<0.05	0.247
Average biomass (1m plot)	Average biomass (5m plot)	0.94	<0.05	0.876
Average mean height (1m plot)	Average cover (1m plot)	0.35	<0.05	0.119
Average mean height (1m plot)	Average biomass (1m plot)	0.56	<0.05	0.316
Average mean height (1m plot)	Average cover (5m plot)	0.09	0.2249	0.008
Average mean height (1m plot)	Average biomass (5m plot)	0.48	<0.05	0.226
Average cover (1m plot)	Average biomass (1m plot)	0.64	<0.05	0.404
Average cover (5m plot)	Average biomass (1m plot)	0.63	<0.05	0.396

Chapter 3: Consequences of within-group competition on the feeding behaviour of individuals.

3.1 Food-site residence time (FSRT)

As mentioned in the objectives, I had wanted to find out whether food-site residence time, which indicates resource value, was correlated with the contestability of females and measured grass abundance variables. The average ± SD of FSRT was small (4.845 ± 6.472 mins), suggesting that individuals could either deplete or be displaced from a feeding site within a short time. The distribution of FSRT was right skewed (See B.2 Appendix B) with most of the individuals having short FSRT and a few individuals with long FSRT. I found using the linear mixed effects model that the average dominance index (ADI) of females and average grass cover of 1-m plots were the best predictors of FSRT. However, there were seven other best models (ΔAICc less than 2) to explain FSRT, in which feeding activity type, age, average mean grass height, and clan identity appeared as explanatory variables (Table 3.1). The best model (ΔAICc = 0) had the least number of explanatory variables, i.e. 2. Average grass cover of 1-m plots was one of the explanatory variables in all the top models, while ADI was an explanatory variable in six out of the top eight models. In all the models in which average grass cover (of 1-m plots) and ADI were present as the explanatory variables, ADI had a higher estimate value than average grass cover. As expected, ADI and average grass cover were positively related with FSRT (Table 3.2). However, the correlations between ADI and FSRT or average grass cover of 1-m plots and FSRT were not high (see B.3, Appendix B).

Table 3.1: Results of linear mixed effect models for food-site residence time (FSRT) as the response variable. Only the top models (ΔAICc ≤ 2) are shown.

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
FSRT ~ 1 + ADI + ave_cover_1m	2	0	2918.36	2918.45	0	2910.4
FSRT ~ 1 + feeding_type + ADI + ave_cover_1m	3	0	2918.72	2918.85	0.4021	2908.7
FSRT ~ 1 + feeding_type + age + ave_cover_1m	3	0	2919	2919.14	0.68602	2909
FSRT ~ 1 + age + ave_cover_1m	2	0	2919.06	2919.15	0.69891	2911.1
FSRT ~ 1 + age + ADI + ave_cover_1m	3	0	2919.93	2920.06	1.61226	2909.9
FSRT ~ 1 + ADI + ave_mean_ht_1m + ave_cover_1m	3	0	2919.96	2920.1	1.6455	2910
FSRT ~ 1 + feeding_type + age + ADI + ave_cover_1m	4	0	2920.07	2920.26	1.81187	2908.1
FSRT ~ 1 + ADI + ave_cover_1m + (1 | clan)	2	1	2920.18	2920.32	1.87071	2910.4
FSRT ~ 1 + ADI + ave_cover_1m + (1 | gp_serial_no)	2	1	2920.32	2920.46	2.00924	2910.4

Table 3.2: Parameter estimates and statistical significance of the best models explaining FSRT.

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *FSRT ~ 1 + ADI + ave_cover_1m*							
Fixed effects							
Intercept	-10.846	3.144	-3.450	443	<0.001	-17.024	-4.668
ADI	2.070	0.858	2.413	443	0.016	0.384	3.756
ave_cover_1m	0.164	0.034	4.815	443	<0.001	0.097	0.231
Random effects							
Error	6.321						
Model: *FSRT ~ 1 + feeding_type + ADI + ave_cover_1m*							
Fixed effects							
Intercept	-12.475	3.385	-3.686	442	<0.001	-19.182	-5.823
feeding_type - Plucking	-0.991	0.772	-1.283	442	0.200	-2.508	0.527
ADI	2.086	0.857	2.435	442	0.015	0.403	3.769
ave_cover_1m	0.185	0.038	4.905	442	<0.001	0.111	0.259
Random effects							
Error	6.309						
Model: *FSRT ~ 1 + feeding_type + age + ave_cover_1m*							
Fixed effects							
Intercept	-11.154	3.285	-3.395	442	<0.001	-17.610	-4.698
feeding_type - Plucking	-1.113	0.775	-1.436	442	0.152	-2.635	0.510
age	0.049	0.021	2.376	442	0.018	0.008	0.090
ave_cover_1m	0.164	0.037	4.377	442	<0.001	0.090	0.237
Random effects							
Error	6.311						

Effect	Estimate	SE	t	df	P value	95% CI	
Model: *FSRT ~ 1 + age + ave_cover_1m*							
Fixed effects							
Intercept	-9.311	3.031	-3.072	443	0.002	-15.268	-3.354
age	0.047	0.021	2.261	443	0.024	0.006	0.087
ave_cover_1m	0.141	0.034	4.152	443	<0.001	0.074	0.208
Random effects							
Error	6.325						
Model: *FSRT ~ 1 + age + ADI + ave_cover_1m*							
Fixed effects							
Intercept	-10.431	3.205	-3.255	442	0.001	-16.729	-4.132
age	0.021	0.032	0.658	442	0.512	-0.042	0.083
ADI	1.408	1.322	1.065	442	0.288	-1.190	4.005
ave_cover_1m	0.156	0.037	4.252	442	<0.001	0.084	0.227
Random effects							
Error	6.317						
Model: *FSRT ~ 1 + ADI + ave_mean_ht_1m + ave_cover_1m*							
Fixed effects							
Intercept	-11.663	3.397	-3.433	442	<0.001	-18.340	-4.986
ADI	2.030	0.860	2.361	442	0.019	0.340	3.720
ave_mean_ht_1m	-0.122	0.192	-0.633	442	0.527	-0.499	0.256
ave_cover_1m	0.181	0.043	4.216	442	<0.001	0.096	0.265
Random effects							
Error	6.318						

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *FSRT ~ 1 + feeding_type + age + ADI + ave_cover_1m*							
Fixed effects							
Intercept	-12.078	3.419	-3.533	441	<0.001	-18.796	-5.359
feeding_type - Plucking	-1.058	0.776	-1.364	441	0.173	-2.583	0.467
age	0.026	0.032	0.804	441	0.422	-0.037	0.088
ADI	1.276	1.327	0.964	441	0.335	-1.324	3.875
ave_cover_1m	0.176	0.039	4.460	441	<0.001	0.098	0.253
Random effects							
Error	6.304						
Model: *FSRT ~ 1 + ADI + ave_cover_1m + (1 / clan)*							
Fixed effects							
Intercept	-10.730	3.240	-3.311	443	<0.001	-17.105	-4.166
ADI	2.153	0.866	2.486	443	0.016	0.424	3.902
ave_cover_1m	0.163	0.035	4.624	443	<0.001	0.091	0.232
Random effects							
clan	0.332			4 levels			
Error	6.312						

3.2 Feeding rates

As mentioned earlier, I had expected feeding rate to be shaped by group size and grass variables. In the case of feeding rate 1 (FR1), which was calculated as the number of trunkfuls eaten in the total time observed feeding or walking between two food sites, the best model had feeding activity type, female age, group size, clan identity, and individual identity as the main predictors (Table 3.3). Feeding rates were higher while plucking (average $\pm$ SD = 2.114 $\pm$ 0.820 trunfuls/min) than while kicking (average $\pm$ SD = 1.688 $\pm$ 0.615 trunfuls/min) because of the effort involved. Feeding rates decreased with increasing female age and marginally increased with increasing group size (Table 3.4). However, 12 other models were equally good, having ΔAICc values less than 2 (Tables 3.3 and 3.4). All of them included feeding activity type as significantly affecting feeding rate, most included age, and all of them included either total group size or the number of adult females as significantly affecting feeding rate (Table 3.4). When average dominance index appeared in a model, it was negatively related to feeding rate (Table 3.4), with more dominant individuals showing slower feeding rates.

In the case of feeding rate 2 (FR2), which was calculated as the number of trunkfuls eaten in the total time observed feeding alone, the best model had feeding activity type, female age, number of adult females, and individual identity as the main predictors (Table 3.5). Again, the feeding rates while plucking (average $\pm$ SD = 2.349 $\pm$ 0.998 trunfuls/min) were higher than while kicking (average $\pm$ SD = 1.844 $\pm$ 0.638 trunfuls/min). There were eight other equally good models (ΔAICc < 2) (Tables 3.5 and 3.6). Here also, total group size or the number of adult females figured in all the best models, as did female age. Group size/number of adult females was positively related with FR2 and female age was negatively related (Table 3.6).

Table 3.3: Results of linear mixed effect models for feeding rate 1 (FR1) as the response variable. Only the top models (ΔAICc ≤ 2) are shown.

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	**Random**				
FR1 ~ 1 + feeding_type + age + gp_size + (1 | clan) + (1 | ind)	3	2	317.242	317.921	0	303.24
FR1 ~ 1 + feeding_type + age + no_AF + (1 | clan) + (1 | ind)	3	2	317.879	318.558	0.63628	303.88
FR1 ~ 1 + feeding_type + age + gp_size + (1 | ind)	3	1	318.248	318.754	0.83301	306.25
FR1 ~ 1 + feeding_type + age + no_AF + (1 | year) + (1 | ind)	3	2	318.226	318.905	0.98364	304.23
FR1 ~ 1 + feeding_type + age + no_AF + (1 | year) + (1 | clan) + (1 | ind)	3	3	318.07	318.948	1.02674	302.07
FR1 ~ 1 + feeding_type + age + gp_size + ave_mean_ht_1m + (1 | clan) + (1 | ind)	4	2	318.217	319.095	1.17333	302.22
FR1 ~ 1 + feeding_type + age + gp_size + (1 | year) + (1 | clan) + (1 | ind)	3	3	318.47	319.348	1.42686	302.47
FR1 ~ 1 + feeding_type + age + no_AF + ave_mean_ht_1m + (1 | clan) + (1 | ind)	4	2	318.495	319.373	1.45205	302.5
FR1 ~ 1 + feeding_type + age + gp_size + (1 | year) + (1 | ind)	3	2	318.89	319.569	1.64749	304.89
FR1 ~ 1 + feeding_type + age + no_AF + (1 | ind)	3	1	319.081	319.587	1.66617	307.08

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
FR1 ~ 1 + feeding_type + ADI + no_AF + (1 | year) + (1 | ind)	3	2	318.985	319.664	1.74265	304.99
FR1 ~ 1 + feeding_type + age + gp_size + ave_cover_5m + (1 | clan) + (1 | ind)	4	2	319.007	319.885	1.96335	303.01
FR1 ~ 1 + feeding_type + ADI + gp_size + (1 | clan) + (1 | ind)	3	2	319.263	319.942	2.02029	305.26

Table 3.4: Parameter estimates and statistical significance of the best models explaining FR1.

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *FR1 ~ 1 + feeding_type + age + gp_size + (1 | clan) + (1 | ind)*							
Fixed effects							
Intercept	1.856	0.250	7.429	169	<0.001	1.363	2.349
feeding_type - Plucking	0.369	0.094	3.925	169	<0.001	0.184	0.555
age	-0.013	0.006	-2.372	169	0.012	-0.024	-0.002
gp_size	0.050	0.016	3.129	169	0.002	0.018	0.081
Random effects							
clan	0.278			4 levels			
ind	0.353			32 levels			
Error	0.514						

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *FR1 ~ 1 + feeding_type + age + no_AF + (1 | clan) + (1 | ind)*							
Fixed effects							
Intercept	1.718	0.263	6.529	169	<0.001	1.199	2.238
feeding_type - Plucking	0.364	0.095	3.852	169	<0.001	0.177	0.550
age	-0.011	0.005	-2.021	169	0.045	-0.021	0.000
no_AF	0.114	0.038	2.980	169	0.003	0.039	0.189
Random effects							
clan	0.272			4 levels			
ind	0.334			32 levels			
Error	0.519						
Model: *FR1 ~ 1 + feeding_type + age + gp_size + (1 | ind)*							
Fixed effects							
Intercept	1.883	0.230	8.788	169	<0.001	1.429	2.337
feeding_type - Plucking	0.390	0.094	4.160	169	<0.001	0.205	0.574
age	-0.016	0.006	-2.528	169	0.012	-0.028	-0.004
gp_size	0.053	0.016	3.387	169	0.001	0.022	0.084
Random effects							
ind	0.447			32 levels			
Error	0.511						
Model: *FR1 ~ 1 + feeding_type + age + no_AF + (1 | year) + (1 | ind)*							
Fixed effects							
Intercept	1.771	0.253	7.000	169	<0.001	1.272	2.271
feeding_type - Plucking	0.452	0.097	4.654	169	<0.001	0.260	0.643

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
age	-0.013	0.006	-2.312	169	0.022	-0.025	-0.002
no_AF	0.107	0.038	2.819	169	0.005	0.032	0.183
Random effects							
year	0.129			2 levels			
ind	0.408			32 levels			
Error	0.511						

Model: *FR1 ~ 1 + feeding_type + age + no_AF + (1 | year) + (1 | clan) + (1 | ind)*

Fixed effects

Intercept	1.752	0.268	6.528	169	<0.001	1.222	2.282
feeding_type - Plucking	0.423	0.098	4.306	169	<0.001	0.229	0.618
age	-0.011	0.005	-2.131	169	0.035	-0.022	-0.001
no_AF	0.103	0.038	2.693	169	0.008	0.028	0.179
Random effects							
year	0.120			2 levels			
clan	0.240			4 levels			
ind	0.336			32 levels			
Error	0.514						

Model: *FR1 ~ 1 + feeding_type + age + gp_size + ave_mean_ht_1m + (1 | clan) + (1 | ind)*

Fixed effects

Intercept	2.012	0.298	6.752	168	<0.001	1.424	2.601
feeding_type - Plucking	0.407	0.100	4.061	168	<0.001	0.209	0.605
age	-0.013	0.006	-2.342	168	0.020	-0.025	-0.002
gp_size	0.050	0.016	3.180	168	0.002	0.019	0.082

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
ave_mean_ht_1m	-0.028	0.027	-1.054	168	0.294	-0.080	0.024
Random effects							
clan	0.288			4 levels			
ind	0.372			32 levels			
Error	0.509						

Model: *FR1 ~ 1 + feeding_type + age + gp_size + (1 | year) + (1 | clan) + (1 | ind)*

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Fixed effects							
Intercept	1.881	0.253	7.450	169	<0.001	1.383	2.380
feeding_type - Plucking	0.409	0.097	4.200	169	<0.001	0.217	0.602
age	-0.013	0.006	-2.402	169	0.017	-0.024	-0.002
gp_size	0.044	0.016	2.702	169	0.008	0.012	0.076
Random effects							
year	0.095			2 levels			
clan	0.256			4 levels			
ind	0.351			32 levels			
Error	0.512						

Model: *FR1 ~ 1 + feeding_type + age + no_AF + ave_mean_ht_1m + (1 | clan) + (1 | ind)*

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Fixed effects							
Intercept	1.891	0.305	6.192	168	<0.001	1.288	2.494
feeding_type - Plucking	0.409	0.101	4.047	168	<0.001	0.209	0.608
age	-0.011	0.006	-2.002	168	0.047	-0.022	0.000
no_AF	0.118	0.038	3.096	168	0.002	0.043	0.193
ave_mean_ht_1m	-0.033	0.027	-1.222	168	0.224	-0.085	0.020

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Random effects							
clan	0.284			4 levels			
ind	0.355			32 levels			
Error	0.512						
Model: *FR1 ~ 1 + feeding_type + age + gp_size + (1 / year) + (1 / ind)*							
Fixed effects							
Intercept	1.910	0.236	8.082	169	<0.001	1.443	2.377
feeding_type - Plucking	0.436	0.096	4.519	169	<0.001	0.245	0.626
age	-0.016	0.006	-2.548	169	0.012	-0.028	-0.004
gp_size	0.045	0.016	2.785	169	0.006	0.013	0.077
Random effects							
year	0.105			2 levels			
ind	0.431			32 levels			
Error	0.509						
Model: *FR1 ~ 1 + feeding_type + age + no_AF + (1 / ind)*							
Fixed effects							
Intercept	1.734	0.243	7.139	169	<0.001	1.255	2.214
feeding_type - Plucking	0.386	0.094	4.102	169	<0.001	0.200	0.571
age	-0.013	0.006	-2.190	169	0.030	-0.025	-0.001
no_AF	0.123	0.038	3.232	169	0.002	0.048	0.198
Random effects							
ind	0.427			32 levels			
Error	0.516						

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *FR1 ~ 1 + feeding_type + ADI + no_AF + (1 / year) + (1 / ind)*							
Fixed effects							
Intercept	1.589	0.213	7.478	169	<0.001	1.169	2.008
feeding_type - Plucking	0.432	0.097	4.465	169	<0.001	0.241	0.623
ADI	-0.526	0.250	-2.101	169	0.037	-1.020	-0.032
no_AF	0.102	0.038	2.669	169	0.008	0.026	0.177
Random effects							
year	0.131			2 levels			
ind	0.419			32 levels			
Error	0.51						
Model: *FR1 ~ 1 + feeding_type + age + gp_size + ave_cover_5m + (1 / clan) + (1 / ind)*							
Fixed effects							
Intercept	1.700	0.405	4.200	168	<0.001	0.901	2.500
feeding_type - Plucking	0.357	0.098	3.657	168	<0.001	0.169	0.550
age	-0.013	0.006	-2.400	168	0.018	-0.024	-0.002
gp_size	0.056	0.021	2.737	168	0.007	0.016	0.097
ave_cover_5m	0.002	0.003	0.488	168	0.627	-0.005	0.008
Random effects							
clan	0.273			4 levels			
ind	0.351			32 levels			
Error	0.514						

Table 3.5: Results of linear mixed effect models for feeding rate 2 (FR2) as the response variable. Only the top models (ΔAICc ≤ 2) are shown.

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
FR2 ~ 1 + feeding_type + age + no_AF + (1 | ind)	3	1	363.396	363.902	0	351.4
FR2 ~ 1 + feeding_type + age + gp_size + (1 | ind)	3	1	363.891	364.397	0.49527	351.89
FR2 ~ 1 + feeding_type + age + no_AF + (1 | month) + (1 | ind)	3	2	364.074	364.753	0.85086	350.07
FR2 ~ 1 + feeding_type + age + gp_size + (1 | month) + (1 | ind)	3	2	364.177	364.856	0.95436	350.18
FR2 ~ 1 + feeding_type + age + no_AF + (1 | year) + (1 | ind)	3	2	364.417	365.096	1.19377	350.42
FR2 ~ 1 + feeding_type + age + no_AF + (1 | clan) + (1 | ind)	3	2	364.498	365.177	1.27515	350.5
FR2 ~ 1 + feeding_type + age + no_AF + ave_biomass_1m + (1 | ind)	4	1	364.82	365.499	1.59664	350.82
FR2 ~ 1 + feeding_type + age + gp_size + (1 | clan) + (1 | ind)	3	2	365.066	365.745	1.84312	351.07
FR2 ~ 1 + feeding_type + age + no_AF + ave_biomass_5m + (1 | ind)	4	1	365.106	365.785	1.88311	351.11
FR2 ~ 1 + feeding_type + age + ADI + no_AF + (1 | ind)	4	1	365.359	366.037	2.13547	351.36

Table 3.6: Parameter estimates and statistical significance of the best models explaining FR2.

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *FR2 ~ 1 + feeding_type + age + no_AF + (1 | ind)*							
Fixed effects							
Intercept	2.007	0.268	7.499	169	<0.001	1.479	2.536
feeding_type - Plucking	0.506	0.108	4.707	169	<0.001	0.294	0.718
age	-0.015	0.007	-2.287	169	0.024	-0.028	-0.002
no_AF	0.111	0.043	2.547	169	0.012	0.025	0.196
Random effects							
ind	0.457			32 levels			
Error	0.592						
Model: *FR2 ~ 1 + feeding_type + age + gp_size + (1 | ind)*							
Fixed effects							
Intercept	2.156	0.253	8.534	169	<0.001	1.658	2.655
feeding_type - Plucking	0.506	0.107	4.713	169	<0.001	0.294	0.718
age	-0.017	0.007	-2.488	169	0.014	-0.031	-0.004
gp_size	0.045	0.018	2.470	169	0.015	0.009	0.080
Random effects							
ind	0.481			32 levels			
Error	0.588						
Model: *FR2 ~ 1 + feeding_type + age + no_AF + (1 | month) + (1 | ind)*							
Fixed effects							
Intercept	2.012	0.273	7.382	169	<0.001	1.474	2.550

Effect	Estimate	SE	t	df	P value	95% CI	
feeding_type - Plucking	0.547	0.111	4.911	169	<0.001	0.327	0.767
age	-0.015	0.006	-2.303	169	0.023	-0.027	-0.002
no_AF	0.104	0.045	2.299	169	0.023	0.015	0.193
Random effects							
month	0.115			4 levels			
ind	0.445			32 levels			
Error	0.586						
Model: *FR2 ~ 1 + feeding_type + age + gp_size + (1 | month) + (1 | ind)*							
Fixed effects							
Intercept	2.150	0.256	8.409	169	<0.001	1.645	2.655
feeding_type - Plucking	0.557	0.112	4.998	169	<0.001	0.337	0.777
age	-0.017	0.007	-2.515	169	0.013	-0.030	-0.004
gp_size	0.042	0.019	2.269	169	0.025	0.006	0.079
Random effects							
month	0.125			4 levels			
ind	0.466			32 levels			
Error	0.582						
Model: *FR2 ~ 1 + feeding_type + age + no_AF + (1 | year) + (1 | ind)*							
Fixed effects							
Intercept	2.034	0.273	7.447	169	<0.001	1.494	2.573
feeding_type - Plucking	0.552	0.111	4.988	169	<0.001	0.334	0.771
age	-0.015	0.006	-2.370	169	0.019	-0.028	-0.003

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
no_AF	0.100	0.044	2.281	169	0.024	0.013	0.186
Random effects							
ind	0.443			32 levels			
Error	0.59						

Model: *FR2 ~ 1 + feeding_type + age + no_AF + (1 | clan) + (1 | ind)*

Fixed effects

Intercept	2.005	0.282	7.107	169	<0.001	1.448	2.561
feeding_type - Plucking	0.488	0.108	4.514	169	<0.001	0.274	0.701
age	-0.013	0.006	-2.163	169	0.032	-0.026	-0.001
no_AF	0.104	0.044	2.390	169	0.018	0.018	0.191
Random effects							
clan	0.209			4 levels			
ind	0.407			32 levels			
Error	0.593						

Model: *FR2 ~ 1 + feeding_type + age + no_AF + ave_biomass_1m + (1 | ind)*

Fixed effects

Intercept	2.132	0.315	6.777	168	<0.001	1.511	2.753
feeding_type - Plucking	0.541	0.117	4.622	168	<0.001	0.310	0.773
age	-0.015	0.007	-2.257	168	0.025	-0.028	-0.002
no_AF	0.107	0.044	2.455	168	0.015	0.021	0.193
ave_biomass_1m	0.000	0.000	-0.764	168	0.446	-0.001	0.000
Random effects							
ind	0.463			32 levels			

| Error | 0.59 | | | | | | |

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *FR2 ~ 1 + feeding_type + age + gp_size + (1 | clan) + (1 | ind)*							
Fixed effects							
Intercept	2.148	0.266	8.077	169	<0.001	1.623	2.673
feeding_type - Plucking	0.490	0.108	4.533	169	<0.001	0.276	0.703
age	0.016	0.007	-2.370	169	0.019	-0.029	-0.003
gp_size	0.042	0.018	2.303	169	0.023	0.006	0.078
Random effects							
clan	0.212			4 levels			
ind	0.431			32 levels			
Error	0.590						
Model: *FR2 ~ 1 + feeding_type + age + no_AF + ave_biomass_5m + (1 | ind)*							
Fixed effects							
Intercept	2.108	0.326	6.461	168	<0.001	1.464	2.752
feeding_type - Plucking	0.533	0.119	4.488	168	<0.001	0.299	0.767
age	-0.015	0.007	-2.291	168	0.023	-0.028	-0.002
no_AF	0.100	0.047	2.112	168	0.036	0.007	0.194
ave_biomass_5m	0.000	0.000	-0.543	168	0.588	0.000	0.000
Random effects							
ind	0.462			32 levels			
Error	0.590						

As feeding activity type was important in all the top models (ΔAICc < 2) of FR1 and FR2, we separated the data set based on the feeding activity type, whether kicking or plucking, and refitted the linear mixed effects model for the top models. Tables 3.7 and 3.8 show the results for FR1 for the same models as mentioned in Table 3.3, for kicking and plucking respectively. For the feeding activity type kicking, the top model had age, number of adult females, average mean grass height (of 1-m plots), clan identity, and individual identity as explanators in the best model. There was only one other best model (ΔAICc < 2) with the same explanatory variables as the best model, except for number of adult females being replaced by the group size. In case of the feeding activity type plucking, the best model has fewer explanatory variables including age, group size and individual identity, as compared to the data set with kicking as the feeding activity type. The only other best model (ΔAICc < 2) had the same explanatory variables, except for group size being replaced by number of adult females. Tables 3.9 and 3.10 shows the parameter estimates and statistical significance for the models in 3.7 and 3.8 respectively. Thus, FR1 was additionally affected by the average mean grass height when only kicking was examined and not plucking, with feeding rate surprisingly being negative related to grass height.

Tables 3.11 and 3.12 show the results for FR2 for the same models as mentioned in Table 3.5, for feeding activity types kicking and plucking, respectively. For the feeding activity type kicking, the top model had age, group size, clan identity, and individual identity as the main explanators. In the only other best model (ΔAICc < 2) had the same explanatory variables, except for group size being replaced by number of adult females. In case of the feeding activity type as plucking, the top model had age, ADI, number of adult females, and individual identity as the explanators. There were two other best models (ΔAICc < 2). Tables 3.13 and 3.14 shows the parameter estimates and statistical significance for the models in 3.11 and 3.12 respectively. In case of both FR1 and FR2, the estimate values for the predictor variables in each of the refitted models was very small, indicating that feeding activity type is the main predictor of both the feeding rates (Tables 3.9, 3.10, 3.13 and 3.14).

Table 3.7: Results of linear mixed effect models for feeding rate 1 (FR1) as the response variable with the data set having feeding activity type as kicking. All the top models in Table 3.3 are refitted to linear mixed effects models and ranked according to recalculated ΔAICc values.

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
FR_1 ~ Age + No_AF + Av_mean_ht_1m + (1 | Clan) + (1 | Individual)	3	2	135.3	136.339	0	121.3
FR_1 ~ Age + Gp_size + Av_mean_ht_1m + (1 | Clan) + (1 | Individual)	3	2	136.3	137.406	1.0676	122.3
FR_1 ~ Age + Gp_size + (1 | Clan) + (1 | Individual)	2	2	141	141.742	5.4034	129
FR_1 ~ Age + No_AF + (1 | Clan) + (1 | Individual)	2	2	141.1	141.933	5.5944	129.1
FR_1 ~ ADI + Gp_size + (1 | Clan) + (1 | Individual)	2	2	142.8	143.582	7.2432	130.8
FR_1 ~ Age + No_AF + (1 | Year) + (1 | Clan) + (1 | Individual)	2	3	142.6	143.637	7.2987	128.6
FR_1 ~ Age + Gp_size + Av_cover_5m + (1 | Clan) + (1 | Individual)	3	2	142.6	143.701	7.3625	128.6
FR_1 ~ Age + Gp_size + (1 | Year) + (1 | Clan) + (1 | Individual)	2	3	142.9	143.986	7.6478	128.9
FR_1 ~ Age + No_AF + (1 | Individual)	2	1	147.4	147.936	11.597	137.4
FR_1 ~ Age + Gp_size + (1 | Individual)	2	1	147.9	148.498	12.1596	137.9
FR_1 ~ Age + No_AF + (1 | Year) + (1 | Individual)	2	2	148.1	148.924	12.5849	136.1

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
FR_1 ~ Age + Gp_size + (1 | Year) + (1 | Individual)	2	2	149.8	150.55	14.2116	137.8
FR_1 ~ Age + ADI + No_AF + (1 | Year) + (1 | Individual)	3	2	149.6	150.667	14.3286	135.6

Table 3.8: Results of linear mixed effect models for feeding rate 1 (FR1) as the response variable with the data set having feeding activity type as plucking. All the top models in Table 3.3 are refitted to linear mixed effects model and ranked according to recalculated ΔAICc values.

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
FR_1 ~ Age + Gp_size + (1 | Individual)	2	1	144.9	146.033	0	134.9
FR_1 ~ Age + No_AF + (1 | Individual)	2	1	145.3	146.474	0.4407	135.3
FR_1 ~ Age + Gp_size + (1 | Clan) + (1 | Individual)	2	2	146.9	148.516	2.4833	134.9
FR_1 ~ Age + Gp_size + (1 | Year) + (1 | Individual)	2	2	146.9	148.516	2.4833	134.9
FR_1 ~ Age + No_AF + (1 | Clan) + (1 | Individual)	2	2	147.3	148.957	2.924	135.3
FR_1 ~ Age + No_AF + (1 | Year) + (1 | Individual)	2	2	147.3	148.957	2.924	135.3
FR_1 ~ ADI + Gp_size + (1 | Clan) + (1 | Individual)	2	2	148.1	149.736	3.7033	136.1
FR_1 ~ Age + Gp_size + Av_mean_ht_1m + (1 | Clan) + (1 | Individual)	3	2	147.7	149.847	3.8141	133.7

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
FR_1 ~ Age + Gp_size + Av_cover_5m + (1 | Clan) + (1 | Individual)	3	2	148.3	150.542	4.5088	134.3
FR_1 ~ Age + No_AF + Av_mean_ht_1m + (1 | Clan) + (1 | Individual)	3	2	148.4	150.57	4.5371	134.4
FR_1 ~ Age + Gp_size + (1 | Year) + (1 | Clan) + (1 | Individual)	2	3	148.9	151.097	5.064	134.9
FR_1 ~ Age + ADI + No_AF + (1 | Year) + (1 | Individual)	3	2	149	151.168	5.1353	135
FR_1 ~ Age + No_AF + (1 | Year) + (1 | Clan) + (1 | Individual)	2	3	149.3	151.538	5.5047	135.3

Table 3.9: Parameter estimates and statistical significance of the best models explaining FR1 for data set with feeding activity type as kicking.

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *FR_1 ~ 1 + age + no_AF + ave_mean_ht_1m + (1 | clan) + (1 | ind)*							
Fixed effects							
Intercept	2.112	0.300	7.044	110	<0.001	1.518	2.706
age	-0.010	0.005	-1.932	110	0.056	-0.019	0.002
no_AF	0.098	0.034	2.844	110	0.005	0.030	0.165
av_mean_ht_1m	-0.065	0.023	-2.910	110	0.004	-0.110	-0.021
Random effects							
clan	0.396			4 levels			
ind	0.318			30 levels			
Error	0.329						
Model: *FR_1 ~ 1 + age + gp_size + ave_mean_ht_1m + (1 | clan) + (1 | ind)*							
Fixed effects							
Intercept	2.213	0.297	7.443	110	<0.001	1.624	2.802
age	-0.011	0.005	-2.223	110	0.028	-0.021	-0.001
gp_size	0.038	0.014	2.630	110	0.010	0.009	0.066
av_mean_ht_1m	-0.059	0.022	-2.659	110	0.009	-0.103	-0.015
Random effects							
clan	0.410			4 levels			
ind	0.316			30 levels			
Error	0.331						

Table 3.10: Parameter estimates and statistical significance of the best models explaining FR1 for data set with feeding activity type as plucking.

Effect	Estimate	SE	t	df	P value	95% CI	
Model: *FR_1 ~ 1 + age + gp_size + (1 | ind)*							
Fixed effects							
Intercept	2.349	0.401	5.860	56	<0.001	1.546	3.152
age	-0.015	0.010	-1.460	56	0.150	-0.035	0.006
gp_size	0.056	0.030	1.891	56	0.064	-0.003	0.115
Random effects							
ind	0.616			21 levels			
Error	0.611						
Model: *FR_1 ~ 1 + age + no_AF + (1 | ind)*							
Fixed effects							
Intercept	2.191	0.431	5.082	56	<0.001	1.327	3.055
age	-0.012	0.010	-1.230	56	0.224	-0.031	0.007
no_AF	0.124	0.073	1.701	56	0.095	-0.022	0.271
Random effects							
ind	0.565			21 levels			
Error	0.630						

Table 3.11: Results of linear mixed effect models for feeding rate 2 (FR2) as the response variable with the data set having feeding activity type as kicking. All the top models in Table 3.5 are refitted to linear mixed effects model and ranked according to recalculated ΔAICc values.

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	**Random**				
FR_2 ~ Age + Gp_size + (1 | Clan) + (1 | Individual)	2	2	154.7	155.437	0	142.7
FR_2 ~ Age + No_AF + (1 | Clan) + (1 | Individual)	2	2	155.2	155.997	0.5607	143.2
FR_2 ~ Age + Gp_size + (1 | Individual)	2	1	160.7	161.206	5.7698	150.7
FR_2 ~ Age + No_AF + (1 | Individual)	2	1	160.9	161.455	6.0183	150.9
FR_2 ~ Age + Gp_size + (1 | Month) + (1 | Individual)	2	2	160.8	161.537	6.1002	148.8
FR_2 ~ Age + No_AF + (1 | Month) + (1 | Individual)	2	2	160.8	161.581	6.1441	148.8
FR_2 ~ Age + No_AF + (1 | Year) + (1 | Individual)	2	2	162.4	163.165	7.728	150.4
FR_2 ~ Age + No_AF + Av_biomass_1m + (1 | Individual)	3	1	162.4	163.205	7.768	150.4
FR_2 ~ Age + No_AF + Av_biomass_5m + (1 | Individual)	3	1	162.6	163.365	7.9288	150.6
FR_2 ~ Age + ADI + No_AF + (1 | Individual)	3	1	162.6	163.388	7.9516	150.6

Table 3.12: Results of linear mixed effect models for feeding rate 2 (FR2) as the response variable with the data set having feeding activity type as plucking. All the top models in Table 3.5 are refitted to linear mixed effects model and ranked according to recalculated ΔAICc values.

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	**Random**				
FR_2 ~ Age + ADI + No_AF + (1 | Individual)	3	1	165	166.644	0	153
FR_2 ~ Age + No_AF + (1 | Individual)	2	1	165.8	166.98	0.3351	155.8
FR_2 ~ Age + Gp_size + (1 | Individual)	2	1	166.3	167.449	0.8047	156.3
FR_2 ~ Age + No_AF + (1 | Month) + (1 | Individual)	2	2	167.7	169.306	2.6616	155.7
FR_2 ~ Age + No_AF + Av_biomass_1m + (1 | Individual)	3	1	167.8	169.435	2.7902	155.8
FR_2 ~ Age + No_AF + Av_biomass_5m + (1 | Individual)	3	1	167.8	169.445	2.8005	155.8
FR_2 ~ Age + No_AF + (1 | Clan) + (1 | Individual)	2	2	167.8	169.463	2.8184	155.8
FR_2 ~ Age + No_AF + (1 | Year) + (1 | Individual)	2	2	167.8	169.463	2.8184	155.8
FR_2 ~ Age + Gp_size + (1 | Month) + (1 | Individual)	2	2	168	169.614	2.9694	156
FR_2 ~ Age + Gp_size + (1 | Clan) + (1 | Individual)	2	2	168.3	169.932	3.288	156.3

Table 3.13: Parameter estimates and statistical significance of the best models explaining FR2 for data set with feeding activity type as kicking.

Effect	Estimate	SE	t	df	P value	95% CI	
Model: *FR_2 ~ 1 + age + gp_size + (1 | clan) + (1 | ind)*							
Fixed effects							
Intercept	2.202	0.258	8.545	111	<0.001	1.692	2.713
age	-0.012	0.005	-2.345	111	0.021	-0.022	-0.002
gp_size	0.023	0.016	1.430	111	0.156	-0.009	0.054
Random effects							
clan	0.351			4 levels			
ind	0.312			30 levels			
Error	0.372						
Model: *FR_2 ~ 1 + age + no_AF + (1 | clan) + (1 | ind)*							
Fixed effects							
Intercept	2.162	0.272	7.954	111	<0.001	1.624	2.701
age	-0.011	0.005	-2.184	111	0.031	-0.021	-0.001
no_AF	0.046	0.038	1.208	111	0.230	-0.029	0.121
Random effects							
clan	0.343			4 levels			
ind	0.310			30 levels			
Error	0.374						

Table 3.14: Parameter estimates and statistical significance of the best models explaining FR2 for data set with feeding activity type as plucking.

Effect	Estimate	SE	t	df	P value	95% CI	
Model: *FR_2 ~ 1 + age + ADI + no_AF + (1 | ind)*							
Fixed effects							
Intercept	3.080	0.524	5.874	55	<0.001	2.029	4.131
age	-0.044	0.019	-2.355	55	0.022	-0.081	-0.007
ADI	1.425	0.799	1.783	55	0.080	-0.177	3.027
no_AF	0.106	0.086	1.236	55	0.222	-0.066	0.279
Random effects							
ind	0.619			21 levels			
Error	0.744						
Model: *FR_2 ~ 1 + age + no_AF + (1 | ind)*							
Fixed effects							
Intercept	2.790	0.532	5.242	56	<0.001	1.724	3.856
age	-0.017	0.012	-1.379	56	0.173	-0.041	0.008
no_AF	0.093	0.085	1.095	56	0.278	-0.077	0.264
Random effects							
ind	0.745			21 levels			
Error	0.727						

3.3 Number of steps / time between successive food-sites

As mentioned in the introduction, I had wanted to examine whether the distances moved between food sites by individuals was related to dominance, group size, and grass abundance variables. I found that the best model for the number of steps taken between successive food sites (steps_bet) had feeding activity type and average mean grass height as the main predictors (Table 3.15). The number of steps between feeding sites were similar while plucking (average ± SD = 9.255 ± 5.789) and while kicking (average ± SD = 10.540 ± 8.300). The number of steps also increased with greater mean grass height (Table 3.16). However, there were 15 other equally good models with ΔAICc < 2. All the models included feeding type and average mean grass height of 1-m plots as significant predictors and some models additionally included cover or biomass variables (Table 3.15).

In case of the time taken to move between successive food sites (time_bet), feeding activity type, number of adult females, average mean grass height, average grass biomass (5m plots), year, and group feeding event were the main predictors in the top-most model (Table 3.17). There were 11 alternative best models (ΔAICc < 2, see Tables 3.17 and 3.18). However, all these top models had at least 5 predictor variables. All the top models included feeding activity type, average mean height of 1-m plots, and average biomass of 5-m plots as significant predictors, and some models additionally included female age and the number of adult females (Table 3.17). The time taken to move between successive food sites was similar while plucking (average ± SD = 0.300 ± 0.234 mins) than while kicking (average ± SD = 0.451 ± 0.472 mins). The time taken increased slightly with greater mean grass height and although average grass biomass featured in the models, the estimate values approximated zero (Table 3.18).

Table 3.15: Results of linear mixed effect models with the number of steps taken between successive food-sites (steps_bet) as the response variable. Only the top models (ΔAICc ≤ 2) are shown.

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	**Random**				
steps_bet ~ 1 + feeding_type + ave_mean_ht_1m	2	0	2783.93	2784.03	0	2775.9
steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m	3	0	2784.06	2784.21	0.18634	2774.1
steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_cover_5m	3	0	2784.38	2784.53	0.50558	2774.4
steps_bet ~ 1 + feeding_type + age + ave_mean_ht_1m	3	0	2784.85	2785	0.97759	2774.9
steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_1m	3	0	2785.11	2785.26	1.23531	2775.1
steps_bet ~ 1 + feeding_type + no_AF + ave_mean_ht_1m + ave_cover_5m	4	0	2785.08	2785.29	1.26784	2773.1
steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_cover_1m	3	0	2785.2	2785.35	1.32125	2775.2
steps_bet ~ 1 + feeding_type + no_AF + ave_mean_ht_1m + ave_biomass_5m	4	0	2785.16	2785.38	1.34926	2773.2

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + (1 | gp_serial_no)	3	1	2785.18	2785.39	1.36572	2774.1
steps_bet ~ 1 + feeding_type + age + ave_mean_ht_1m + ave_biomass_5m	4	0	2785.26	2785.47	1.44257	2773.3
steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + (1 | gp_serial_no)	2	1	2785.44	2785.59	1.56547	2775.9
steps_bet ~ 1 + feeding_type + ADI + ave_mean_ht_1m	3	0	2785.75	2785.9	1.87098	2775.7
steps_bet ~ 1 + feeding_type + no_AF + ave_mean_ht_1m	3	0	2785.78	2785.93	1.90076	2775.8
steps_bet ~ 1 + feeding_type + gp_size + ave_mean_ht_1m	3	0	2785.82	2785.97	1.94328	2775.8
steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_cover_5m + (1 | gp_serial_no)	3	1	2785.8	2786.02	1.98951	2774.4
steps_bet ~ 1 + feeding_type + age + ave_mean_ht_1m + ave_cover_5m	4	0	2785.81	2786.03	1.99968	2773.8
steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + (1 | year)	2	1	2785.93	2786.08	2.05076	2775.9

Table 3.16: Parameter estimates and statistical significance of the best models explaining number of steps taken between successive food-sites.

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *steps_bet ~ 1 + feeding_type + ave_mean_ht_1m*							
Fixed effects							
Intercept	6.768	1.218	5.556	399	<0.001	4.373	9.163
feeding_type_Plucking and feeding	-3.662	1.141	-3.210	399	0.001	-5.904	-1.419
ave_mean_ht_1m	0.825	0.249	3.318	399	0.001	0.336	1.313
Random effects							
Error	7.642						
Model: *steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m*							
Fixed effects							
Intercept	7.371	1.293	5.701	398	<0.001	4.829	9.912
feeding_type_Plucking and feeding	-3.077	1.216	-2.531	398	0.012	-5.467	-0.687
ave_mean_ht_1m	0.971	0.270	3.595	398	<0.001	0.440	1.502
ave_biomass_5m	-0.003	0.002	-1.367	398	0.172	-0.006	0.001
Random effects							
Error	7.625						
Model: *steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_cover_5m*							
Fixed effects							
Intercept	8.996	2.164	4.156	398	<0.001	4.741	13.251
feeding_type_Plucking and feeding	-3.243	1.187	-2.732	398	0.007	-5.577	-0.909
Effect	Estimate	SE	*t*	df	*P* value	95% CI	
ave_mean_ht_1m	0.845	0.249	3.399	398	0.001	0.356	1.333
ave_cover_5m	-0.031	0.025	-1.244	398	0.214	-0.081	0.018

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Random effects							
Error	7.628						

Model: *steps_bet ~ 1 + feeding_type + age + ave_mean_ht_1m*

Fixed effects

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Intercept	5.947	1.452	4.096	398	<0.001	3.092	8.801
feeding_type_Plucking and feeding	-3.736	1.142	-3.273	398	0.001	-5.981	-1.492
ave_mean_ht_1m	0.827	0.248	3.332	398	0.001	0.339	1.315
age	0.027	0.026	1.037	398	0.301	-0.024	0.077

Random effects

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Error	7.632						

Model: *steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_1m*

Fixed effects

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Intercept	7.272	1.339	5.432	398	<0.001	4.640	9.904
feeding_type_Plucking and feeding	-3.423	1.170	-2.927	398	0.004	-5.723	-1.124
ave_mean_ht_1m	0.978	0.301	3.251	398	0.001	0.387	1.570
ave_biomass_1m	-0.002	0.002	-0.904	398	0.367	-0.006	0.002

Random effects

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Error	7.635						

Model: *steps_bet ~ 1 + feeding_type + no_AF + ave_mean_ht_1m + ave_cover_5m*

Fixed effects

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Intercept	11.522	3.095	3.723	397	<0.001	5.439	17.606
feeding_type_Plucking and feeding	-3.409	1.194	-2.855	397	0.005	-5.757	-1.061
no_AF	-0.565	0.495	-1.141	397	0.255	-1.538	0.409
ave_mean_ht_1m	0.938	0.261	3.591	397	<0.001	0.424	1.451

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
ave_cover_5m	-0.047	0.029	-1.644	397	0.101	-1.104	0.009
Random effects							
Error	7.615						

Model: *steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_cover_1m*

Fixed effects

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Intercept	10.304	4.313	2.389	398	0.017	1.824	18.784
feeding_type_Plucking and feeding	-3.635	1.140	-3.188	398	0.002	-5.876	-1.393
ave_mean_ht_1m	0.943	0.284	3.316	398	0.001	0.384	1.502
ave_cover_1m	-0.046	0.054	-0.855	398	0.393	-0.153	0.060
Random effects							
Error	7.635						

Model: *steps_bet ~ 1 + feeding_type + no_AF + ave_mean_ht_1m + ave_biomass_5m*

Fixed effects

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Intercept	8.614	1.841	4.680	397	<0.001	4.996	12.233
feeding_type_Plucking and feeding	-3.216	1.223	-2.629	397	0.009	-5.621	-0.811
no_AF	-0.440	0.464	-0.948	397	0.344	-1.352	0.472
ave_mean_ht_1m	1.075	0.291	3.632	397	<0.001	0.502	1.647
ave_biomass_5m	-0.003	0.002	-1.619	397	0.106	-0.007	0.001
Random effects							
Error	7.616						

Model: *steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + (1 | gp_serial_no)*

Fixed effects

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Intercept	7.371	1.293	5.701	398	<0.001	4.829	9.912

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
feeding_type_Plucking and feeding	-3.077	1.216	-2.531	398	0.012	-5.467	-0.687
ave_mean_ht_1m	0.971	0.270	3.560	398	<0.001	0.440	1.502
ave_biomass_5m	-0.003	0.002	-1.367	398	0.172	-0.006	0.001
Random effects							
gp_serial_no	0			60 levels			
Error	7.625						

Model: *steps_bet ~ 1 + feeding_type + age + ave_mean_ht_1m + ave_biomass_5m*

Fixed effects

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Intercept	6.614	1.542	4.289	397	<0.001	3.582	9.646
feeding_type_Plucking and feeding	-3.183	1.220	-2.609	397	0.009	-5.583	-0.784
age	0.023	0.026	0.898	397	0.370	-0.028	0.074
ave_mean_ht_1m	0.963	0.270	3.566	397	<0.001	0.432	1.493
ave_biomass_5m	-0.002	0.002	-1.265	397	0.207	-0.006	0.001
Random effects							
Error	7.617						

Model: *steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + (1 | gp_serial_no)*

Fixed effects

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Intercept	6.768	1.218	5.556	399	<0.001	4.373	9.163
feeding_type_Plucking and feeding	-3.662	1.141	-3.210	399	0.001	-5.904	-1.419
ave_mean_ht_1m	0.825	0.250	3.318	399	0.001	0.336	1.313
Random effects							
gp_serial_no	0			60 levels			
Error	7.642						

Effect	Estimate	SE	t	df	P value	95% CI	
Model: *steps_bet ~ 1 + feeding_type + ADI + ave_mean_ht_1m*							
Fixed effects							
Intercept	6.485	1.389	4.669	398	<0.001	3.754	9.215
feeding_type_Plucking and feeding	-3.662	1.141	-3.211	398	0.001	-5.904	-1.419
ave_mean_ht_1m	0.840	0.251	3.346	398	0.001	0.346	1.333
ADI	0.471	1.111	0.424	398	0.672	-1.713	2.655
Random effects							
Error	7.641						
Model: *steps_bet ~ 1 + feeding_type + no_AF + ave_mean_ht_1m*							
Fixed effects							
Intercept	7.181	1.619	4.436	398	<0.001	3.998	10.364
feeding_type_Plucking and feeding	-3.775	1.177	-3.206	398	0.002	-6.089	-1.460
ave_mean_ht_1m	0.849	0.256	3.311	398	0.001	0.345	1.353
no_AF	-0.168	0.434	-0.387	398	0.699	-1.021	0.685
Random effects							
Error	7.641						
Model: *steps_bet ~ 1 + feeding_type + gp_size + ave_mean_ht_1m*							
Fixed effects							
Intercept	6465.000	1.528	4.231	398	<0.001	3.461	9.469
feeding_type_Plucking and feeding	-3.596	1.158	-3.105	398	0.002	-5.873	-1.320
ave_mean_ht_1m	0.821	0.249	3.299	398	0.001	0.332	1.310
gp_size	0.050	0.152	0.328	398	0.743	-0.249	0.349
Random effects							
Error	7.641						

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *steps_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_cover_5m + (1 | gp_serial_no)*							
Fixed effects							
Intercept	8.996	2.164	4.156	398	<0.001	4.741	13.251
feeding_type_Plucking and feeding	-3.243	1.187	-2.732	398	0.007	-5.577	-0.909
ave_mean_ht_1m	0.845	0.249	3.399	398	0.001	0.356	1.333
ave_cover_5m	-0.031	0.025	-1.244	398	0.214	-0.081	0.018
Random effects							
gp_serial_no	0			60 levels			
Error	7.628						
Model: *steps_bet ~ 1 + feeding_type + age + ave_mean_ht_1m + ave_cover_5m*							
Fixed effects							
Intercept	8.036	2.210	3.202	397	0.002	3.102	12.971
feeding_type_Plucking and feeding	-3.364	1.197	-2.810	397	0.005	-5.717	-1.010
age	0.020	0.026	0.753	397	0.452	-0.032	0.072
ave_mean_ht_1m	0.843	0.248	3.396	397	0.001	0.355	1.332
ave_cover_5m	-0.027	0.026	-1.020	397	0.308	-0.078	0.025
Random effects							
Error	7.622						

Table 3.17: Results of linear mixed effect models for the time taken to move between successive food-sites (time_bet) as the response variable. Only the top models (ΔAICc ≤ 2) are shown.

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + no_AF + (1 | year) + (1 | gp_serial_no)	4	2	438.93	439.296	0	422.93
time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + (1 | year) + (1 | gp_serial_no)	3	2	439.363	439.647	0.3508	425.36
time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + ADI + age + no_AF + (1 |year) + (1 | gp_serial_no)	6	2	439.32	439.883	0.58665	419.32
time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + age + no_AF + (1 |year) + (1 | gp_serial_no)	5	2	439.531	439.99	0.69373	421.53
time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + age + (1 |year) + (1 | gp_serial_no)	4	2	440.165	440.532	1.23586	424.17
time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + age + gp_size + (1 |year) + (1 | gp_serial_no)	5	2	440.163	440.622	1.32621	422.16
time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + gp_size + (1 |year) + (1 | gp_serial_no)	4	2	440.323	440.69	1.39376	424.32
time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + ADI + age + (1 |year) + (1 | gp_serial_no)	5	2	440.274	440.733	1.43728	422.27

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + ADI + age + gp_size + (1 |year) + (1 | gp_serial_no)	6	2	440.208	440.771	1.47507	420.21
time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + (1 | ind) + (1 |year) + (1 | gp_serial_no)	3	3	440.461	440.827	1.53105	424.46
time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + no_AF + (1 | ind) + (1 |year) + (1 | gp_serial_no)	4	3	440.382	440.841	1.54547	422.38
time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + ave_cover_5m + no_AF + (1 |year) + (1 | gp_serial_no)	5	2	440.647	441.106	1.81045	422.65
time_bet ~ 1 + feeding_type + no_AF + ave_mean_ht_1m + ave_biomass_5m + (1 | gp_serial_no)	4	1	441.042	441.326	2.02998	427.04

Table 3.18: Parameter estimates and statistical significance of the best models explaining time taken to move between successive food-sites.

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + no_AF + (1 / year) + (1 / gp_serial_no)*							
Fixed effects							
Intercept	0.510	0.140	3.64	397	<0.001	0.234	0.785
feeding_type_Plucking and feeding	-0.230	0.072	-3.195	397	0.002	-0.372	-0.089
no_AF	-0.046	0.029	-1.572	397	0.117	-0.103	0.012
ave_mean_ht_1m	0.066	0.019	3.518	397	0.001	0.029	0.103
ave_biomass_5m	0.000	0.000	-2.928	397	0.004	-0.001	0.000
Random effects							
year	0.087			2 levels			
gp_serial_no	0.115			60 levels			
Error	0.396						
Model: *time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + (1 / year) + (1 / gp_serial_no)*							
Fixed effects							
Intercept	0.379	0.114	3.322	398	0.001	0.155	0.603
feeding_type_Plucking and feeding	-0.220	0.073	-3.031	398	0.003	-0.363	-0.077
ave_mean_ht_1m	0.056	0.018	3.124	398	0.002	0.021	0.091
ave_biomass_5m	0.000	0.000	-2.530	398	0.012	-0.001	0.000
Random effects							
year	0.089			2 levels			
gp_serial_no	0.121			60 levels			
Error	0.396						

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + ADI + age + no_AF + (1 |year) + (1 | gp_serial_no)*							
Fixed effects							
Intercept	0.458	0.145	3.167	395	0.002	0.173	0.742
feeding_type_Plucking and feeding	-0.248	0.072	-3.460	395	0.001	-0.389	-0.107
ADI	-0.140	0.094	-1.490	395	0.137	-0.325	0.045
age	0.004	0.002	1.911	395	0.057	0.000	0.009
no_AF	-0.050	0.029	-1.741	395	0.083	-0.106	0.007
ave_mean_ht_1m	0.063	0.019	3.367	395	0.008	0.026	0.099
ave_biomass_5m	0.000	0.000	-2.838	395	0.005	-0.001	0.000
Random effects							
year	0.082			2 levels			
gp_serial_no	0.108			60 levels			
Error	0.395						
Model: *time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + age + no_AF + (1 |year) + (1 | gp_serial_no)*							
Fixed effects							
Intercept	0.450	0.146	3.084	396	0.002	0.163	0.737
feeding_type_Plucking and feeding	-0.242	0.072	-3.369	396	0.001	-0.383	-0.101
age	0.002	0.002	1.195	396	0.233	-0.002	0.005
no_AF	-0.047	0.029	-1.639	396	0.102	-0.104	0.009
ave_mean_ht_1m	0.066	0.019	3.548	396	<0.001	0.029	0.102
ave_biomass_5m	0.000	0.000	-2.851	396	0.005	-0.001	0.000
Random effects							
year	0.083			2 levels			

Effect	Estimate	SE	t	df	P value	95% CI	
gp_serial_no	0.109			60 levels			
Error	0.396						

Model: *time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + age + (1 |year) + (1 | gp_serial_no)*

Fixed effects

Effect	Estimate	SE	t	df	P value	95% CI	
Intercept	0.320	0.124	2.579	397	0.010	0.076	0.564
feeding_type_Plucking and feeding	-0.230	0.072	-3.174	397	0.002	-0.372	-0.088
age	0.002	0.002	1.103	397	0.271	-0.001	0.005
ave_mean_ht_1m	0.055	0.178	3.125	397	0.002	0.021	0.090
ave_biomass_5m	0.000	0.000	-2.431	397	0.016	-0.001	0.000

Random effects

Effect	Estimate	SE	t	df	P value	95% CI	
year	0.088			2 levels			
gp_serial_no	0.116			60 levels			
Error	0.396						

Model: *time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + age + gp_size + (1 |year) + (1 | gp_serial_no)*

Fixed effects

Effect	Estimate	SE	t	df	P value	95% CI	
Intercept	0.401	0.135	2.977	396	0.003	0.136	0.665
feeding_type_Plucking and feeding	-0.233	0.072	-3.230	396	0.001	-0.374	-0.091
age	0.002	0.002	1.489	396	0.137	-0.001	0.005
gp_size	-0.016	0.011	-1.426	396	0.155	-0.038	0.006
ave_mean_ht_1m	0.062	0.018	3.423	396	0.001	0.025	0.098
ave_biomass_5m	0.000	0.000	-2.768	396	0.006	-0.001	0.000

Random effects

Effect	Estimate	SE	t	df	P value	95% CI	
year	0.081			2 levels			

Effect	Estimate	SE	t	df	P value	95% CI	
gp_serial_no	0.113			60 levels			
Error	0.396						

Model: *time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + gp_size + (1 |year) + (1 | gp_serial_no)*

Fixed effects

Effect	Estimate	SE	t	df	P value	95% CI	
Intercept	0.452	0.134	3.366	397	0.001	0.188	0.716
feeding_type_Plucking and feeding	-0.218	0.073	-3.011	397	0.003	-0.361	-0.076
gp_size	-0.011	0.011	-1.024	397	0.307	-0.033	0.010
ave_mean_ht_1m	0.061	0.019	3.295	397	0.001	0.025	0.097
ave_biomass_5m	0.000	0.000	-2.718	397	0.007	-0.001	0.000

Random effects

Effect	Estimate	SE	t	df	P value	95% CI	
year	0.084			2 levels			
gp_serial_no	0.121			60 levels			
Error	0.395						

Model: *time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + ADI + age + (1 |year) + (1 | gp_serial_no)*

Fixed effects

Effect	Estimate	SE	t	df	P value	95% CI	
Intercept	0.320	0.123	2.602	396	0.010	0.078	0.562
feeding_type_Plucking and feeding	-0.234	0.073	-3.226	396	0.001	-0.376	-0.091
ADI	-0.130	0.094	-1.378	396	0.169	-0.316	0.056
age	0.004	0.002	1.761	396	0.079	-0.001	0.008
ave_mean_ht_1m	0.052	0.018	2.896	396	0.004	0.017	0.087
ave_biomass_5m	0.000	0.000	-2.383	396	0.018	-0.001	0.000

Random effects

Effect	Estimate	SE	t	df	P value	95% CI	
year	0.085			2 levels			

Effect	Estimate	SE	t	df	P value	95% CI	
gp_serial_no	0.117			60 levels			
Error	0.395						

Model: *time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + ADI + age + gp_size + (1 |year) + (1 | gp_serial_no)*

Fixed effects

Effect	Estimate	SE	t	df	P value	95% CI	
Intercept	0.402	0.134	3.008	395	0.003	0.139	0.067
feeding_type_Plucking and feeding	-0.237	0.072	-3.285	395	0.001	-0.378	-0.095
ADI	-0.132	0.094	-1.402	395	0.162	0.000	0.009
age	0.005	0.002	2.042	395	0.042	-0.317	-0.095
gp_size	-0.016	0.011	-1.449	395	0.148	-0.038	0.006
ave_mean_ht_1m	0.059	0.018	3.204	395	0.002	0.023	0.095
ave_biomass_5m	0.000	0.000	-2.729	395	0.007	-0.001	0.000

Random effects

Effect	Estimate	SE	t	df	P value	95% CI	
year	0.077			2 levels			
gp_serial_no	0.114			60 levels			
Error	0.394						

Model: *time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + (1 | ind) + (1 |year) + (1 | gp_serial_no)*

Fixed effects

Effect	Estimate	SE	t	df	P value	95% CI	
Intercept	0.375	0.117	3.207	398	0.002	0.145	0.604
feeding_type_Plucking and feeding	-0.214	0.073	-2.931	398	0.004	-0.358	-0.070
ave_mean_ht_1m	0.057	0.019	3.059	398	0.002	0.020	0.093
ave_biomass_5m	0.000	0.000	-2.514	398	0.012	-0.001	0.000

Random effects

Effect	Estimate	SE	t	df	P value	95% CI	
ind	0.062			32 levels			

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
year	0.085			2 levels			
gp_serial_no	0.124			60 levels			
Error	0.391						

Model: *time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + no_AF + (1 | ind) + (1 |year) + (1 | gp_serial_no)*

Fixed effects

Intercept	0.499	0.142	3.507	397	0.001	0.219	0.779
feeding_type_Plucking and feeding	-0.225	0.072	-3.108	397	0.002	-0.367	-0.083
no_AF	-0.044	0.030	-1.470	397	0.142	-0.102	0.015
ave_mean_ht_1m	0.066	0.019	3.435	397	0.001	0.028	0.104
ave_biomass_5m	0.000	0.000	-2.881	397	0.004	-0.001	0.000

Random effects

ind	0.054			32 levels			
year	0.084			2 levels			
gp_serial_no	0.117			60 levels			
Error	0.392						

Model: *time_bet ~ 1 + feeding_type + ave_mean_ht_1m + ave_biomass_5m + ave_cover_5m + no_AF + (1 |year) + (1 | gp_serial_no)*

Fixed effects

Intercept	0.607	0.231	2.626	396	0.009	0.153	1.062
feeding_type_Plucking and feeding	-0.232	0.072	-3.226	396	0.001	-0.373	-0.091
no_AF	-0.052	0.031	-1.665	396	0.097	-0.114	0.009
ave_mean_ht_1m	0.064	0.019	3.343	396	0.001	0.026	0.102
ave_cover_5m	-0.001	0.003	-0.536	396	0.592	-0.007	0.004
ave_biomass_5m	0.000	0.000	-1.806	396	0.072	-0.001	0.000

Effect	Estimate	SE	t	df	P value	95% CI
Random effects						
year	0.084			2 levels		
gp_serial_no	0.113			60 levels		
Error	0.396					

As feeding activity type was the main predictor in all the top models (ΔAICc < 2) of the steps between successive food-sites, we split the datasets based on the feeding activity type (kicking or plucking grass) and refitted the linear mixed effects models for the top models in both cases. Tables 3.19 and 3.20 show the results for the steps between successive food-sites for the same models as mentioned in Table 3.15, for kicking and plucking, respectively. For both the datasets (kicking and plucking), the best model had a single explanatory variable, average mean grass height. In case of the feeding activity type kicking, there were eight other equally good models (ΔAICc < 2), while in the case of feeding activity type plucking, there were three other equally good models (ΔAICc < 2). Tables 3.21 and 3.22 shows the parameter estimates and statistical significance for the models in 3.19 and 3.20 respectively.

Table 3.19: Results of linear mixed effect models for number of steps taken between successive food-sites as the response variable with the data set having feeding activity type as kicking. All the top models in Table 3.15 are refitted to linear mixed effects model and ranked according to recalculated ΔAICc values.

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
steps_bet ~ 1 + ave_mean_ht_1m	1	0	2137.3	2137.36	0	2131.3
steps_bet ~ 1 + ave_mean_ht_1m + ave_cover_1m	2	0	2138.3	2138.45	1.088	2130.3
steps_bet ~ 1 + ADI + ave_mean_ht_1m	2	0	2138.9	2139.08	1.717	2130.9
steps_bet ~ 1 + ave_mean_ht_1m + ave_cover_5m	2	0	2139	2139.12	1.753	2131
steps_bet ~ 1 + no_AF + ave_mean_ht_1m	2	0	2139	2139.15	1.786	2131
steps_bet ~ 1 + ave_mean_ht_1m + (1 | gp_serial_no)	1	1	2139.3	2139.18	1.812	2131.3
steps_bet ~ 1 + ave_mean_ht_1m + ave_biomass_5m	2	0	2139.1	2139.24	1.878	2131.1
steps_bet ~ 1 + ave_mean_ht_1m + ave_biomass_1m	2	0	2139.2	2139.35	1.99	2131.2
steps_bet ~ 1 + age + ave_mean_ht_1m	2	0	2139.2	2139.36	1.997	2131.2
steps_bet ~ 1 + gp_size + ave_mean_ht_1m	2	0	2139.3	2139.4	2.032	2131.3
steps_bet ~ 1 + ave_mean_ht_1m + (1 | year)	1	1	2139.3	2139.42	2.053	2131.3

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
steps_bet ~ 1 + no_AF + ave_mean_ht_1m + ave_cover_5m	3	0	2140.3	2140.52	3.159	2130.3
steps_bet ~ 1 + no_AF + ave_mean_ht_1m + ave_cover_5m	3	0	2140.3	2140.88	3.518	2130.3
steps_bet ~ 1 + ave_mean_ht_1m + ave_cover_5m + (1 | gp_serial_no)	2	1	2141	2140.89	3.528	2131
steps_bet ~ 1 + ave_mean_ht_1m + ave_cover_5m + (1 | gp_serial_no)	2	1	2141	2140.93	3.568	2131
steps_bet ~ 1 + age + ave_mean_ht_1m + ave_cover_5m	3	0	2141	2141.16	3.8	2131
steps_bet ~ 1 + age + ave_mean_ht_1m + ave_biomass_5m	3	0	2141.1	2141.26	3.899	2131.1

Table 3.20: Results of linear mixed effect models for number of steps taken between successive food-sites as the response variable with the data set having feeding activity type as plucking. All the top models in Table 3.15 are refitted to linear mixed effects model and ranked according to recalculated ΔAICc values.

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
steps_bet ~ 1 + ave_mean_ht_1m	1	0	626.4	626.655	0	620.4
steps_bet ~ 1 + ADI + ave_mean_ht_1m	2	0	627.31	627.738	1.0836	619.31
steps_bet ~ 1 + ave_mean_ht_1m + ave_cover_1m	2	0	627.39	627.822	1.167	619.39
steps_bet ~ 1 + no_AF + ave_mean_ht_1m	2	0	628.14	628.571	1.9162	620.14
steps_bet ~ 1 + age + ave_mean_ht_1m	2	0	628.27	628.697	2.0418	620.27
steps_bet ~ 1 + ave_mean_ht_1m + ave_biomass_1m	2	0	628.37	628.795	2.1405	620.37
steps_bet ~ 1 + ave_mean_ht_1m + ave_cover_5m	2	0	628.38	628.808	2.1534	620.38
steps_bet ~ 1 + ave_mean_ht_1m + ave_biomass_5m	2	0	628.4	628.825	2.1707	620.4
steps_bet ~ 1 + gp_size + ave_mean_ht_1m	2	0	628.4	628.826	2.1715	620.4
steps_bet ~ 1 + ave_mean_ht_1m + (1 | gp_serial_no)	1	1	628.4	628.83	2.1748	620.4
steps_bet ~ 1 + ave_mean_ht_1m + (1 | year)	1	1	628.4	628.83	2.1748	620.4

Model	Number of Parameters		AIC	AICc	ΔAICc	Deviance
	Fixed	Random				
steps_bet ~ 1 + no_AF + ave_mean_ht_1m + ave_cover_5m	3	0	630.03	630.68	4.0248	620.03
steps_bet ~ 1 + no_AF + ave_mean_ht_1m + ave_biomass_5m	3	0	630.07	630.723	4.068	620.07
steps_bet ~ 1 + age + ave_mean_ht_1m + ave_cover_5m	3	0	630.2	630.852	4.1969	620.2
steps_bet ~ 1 + age + ave_mean_ht_1m + ave_biomass_5m	3	0	630.26	630.915	4.2602	620.26
steps_bet ~ 1 + ave_mean_ht_1m + ave_cover_5m + (1 | gp_serial_no)	2	1	630.38	631.03	4.3755	620.38
steps_bet ~ 1 + ave_mean_ht_1m + ave_biomass_5m + (1 | gp_serial_no)	2	1	630.4	631.048	4.3928	620.4

Table 3.21: Parameter estimates and statistical significance of the best models explaining number of steps taken between successive food-sites for data set with feeding activity type as kicking.

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *steps_bet ~ 1 + ave_mean_ht_1m*							
Fixed effects							
Intercept	4.544	1.503	3.023	302	0.003	1.586	7.502
ave_mean_ht_1m	1.311	0.313	4.192	302	<0.001	0.695	1.926
Random effects							
Error	8.056						
Model: *steps_bet ~ 1 + ave_mean_ht_1m + ave_cover_1m*							
Fixed effects							
Intercept	8.900	4.678	1.903	301	0.058	-0.306	18.106
ave_mean_ht_1m	1.478	0.356	4.156	301	<0.001	0.778	2.178
ave_cover_1m	-0.058	0.059	-0.983	301	0.326	-0.175	0.058
Random effects							
Error	8.044						
Model: *steps_bet ~ 1 + ADI + ave_mean_ht_1m*							
Fixed effects							
Intercept	4.920	1.636	3.008	301	0.003	1.701	8.138
ADI	-0.792	1.366	-0.580	301	0.562	-3.481	1.900
ave_mean_ht_1m	1.307	0.313	4.183	301	<0.001	0.692	1.923
Random effects							
Error	8.052						
Model: *steps_bet ~ 1 + ave_mean_ht_1m + ave_cover_5m*							
Fixed effects							
Intercept	5.875	2.854	2.059	301	0.040	0.259	11.491

Effect	Estimate	SE	t	df	P value	95% CI	
ave_mean_ht_1m	1.293	0.314	4.116	301	<0.001	0.675	1.911
ave_cover_5m	-0.017	0.031	-0.548	301	0.584	-0.078	0.044
Random effects							
Error	8.052						

Model: *steps_bet ~ 1 + no_AF + ave_mean_ht_1m*

Fixed effects

Effect	Estimate	SE	t	df	P value	95% CI	
Intercept	5.179	1.940	2.669	301	0.008	1.361	8.996
no_AF	-0.276	0.533	-0.517	301	0.606	-1.324	0.773
ave_mean_ht_1m	1.360	0.327	4.160	301	<0.001	0.717	2.004
Random effects							
Error	8.053						

Model: *steps_bet ~ 1 + ave_mean_ht_1m + (1 | gp_serial_no)*

Fixed effects

Effect	Estimate	SE	t	df	P value	95% CI	
Intercept	4.544	1.503	3.023	302	0.003	1.586	7.502
ave_mean_ht_1m	1.311	0.313	4.192	302	<0.001	0.695	1.926
Random effects							
gp_serial_no	0			48 levels			
Error	8.057						

Model: *steps_bet ~ 1 + ave_mean_ht_1m + ave_biomass_5m*

Fixed effects

Effect	Estimate	SE	t	df	P value	95% CI	
Intercept	4.952	1.790	2.766	301	0.006	1.428	8.475
ave_mean_ht_1m	1.340	0.320	4.182	301	<0.001	0.710	1.970
ave_biomass_5m	-0.001	0.003	-0.419	301	0.676	-0.006	0.004
Random effects							
Error	8.054						

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *steps_bet ~ 1 + ave_mean_ht_1m + ave_biomass_1m*							
Fixed effects							
Intercept	4.763	1.738	2.741	301	0.007	1.343	8.184
ave_mean_ht_1m	1.353	0.355	3.807	301	<0.001	0.654	2.052
ave_biomass_1m	-0.001	0.003	-0.251	301	0.802	-0.006	0.005
Random effects							
Error	8.056						
Model: *steps_bet ~ 1 + age + ave_mean_ht_1m*							
Fixed effects							
Intercept	4.350	1.713	2.540	301	0.012	0.980	7.720
age	0.008	0.034	0.237	301	0.813	-0.059	0.074
ave_mean_ht_1m	1.300	0.316	4.114	301	<0.001	0.678	1.922
Random effects							
Error	8.056						

Table 3.22: Parameter estimates and statistical significance of the best models explaining number of steps taken between successive food-sites for data set with feeding activity type as plucking.

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *steps_bet ~ 1 + ave_mean_ht_1m*							
Fixed effects							
Intercept	11.639	2.611	4.458	96	<0.001	6.456	16.822
ave_mean_ht_1m	-0.320	0.341	-0.936	96	0.352	-0.997	0.358
Random effects							

| Error | 5.734 | | | | | | |

Effect	Estimate	SE	t	df	P value	95% CI	
Model: *steps_bet ~ 1 + ADI + ave_mean_ht_1m*							
Fixed effects							
Intercept	9.662	3.210	3.010	95	0.003	3.290	16.035
ADI	1.814	1.732	1.048	95	0.298	-1.624	5.251
ave_mean_ht_1m	-0.143	0.379	-0.377	95	0.707	-0.896	0.610
Random effects							
Error	5.702						
Model: *steps_bet ~ 1 + ave_mean_ht_1m + ave_cover_1m*							
Fixed effects							
Intercept	25.677	14.188	1.810	95	0.074	-2.489	53.843
ave_mean_ht_1m	-0.014	0.456	-0.031	95	0.975	-0.919	0.890
ave_cover_1m	-0.170	0.169	-1.007	95	0.317	-0.506	0.166
Random effects							
Error	5.704						
Model: *steps_bet ~ 1 + no_AF + ave_mean_ht_1m*							
Fixed effects							
Intercept	12.418	3.024	4.106	95	<0.001	6.415	18.422
no_AF	-0.327	0.643	-0.529	95	0.612	-1.604	0.950
ave_mean_ht_1m	-0.298	0.344	-0.867	95	0.388	-0.980	0.384
Random effects							
Error	5.726						

3.4 Patch Depletion by Foraging Groups

As mentioned in the introduction, I had wanted to examine whether there was significant within-group scramble competition using the patch-depletion method. The number of trunkfuls eaten in all the 5-minute intervals was normally distributed (See B.2, Appendix B). There was no difference in the number of trunkfuls eaten in the first (average ± SD number of trunkfuls = 8.690 ± 3.666) and the last (average ± SD number of trunkfuls = 8.966 ± 3.235) 5-minute intervals (paired t-test, *t=-0.492, N=29, P=0.627*, Figure 4.1). The difference in the number of trunkfuls between the last and the first 5-minute interval was not significantly correlated with the duration between the two intervals (Spearman's *r=-0.317, R²=0.101, N=29, P=0.094*). Thus, the variance in the duration between the two time intervals did not affect the feeding rates in the first and last intervals. There was also no difference in the number of trunkfuls taken in 5-minute intervals separated by 10 minutes (paired t-test, *t =-0.333, N=38, P=0.741*, Figure 4.2).
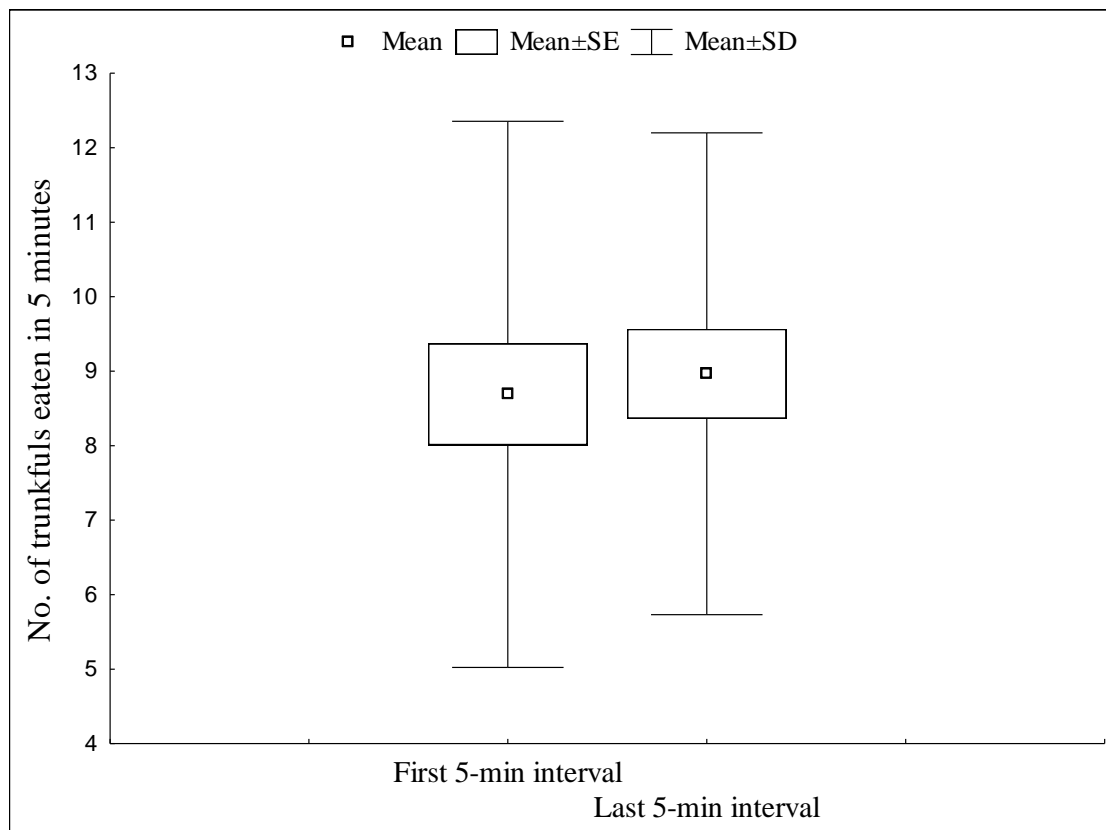
Figure 3.1: Box-plot of number of trunkfuls eaten in first and last 5-minute intervals.
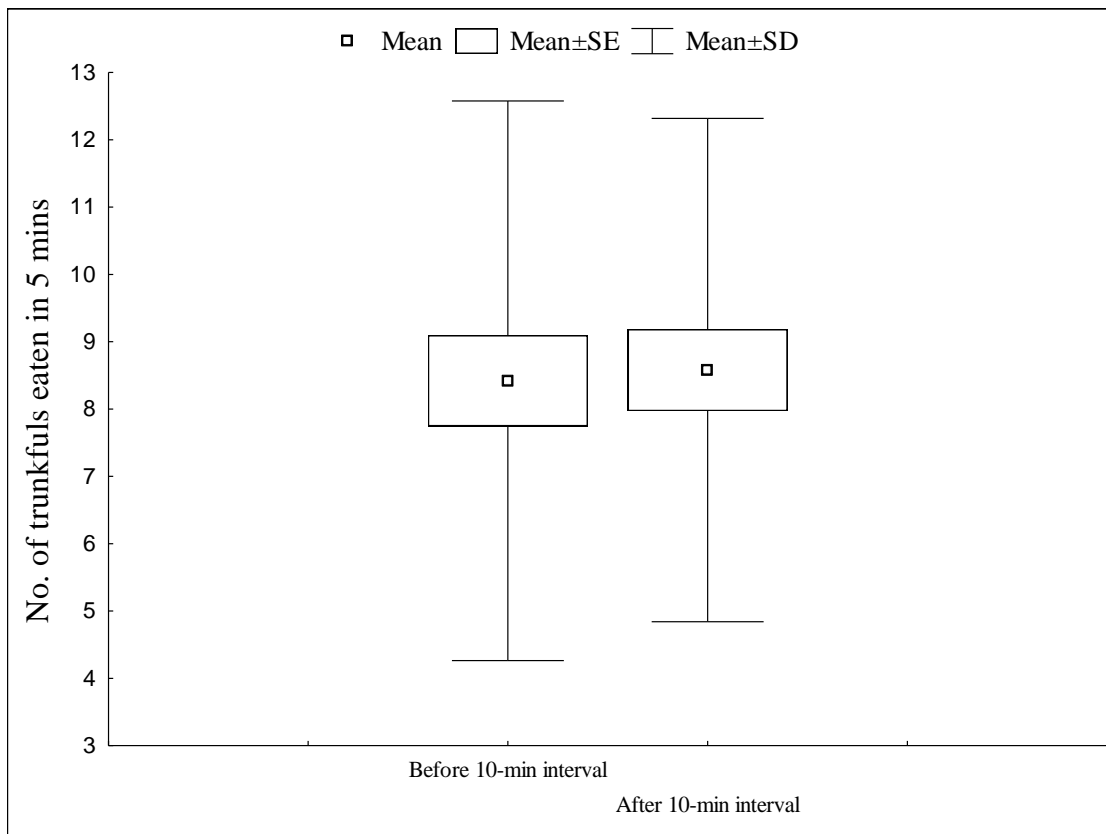
Figure 3.2: Box-plot of number of trunkfuls eaten in 5-minute intervals before and after a 10-minute interval.

Chapter 4: Discussion

This is the first study to examine the relationship between the distribution of food resource and expected contest and scramble competition, and how it affects the within-group feeding behaviour of females in any species of elephant. I had wanted to find out whether the food resource was patchy or not based on the distances moved by individuals between feeding sites, whether usurpability of food resource was related to the contesting ability of individuals, and whether there was significant scramble competition based on feeding rates and patch depletion. Based on the somewhat short average food-site residence time of about 5 minutes and an average number of ~10 steps between feeding sites, there appears to be moderate patchiness in grass resource at a very small spatial scale. One might, therefore, expect some level of within-group contest competition, as well as scramble competition because the patches are close together.

4.1 Food-site residence time (FSRT) and within-group contest competition

I expected more dominant females to have longer FSRT (the behavioural proxy for usurpability of a resource) than less dominant females as the former might be able to garner high resource patches and also be less susceptible to displacement by others. I also expected contest competition to increase with group size and, therefore, the FSRT of females in larger groups to be shorter than those of females in smaller groups due to greater interference competition. Females feeding in areas with greater grass abunance were also expected to have longer FSRT. Despite somewhat low levels of within-clan female dominance in the Kabini population, I found that FSRT was best explained by the average dominance index (ADI) of females and average grass cover of 1-m plots. Higher ADI and average grass cover were related to longer FSRT. The ADI had a beta estimate value of

2.07, while average grass cover (1m plot) had a beta estimate value of 0.164, indicating that ADI explains more variation in FSRT than does average grass cover. These results are consistent with other studies in female primate groups with egalitarian or less defined dominance hierarchies such as vervets (Isbell *et al.* 1998) and mountain gorillas (Wright and Robbins 2014, Grueter *et al.* 2017). Surprisingly, it was average grass cover (of 1-m plots) rather than grass biomass that appeared in all the top (ΔAICc < 2) linear mixed-effects models of FSRT. This may indicate that, perhaps, elephants select food-sites based on the average grass cover similar to that perceived by us. Grass cover may be important in terms of the amount of overground grass available as opposed to the roots also, although the roots may also be nutritious.

4.2 Feeding rates and within-group scramble competition

Scramble competition was measured in terms of feeding rates, which were calculated in 2 ways: FR1 was calculated as the number of trunkfuls eaten in the total time spent feeding and moving between two food-sites, while FR2 was calculated as the number of trunkfuls eaten in the total time observed feeding alone. As mentioned in the introduction, since feeding rate is expected to be shaped by scramble competition, the most dominant individuals were not expected to have the highest feeding rates. However, scramble competition increases with group size and females in larger groups were expected to show slower feeding rates on average if there was a searching component involved but to show faster feeding rates if feeding effort was simply increased in the presence of competitors. Individuals feeding in areas with taller grass, more grass cover and biomass were expected to have higher feeding rates because of the smaller processing time required. We found both FR1 and FR2 to be greatly affected by the type of feeding activity, plucking grass or kicking (scraping out) at the grass. Understandably, feeding rates were higher while plucking than while kicking because of the lower effort required. As FR1 accounts for the time spent in searching for food-sites, FR1 might be expected to be negatively related to group size and FR2 to be positively related to group size. However, the best models explaining FR1 and FR2 were all positively related to either total group size or the number of adult females. Since the time taken between feeding sites was small, it appears that searching costs were not high. When average dominance index appeared in a model to explain FR1, it was negatively related to feeding rate. Since searching times were not high,

this negative dependence is not likely to be due to more dominant females obtaining access to feeding sites faster and may reflect an advantage, if at all, of being able to feed more slowly without fear of a feeding site being usurped. I also found both FR1 and FR2 to be negatively related to female age. It is not clear if the negative relationship is related to older individuals being able to take larger amounts of grass in a trunkful because of their larger body sizes (although their larger body size would also demand more food) or if they gather grass also more slowly than younger individuals. When feeding rates of specific activity types – plucking or kicking – were examined, FR1 was additionally affected by the average mean grass height when only kicking was examined and not plucking, with feeding rate being negative related to grass height. In case of both FR1 and FR2, after splitting the dataset by feeding activity type, the estimate values for the predictor variables in each of the refitted models was very small, and most of the models lost their explanatory power on removing feeding activity type as a fixed predictor.

4.3 Feeding costs incurred by individuals

I had also examined the steps or time taken between food-sites as a measure of the costs incurred by individuals while feeding. I had expected more dominant (or older) individuals to spend shorter lengths of time between food sites than less dominant (or younger) individuals as they could presumably usurp other individuals' feeding sites. As competition increases with group size, I expected the number of steps and the time taken to move between two food sites to increase with group size, and to decrease in areas with more abundant grass. I found that all the best models of steps between and time between successive feeding sites included feeding type (plucking versus kicking), as well as average mean grass height of 1-m plots, as significant predictors. Both the steps between and the time between successive feeding sites were positively related to average mean grass height, contradictory to expectation that individuals will incur greater searching costs (i.e. they will have to walk more) if food resources are less abundant (low average mean grass height). However, if in a given area, the variation in grass height is high such that taller grass is patchily distributed but is easier to pluck and requires less time and effort in processing, then individuals may to prefer to forage in these patches more despite having to walk more, than in patches where grass height is lessch requires more time and effort to process. A few best models included ADI, which was negatively related to the time taken between feeding

sites as expected. Some best models of the time taken to move between successive food sites included female age and the number of adult females or group size, with the effect of age being slightly positive and the effect of the number of adult females/group size being slightly negative, both against expectation. However, larger group size can lead to lower times beween sites if there is more contest than scramble competition involved. In general though, the best linear mixed effects models for time taken to move between food-sites had too many explanatory variables, each with very low beta estimate values.

4.4 Extent of scramble competition

To examine the extent of scramble competition, I had examined patch depletion by comparing the feeding rates at the beginning and at the end of group feeding events. If patches were being depleted, the feeding rates of individuals were expected to decrease with the time spent feeding in a patch. However, I found no difference in the feeding rates at the start and end of the group feeding events. I also found no differences in the feeding rates at a smaller temporal scale, when I compared the feeding rates at every 10-minute intervals. Since these analyses looked at the same females feeding at presumably different feeding sites at different times in a group feeding event, it suggests that there are fresh feeding sites available in the patch at the temporal scale that I examined. Note that the duration of group feeding events ranged from ~20 to ~90 minutes. Given that elephants spend most of their time foraging, perhaps this temporal scale is too short to observe patch depletion. The focal group videos analysed for this study were recorded whenever elephant groups came into a particular sampling zone. Perhaps, a better study design for patch depletion analysis requires continuously following individual groups as they move between food patches.

4.5 Summary and Future Directions

In summary, I found some patchiness at the level of feeding sites, that would suggest within-group contest competition, as well as scramble competition because the patches are close together. Within-group contest is expected to lead to dominance hierarchies. I found an effect of average dominance index on feeding-site residence time, with more dominant

females spending more time at feeding sites. Feeding rates, which are measures of scramble competition, were positively related to measures of group size, suggesting that individuals increased their feeding efforts in larger groups. However, searching costs were not high in the Kabini backwaters which has an almost continuous stretch of grass. The time or number of steps taken between feeding sites was small and patch depletion was not found, with new feeding sites presumably being readily available. Thus there was an effect of contest and scramble competition on feeding. However, the absence of patch depletion and the low searching costs are at odds with the constraints on group size inferred in this population based on previous work (Nandini *et al*. 2017, 2018). One possibility is that because there might be a constraint on group size within the forest and groups move out from the forest to the backwaters, small groups are sometimes still maintained, although temporary group fusions into larger groups are also found in the backwaters. It would be interesting to model the movement of groups belonging to clans and their within-group competition based on different patterns of local and larger-scale food distribution, as well as within-group dominance relationships.

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Appendix A

A.1 Details of Grass Abundance Data Collection Method

The backwaters area in Nagarahole National Park and Tiger Reserve (11.888108°-11.932174° N, 76.203550°-76.230827°E) was divided into 6 zones, each zone separated from each other either by forest cover and a narrow strip of grassland or by a stream (Figure A.1.1). Each zone was further divided into 4 plot-clusters. The grass cover, grass height and biomass were measured by Hansraj Gautam (for his Ph.D. thesis) for 5 randomly chosen 1-m plots in each plot-cluster, during each month from February to May in 2015 and 2016. Further, the grass cover of 5-m plots was measured in the same area as the 1-m plot, and the grass biomass of 5-m plots was estimated using the grass biomass data collected for 1-m plots. The grass height, cover and biomass values were averaged across the 5 plots sampled during each month in each of the plot-clusters. These analyses were carried out by Hansraj Gautam for his Ph.D. thesis.
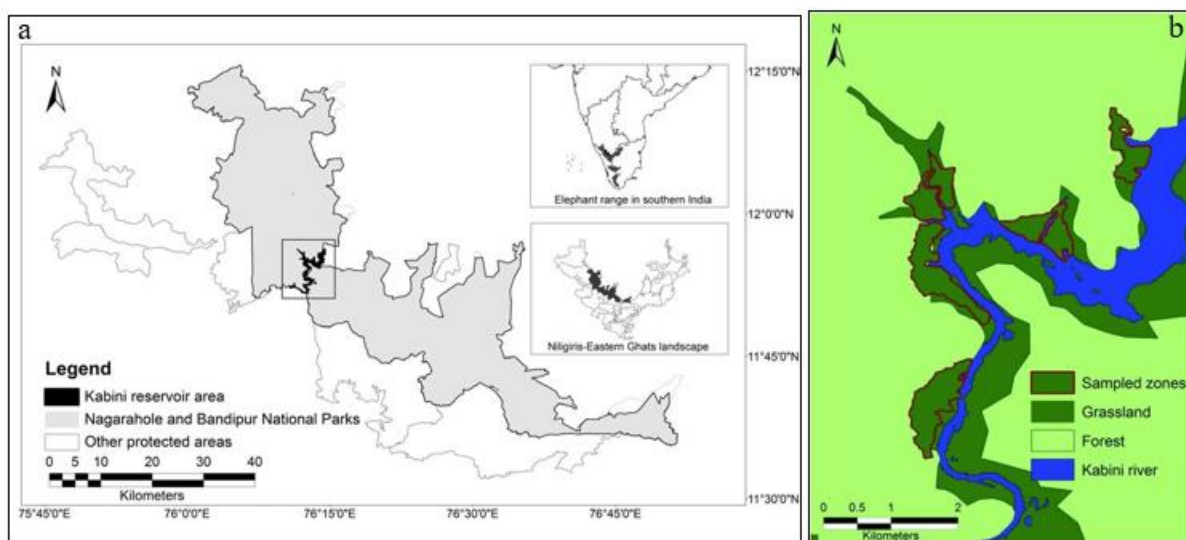

Figure A.1: Maps (courtesy Hansraj Gautam) of (a) Nagarahole and Bandipur National Parks and Tiger Reserves and (b) Kabini reservoir area showing zones sampled by Hansraj Gautam.

A.2 Average Dominance Index (ADI) Calculation

Behavioural *ad libitum* and focal group sampling (15 minutes long) were carried out by Nandini Shetty during her Ph.D. Agonistic interactions between the same pair of individuals were considered to be independent of each other if they were interrupted by other behaviours such as feeding. Behavioural interactions between individuals were categorized as dominant or subordinate behaviours (Shetty 2016). Depending on the response(s) to the initiator of an agonistic behaviour by the recipient, the outcomes of agonistic interactions were classified into those that had a clear winner or not. Only interactions with clear winners were used. Dominance indices of female A with each of the other females she interacted with in the clan was calculated as the proportions of wins by A against each of those others, respectively (dominance index of A with B = number of times individual A won over individual B divided by the total number of interactions between A and B). The average dominance index of an individual was calculated as the average of all the dominance indices involving the focal individual (Hemelrijk *et al.* 2005). These calculations were carried out by Shetty (2016).

Appendix B

B.1 Means and standard deviations of the response variables and fixed predictors.

*Table B.1:* Mean and standard deviation values for the response and fixed variables.

| Variable	Mean	Standard deviation
Response Variables		
FSRT (mins)	4.845	6.472
FR1 (no. of trunkfuls/min)	1.835	0.705
FR2 (no. of trunkfuls/min)	2.003	0.788
steps_bet	10.120	7.537
time_bet (mins)	0.408	0.416
Fixed Predictors		
Age (years)	29.092	14.840
Group size	6.086	2.830
No. of AF	2.828	1.142
Av mean grass height (cm)	5.291	2.211
Av grass cover (1m plots, in %)	89.498	10.377
Av grass biomass (1m plots, in g/m sq)	643.801	250.799
Av grass cover (5m plots, in %)	80.664	12.837
Av grass biomass (5m plots, in g/m sq)	576.666	245.033

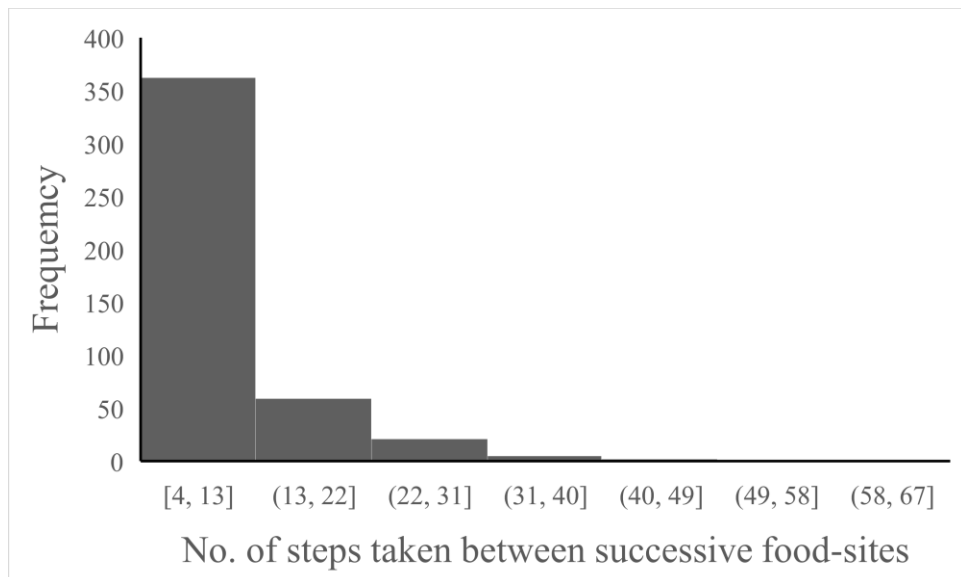*B.2 Frequency distributions of the response variables.*
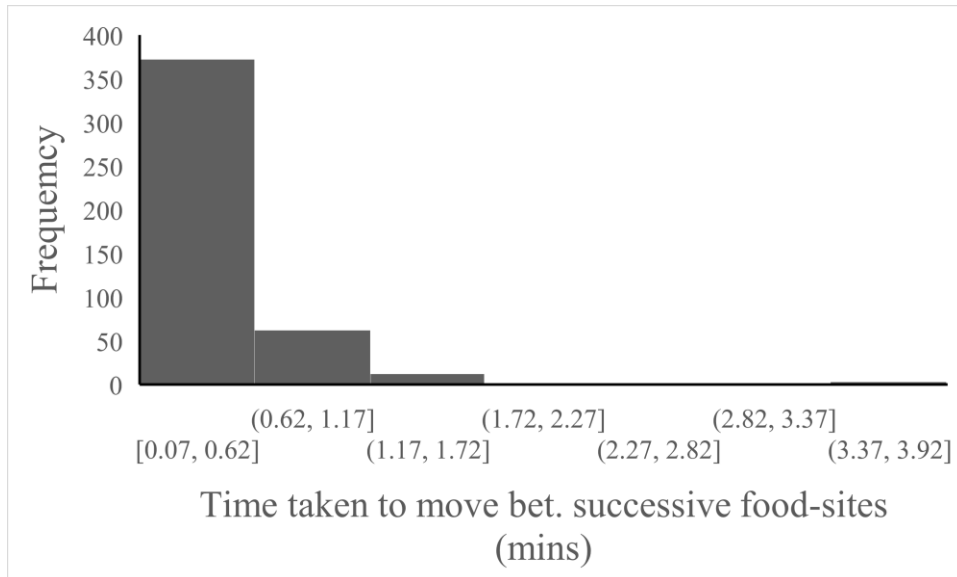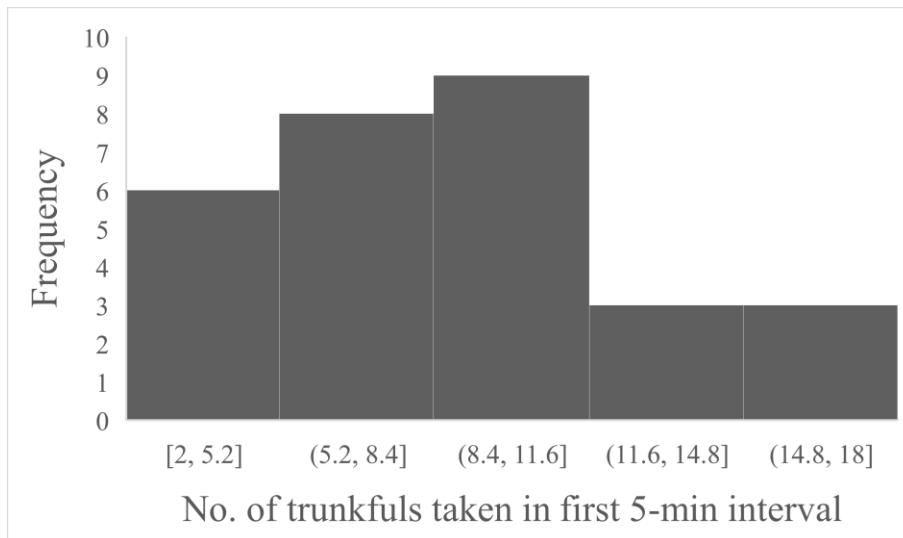
1. FSRT
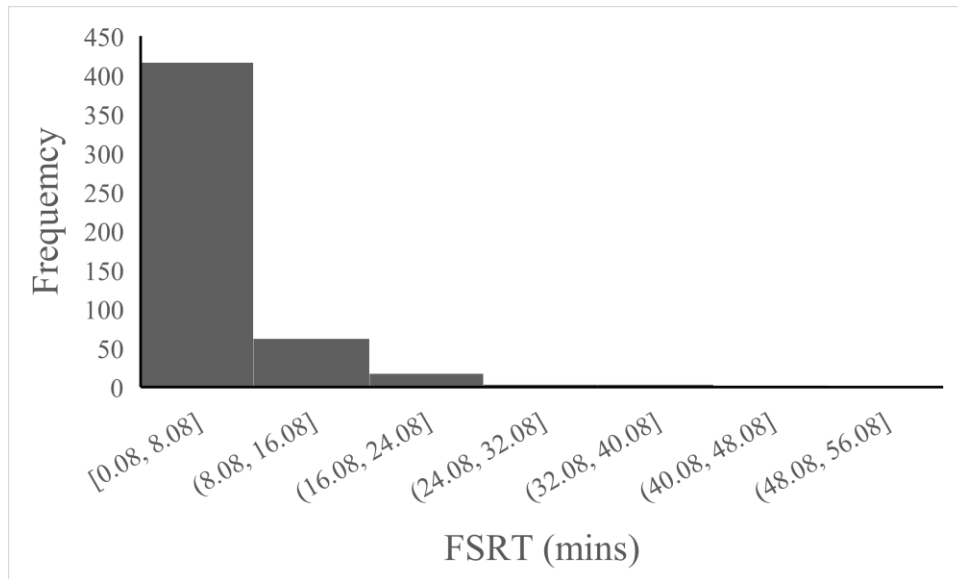
2. FR1
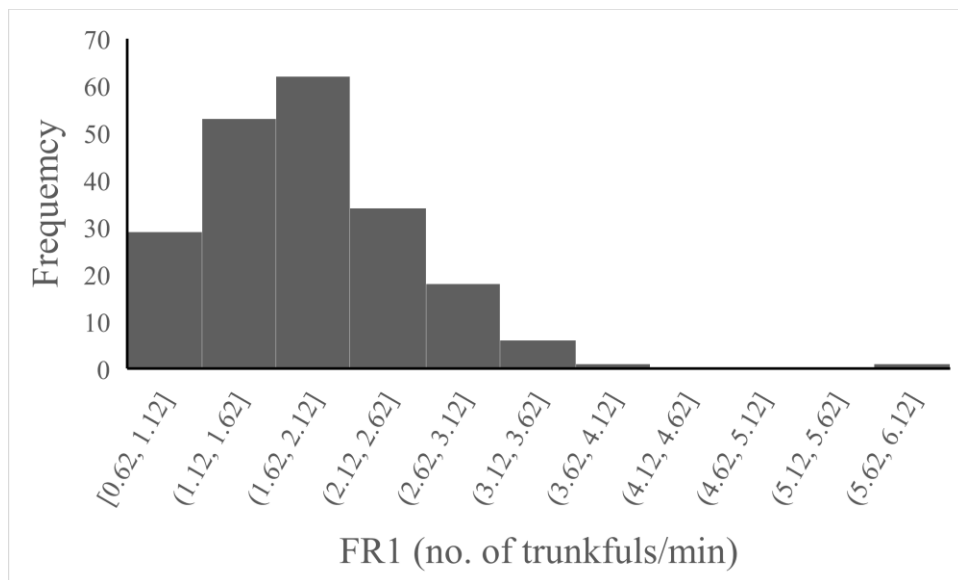
3. FR2
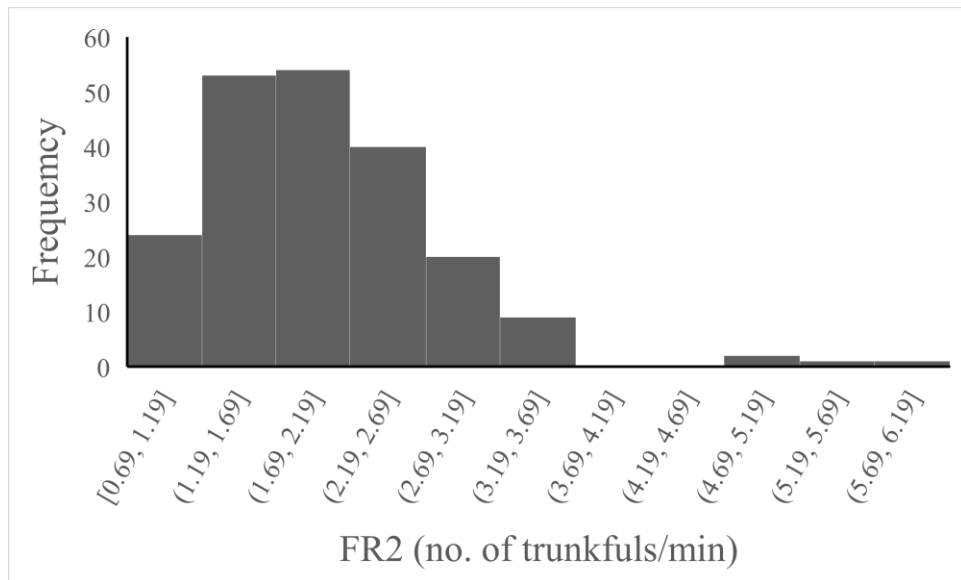
4. Number of steps taken between successive food-sites
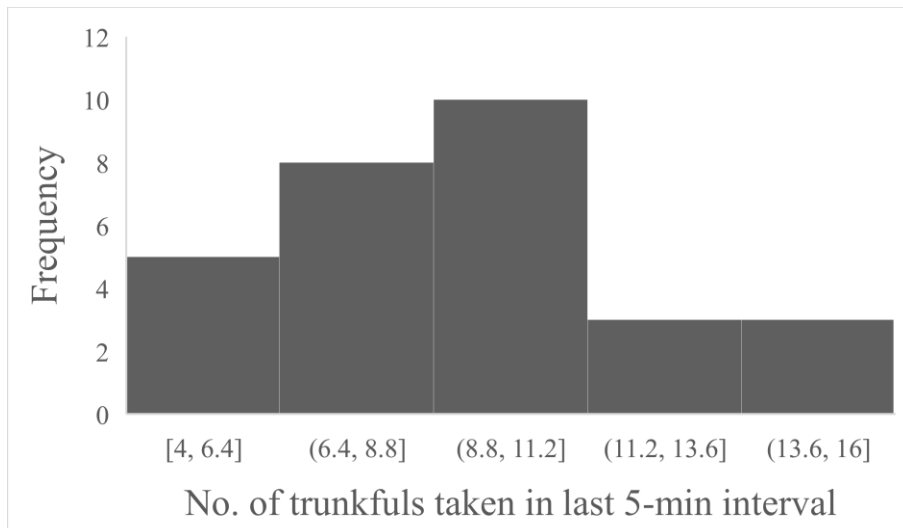
5. Time taken to move between successive food-sites

6. Number of trunkfuls taken in first 5-min interval

7. Number of trunkfuls taken in last 5-min interval

B.3 Correlations between response variables and fixed predictors.

Table B.2: Correlations between response variables and fixed predictors.

Response Variable	Fixed Predictor	Pearson's R	R^2	P
FSRT	Age	0.129	0.017	0.006
FSRT	ADI	0.075	0.006	0.114
FSRT	Gp_size	-0.005	<0.001	0.92
FSRT	No_AF	0.022	0.001	0.641
FSRT	Ave_mean_ht_1m	0.098	0.01	0.039
FSRT	Ave_cover_1m	0.206	0.042	<0.001
FSRT	Ave_biomass_1m	0.132	0.017	0.005
FSRT	Ave_cover_5m	0.116	0.014	0.014
FSRT	Ave_biomass_5m	0.115	0.013	0.016
FR1	Age	-0.171	0.029	0.024
FR1	ADI	-0.190	0.036	0.012
FR1	Gp_size	0.059	0.003	0.771
FR1	No_AF	0.149	0.022	0.051
FR1	Ave_mean_ht_1m	0.231	0.053	0.002
FR1	Ave_cover_1m	0.269	0.072	<0.001
FR1	Ave_biomass_1m	0.171	0.029	0.024
FR1	Ave_cover_5m	0.071	0.005	0.352
FR1	Ave_biomass_5m	0.148	0.022	0.052
FR2	Age	-0.183	0.033	0.016
FR2	ADI	-0.162	0.026	0.034
FR2	Gp_size	-0.013	<0.001	0.867
FR2	No_AF	0.105	0.011	0.168
FR2	Ave_mean_ht_1m	0.269	0.073	<0.001

Response Variable	Fixed Predictor	Pearson's R	R^2	P
FR2	Ave_cover_1m	0.206	0.043	0.007
FR2	Ave_biomass_1m	0.129	0.017	0.091
FR2	Ave_cover_5m	0.077	0.006	0.313
FR2	Ave_biomass_5m	0.124	0.015	0.105
steps_bet	Age	0.044	0.002	0.379
steps_bet	ADI	0.006	<0.001	0.910
steps_bet	Gp_size	0.037	0.001	0.464
steps_bet	No_AF	0.030	0.001	0.547
steps_bet	Ave_mean_ht_1m	0.082	0.007	0.100
steps_bet	Ave_cover_1m	0.012	<0.001	0.815
steps_bet	Ave_biomass_1m	0.005	<0.001	0.926
steps_bet	Ave_cover_5m	-0.074	0.006	0.138
steps_bet	Ave_biomass_5m	-0.041	0.002	0.417
time_bet	Age	0.062	0.004	0.217
time_bet	ADI	-0.006	<0.001	0.907
time_bet	Gp_size	0.003	<0.001	0.954
time_bet	No_AF	0.008	<0.001	0.867
time_bet	Ave_mean_ht_1m	0.045	0.002	0.370
time_bet	Ave_cover_1m	-0.001	<0.001	0.980
time_bet	Ave_biomass_1m	-0.029	0.001	0.564
time_bet	Ave_cover_5m	-0.106	0.011	0.033
time_bet	Ave_biomass_5m	-0.086	0.007	0.085

B.4 Scatter plots of FSRT and fixed predictors