SPATIAL PATTERNS WITHIN GELADA MONKEY ONE MALE UNITS AT GUASSA, ETHIOPIA

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Abstract

I used repeated, accurate positional data, collected between October 2013 and January 2014, on all adult members of nine gelada monkey One-Male Units (OMUs) living at Guassa, Ethiopia to investigate the consequences of a modular, multilevel social organization for the spatial associations of individuals. The results indicate that distances between individuals within OMUs did not change with increasing group size, such that larger OMUs necessarily occupied more space. Unit males were significantly more likely to be in the vanguard. The group geometry of OMUs was distinctive in that all groups, being stretched along the axis of travel, were best described as files. The extent of conformity to a file was best explained by activity and travel speed, rather than by demographic or ecological factors. These results are interpreted in the context of the optimization of foraging by OMU members living in the immediate proximity of other OMUs.

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List of Abbreviations

AF	Adult female
ASTER	Advanced spaceborne thermal emission and reflection radiometer
DEM	Digital elevation model
FM	Follower male
GIS	Geographic information system
GPS	Global positioning system
IID	Inter-individual distance
LM	Leader male
LMM	Linear mixed effects model
NDVI	Normalized difference vegetation index
NND	Nearest neighbour distance
OMU	One male unit
YF	Young adult female

Chapter 1: Introduction

1.1 Overview

There is consistent evidence that gregariousness in primates is driven primarily by predation risk (Dunbar, 1988; Majolo, de Bortoli Vizioli, & Schino, 2008; van Schaik & van Hooff, 1983). As members of coherent groups, individuals benefit from the mere presence of others, which reduces the likelihood that any particular animal will be predated (the ‘dilution’ effect), as well as by their contributions to collective vigilance. Despite these benefits, group membership carries costs to individuals that they are not expected to share equally (Hamilton, 1971). Predation risk, for example, is expected to be higher on the margins of the group (Hamilton, 1971), whereas foraging efficiency, which is regarded as the primary disadvantage of gregariousness (van Schaik, van Noordwijk, de Boer, & den Tonkelaar, 1983), should be better on the group’s leading edge (Robinson, 1981). A third cost of group membership, especially in multimale cercopithecine groups, is the close presence of reproductive rivals in the vicinity of receptive females (Clutton-Brock, 1989).

To the extent to which these and other conflicting demands can be resisted or are traded-off against each other by group members, it is clear that they will underpin individual location in the group (Josephs, 2015), and also the group’s spatial structure, both statically and dynamically (Altmann, 1974). Spatial structure, therefore, is revealing because it reflects the outcome of individual-level processes tied ultimately to the maximization of lifetime reproductive success. Generally, for example, higher ranking animals in cercopithecine groups occupy the center of the group, where their rank still allows them preferential access to resources, whereas subordinate animals occupy the margins, where increased predation risk may possibly be compensated by improved foraging (Hall & Fedigan, 1997; Heesen, Macdonald, Ostner, & Schülke, 2015; Janson, 1990). Sociability may also increase animals' access to desirable spatial positions (Josephs, Bonnell, Dostie, Barrett, & Henzi, 2016). At the same time, animals will need to align themselves relative to others in ways that match as far as possible the local distribution of resources. So, given predation risk, clumped resources might allow for a circular shape at group-level, although this will be sub-optimal when resources are sparse and widely dispersed (Altmann, 1974). While less theoretical and empirical attention has been directed at the spatial consequences of coexistence for individual male competitors, it is clear that, here too, we might expect individual-level interactions among males, both within (Busse, 1984) and across groups (Waser, 1985), to be detectable in spatial structure.

With the exception of leaving and joining dynamics in spider monkeys (Korstjens, Verhoeckx, & Dunbar, 2006; Ramos-Fernandez, Boyer, Aureli, & Vick, 2009), very nearly all the work on spatial structure and movement ecology in monkeys has been conducted on species that form coherent groups with a single layer of social organization. The one exception has been the hamadryas baboon (*Papio hamadryas hamadryas*), a desert species with a flexible multi-level social organization, of which the fundamental social group is the one-male unit (OMU). As Kummer (1968) and Schreier and Swedell (2009) have outlined, OMUs are connect first as clans and then as members of a band, with bands combining to form troops. During the day, bands leave sleeping cliffs to forage and, as they do so, OMUs become more spatially distinct and constitute the basal foraging - as well as - reproductive unit. Sigg (1980) demonstrated that there was a consistent spatial structure within OMUs, with a fundamental division between higher-ranking, younger ‘central’ females and lower-ranking, older ‘peripheral’ females, with the male constituting the unit’s primary social focus. Such multilevel social organizations are spatially interesting because they necessitate at least two levels of coordination - within and across levels - the understanding of which requires us to address individual spatial association patterns, with units at each level treated as independent analytical entities. For example, following the descriptions of Sigg (1980) and Kummer (1968), there is an obvious need to understand spatial processes both within and among OMUs in order to determine the extent to which dynamics at one level structure those at the other.

The other historically pre-eminent multilevel primate society is that of the gelada (*Theropithecus gelada*). Gelada occupy montane uplands in Ethiopia and are, in a way that is superficially similar to hamadryas, characterized by a modular social organization of which the fundamental social group is similarly an OMU, with OMUs aggregated ultimately into herds (Kawai, Ohsawa, Mori, & Dunbar, 1983). Unlike hamadryas, though, related females form the social core of the OMU and, as a consequence of a diet that principally comprises grasses, foraging OMUs are much more consistently likely to be found in the close vicinity of a number of other OMUs (Dunbar & Dunbar, 1975). This means, in turn, that while we expect scramble competition for resources within and between OMUs to set the spatial structure of analytical units, we also expect to see the consequences of the close proximity of reproductive rivals in a system where, unlike savanna baboons, males cannot simply drift to the margins of the herd with a consort partner but need to sustain close proximity to all female unit members.

The overall objective of this dissertation is to use spatially explicit data, obtained by frequent GPS logging of individual members of several OMUs, to begin to address the question of socio-spatial coordination and structure in gelada. I will describe the spatial associations of members of OMUs in relation to a range of potential explanatory variables and use these individual coordinates to abstract global descriptions of group shape in order to explore how OMUs arrange themselves in relation to their neighbours.

1.2 Benefits of Living in Groups

Animals in a group may be less vulnerable to predation than if they were solitary, for several reasons (Krause & Ruxton, 2002). The dilution effect operates when predators can only attack one or a few members of a group, so that each individual has a smaller risk of being targeted (Turner & Pitcher, 1986). Hamilton's selfish herd theory indicates that individual animals can benefit from being part of a group because they can keep other group members between themselves and the predator (Hamilton, 1971). Each animal's domain of danger is the region where, if a predator appeared in the domain of danger, that animal would be the closest and so at the highest risk of attack by the predator. If a predator could approach from any direction, then animals in the center of the group will have smaller domains of danger than those on the periphery. The dilution and selfish herd effects may reduce each individual's risk of being targeted by biting insects (Mooring & Hart, 1992).

Members of a group can also benefit from the vigilance of their fellows. When one group member detects a predator, its reaction will alert other group members to the danger, allowing each individual to spend less time being vigilant (Elgar, 1989; Pulliam, 1973). Many primates produce alarm calls that alert other group members to danger. Vervet monkeys produce different calls in response to different types of predators (Seyfarth, Cheney, & Marler, 1980). Geladas also have a distinctive alarm call used when they detect a predator (Gustison, le Roux, & Bergman, 2012).

As well as alerting conspecifics to the danger, alarm calls can also serve to alert a predator that it has been spotted, which may deter it from attacking (Zuberbühler, Jenny, & Bshary, 1999). Some species that live in groups will come together to mob or harass a predator, a behaviour that may stop or prevent an attack, drive the predator away, and even injure or kill the predator (Crofoot, 2013). Geladas usually respond to a predator by fleeing down the cliff face (Crook, 1966), but males have been known to mob and drive off predators such as domestic dogs and leopards (Iwamoto, Mori, Kawai, & Bekele, 1996) (R. I. M. Dunbar & E. P. Dunbar, 1974). Male baboons have been observed to counter-attack predators, often successfully driving them off, and even killing leopards (Cowlishaw, 1994). Groups of primates such as capuchin monkeys (*Cebus capuchinus*) and Coquerel’s sifakas (*Propithecus coquereli*) have been observed to rescue group members from attacks by constricting snakes (Gardner, Radolalaina, Rajerison, & Greene, 2015; Perry, Manson, Dower, & Wikberg, 2003).

As well as watching for predators, vigilance can also include monitoring fellow group members. Some primates actually spend more time scanning when they have more neighbours (Teichroeb & Sicotte, 2012). Especially among males, vigilance may serve to detect potential mates or rival males, as well as predators (Baldellou & Henzi, 1992; Cowlishaw, 1998). Agent based models where subordinate animals monitor the dominant animals resulted in greater inter individual distances, and increased the tendency of dominant animals to be found in central positions (Evers, de Vries, Spruijt, & Sterck, 2012).

Gelada leader males show much more vigilance towards bachelor males than towards the leader males of other OMUs (U. Mori, 1979). Pappano, Snyder-Mackler, Bergman, and Beehner (2012) have suggested that bachelor males act as “social predators” among geladas. Geladas live in one male units (OMUs) in which one dominant male controls a small group of females, and a bachelor male must take over an OMU in order to reproduce. Bachelor males pose a threat to the incumbent leader male, who, once replaced, is unlikely to ever reproduce again (Dunbar, 1984). Takeovers also pose a threat to females, who may lose their infants to infanticide by the new male, or may spontaneously abort their pregnancies in response to a takeover (Beehner & Bergman, 2008; U. Mori & Dunbar, 1985; Roberts, Lu, Bergman, & Beehner, 2012). Geladas respond to these threats by moving closer together, both within each OMU and between different OMUs, when bachelor males are nearby (Pappano et al., 2012). In snub-nosed monkeys (*Rhinopithecus roxellana*), the leader males from different OMUs will cooperate to defend their females against bachelor males (Zuo-Fu, Bang-He, Yang, & Hui, 2014).

In addition to the anti-predation benefits, there may be situations where animals can feed more efficiently in groups (van Schaik, 1983). By foraging together, groups of animals can regulate how often they return to a particular food patch, and avoid visiting a patch that has been depleted by conspecifics (Altmann, 1974). Capuchins are more successful at catching insect prey when they have more close neighbours, probably because insects escaping from one monkey may flee towards another monkey (Robinson, 1981).

1.3 Costs of Living in Groups

Although there may be many benefits to living together, animals in groups must compete for limited resources (Krause & Ruxton, 2002). Competition may take the form of contest or scramble competition (Janson & van Schaik, 1988; van Schaik & van Noordwijk, 1988). Contest competition occurs when one individual is excluded from a resource by another. This exclusion may take the form of aggression, fighting, or threats, or lower ranking individuals may simply avoid the more dominant ones (Janson & van Schaik, 1988). Scramble competition occurs when one animal has less access to a resource because another animal got there first and depleted the resource; interaction between the two is not required.

To compensate for the increased feeding competition they face, animals in larger groups must often expend more energy to find food (Clutton-Brock & Harvey, 1977). Animals may spend more time travelling, and travel greater distances in a day (Isbell, 1991). Red colobus monkeys *(Procolobus rufomitratus*) spent more time travelling, and less time foraging or grooming, as their group size increased (Gogarten et al., 2014). Orangutans had longer day journeys when several individuals travelled together (van Schaik, 1999). Distance travelled was greater in larger groups of long-tailed macaques, and lower ranking females spent more time walking than did higher ranking females (van Schaik & van Noordwijk, 1988). However, not all species increase their daily travel distance in larger groups. Black-and-white colobus monkeys (*Colobus guereza*) day journeys were not significantly greater in larger groups, indicating that within-group scramble competition may not affect this species (Fashing, 2001). Folivorous colobine monkeys have an abundant source of food, so competition may be less intense than for many other primates, so that day journey length need not increase with group size (Yeager & Kirkpatrick, 1998).

Food is not the only resource for which animals must compete when they live in groups. Males compete over access to females, using both contest and scramble competition (Berghänel, Schülke, & Ostner, 2010; Port & Cant, 2014). Some animals, including baboons, coatis (*Nasua nasua*), and impalas compete over the safer central positions within the group (Blanchard, Sabatier, & Fritz, 2008; Hirsch, 2011; Tkaczynski, MacLarnon, & Ross, 2014).

Central positions can also have their drawbacks. Animals foraging in central positions may face greater feeding competition. Impalas (*Aepyceros melampus*) feeding in a central position were challenged more often than those in peripheral positions, and the central animals spent less time being vigilant (Blanchard et al., 2008). Increased competition, rather than decreased predation risk, may be responsible for lower vigilance rates in larger groups and by central animals (Dalerum, Henrik, Christina, & Tuulikki, 2008).

Primates in larger groups may experience more social stress and harassment, which may limit reproduction and decrease fitness (Sterck, Watts, & van Schaik). Social bonds between females may mitigate this stress and improve fitness (Silk, Alberts, & Altmann, 2003). OMUs may help geladas to cope with their very large group size when foraging in herds of hundreds: a small group of familiar animals can serve as a buffer against stress and harassment (Dunbar, 1993).

Larger group size is also associated with increased risk of parasitism (Rifkin, Nunn, & Garamszegi, 2012). High dominance rank and social centrality were associated with more nematode parasites in Japanese macaques (*Macaca fuscata yakui*) (MacIntosh, Jacobs, Garcia, & Shimizu, 2012).

1.4 Optimal Group Size

The actual sizes of primate groups will result from a balance between the benefits and the costs of sociality (Cowlishaw, 1997; Dunbar, 1996). This balance will vary with ecological conditions, rather than being a characteristic of the species (Dunbar, 1996). Environmental factors, such as rainfall and temperature, will impose a maximum ecologically tolerable group size beyond which the animals will be unable to find sufficient food in the time available (Dunbar, 1992a; Korstjens et al., 2006). The risk of predation limits the minimum group size, as smaller groups provide less protection against predators (Bettridge & Dunbar, 2013).

Another constraint on primate group size is the ability to maintain relationships with other group members. The size of the neocortex in primates’ brains is related to the size of groups they live in (Barton, 1996; Byrne, 1996; Dunbar, 1992b). Neocortex size may limit the number of individuals or relationships that an individual primate can remember, and this may constrain the maximum group size, with overly large groups likely to split up (Dunbar, 1992b).

1.5 Fission-fusion Dynamics and Multilevel Societies

Many social animals, such as savannah baboon troops, live in stable and cohesive groups, while other taxa may have more variable association patterns. Fission-fusion social systems allow animals to adjust their group size flexibly. Here, members, either singly or in conjunction with others, may merge when environmental or social conditions favour or enable larger groups, and split apart, when smaller groups are more beneficial (Couzin & Laidre, 2009). Fission-fusion dynamics can be described as being present to a greater or lesser degree in a range of species or populations, with variation in the spatial cohesion, size, and composition of groups being detectable over time (Aureli et al., 2008). Even a brief splitting of a group can offer group members a choice of different activities or locations, allowing each animal more freedom to choose an option that suits its needs, without having to leave the safety of the group entirely (Jacobs, 2010).

Several primate species show a high degree of fission-fusion dynamics, including chimpanzees (*Pan* spp.), orangutans (*Pongo pygmaeus*), spider monkeys (*Ateles* spp.), and ruffed lemurs (*Varecia varigata* and *V. rubra*) (Boesch, 1996; Campbell, 2008; Symington, 1990; van Schaik, 1999; Vasey, 2007). Fission-fusion systems can also be found in non-primate species, such as hyenas (*Crocuta crocuta*), dolphins (*Tursiops aduncus*) and ungulates, including giraffes (*Giraffa camelopardalis*) and zebras (*Equus grevyi*) (Bercovitch & Berry, 2013; Connor, 2007; Sundaresan, Fischhoff, Dushoff, & Rubenstein, 2007; Watts & Holekamp, 2007).

Modular, ‘multilevel’ social systems express fission-fusion dynamics, but are characterized by a structure where decomposition is modular, such that different levels of groupings such as one-male units (OMUs), bands, or clans can be identified. Multilevel social systems can be found in several primate taxa, including both cercopithecine monkeys (geladas, hamadryas baboons (*Papio hamadryas*)), and colobine monkeys (snub-nosed monkeys (*Rhinopithecus* spp.), and proboscis monkeys (*Nasalis larvatus*)) (Grueter, Chapais, & Zinner, 2012; Matsuda et al., 2012; Yeager & Kirkpatrick, 1998). All these species form OMUs, which come together at sleeping or feeding sites (Matsuda et al., 2012). Multilevel social systems could have evolved in two ways. A large multi-male multi-female group could have divided into OMUs, as is most likely for geladas and hamadryas baboons, or several one-male groups could have come together, as is likely for the snub-nosed monkeys and proboscis monkeys (Grueter et al., 2012).

Geladas, along with the colobine species that form multilevel societies, feed on abundant foods such as grass and leaves, so that ecological conditions permit very large groups (Dunbar & Bose, 1991; Yeager & Kirkpatrick, 1998). Snub-nosed monkeys consume considerable amounts of filamentous lichen, which is low in nutrients and very widely distributed, permitting larger group sizes (Kirkpatrick & Grueter, 2010).

Daily patterns of association vary between these species. Gelada and snub-nosed monkey OMUs both forage and sleep in large groups. In proboscis monkeys and hamadryas baboons, OMUs forage independently, but congregate in larger groups at night (Bennett & Sebastian, 1988; Kummer, 1968).

Some non-primate species also live in multilevel societies, including elephants (*Loxodonta africana*), sperm whales (*Physeter macrocephalus),* and bats (*Myotis bechsteinii*) (Kerth, Perony, & Schweitzer, 2011; Whitehead et al., 2012; Wittemyer, Douglas-Hamilton, & Getz, 2005). In several species whose societies have multiple hierarchical levels, including geladas, each level contains approximately three times more individuals than the level below (Hill, Bentley, & Dunbar, 2008). Deviations from this ratio may suggest the presence of another intermediate level of organization, such as the level between the OMU and the clan in the population of hamadryas baboons studied by (Schreier & Swedell, 2012b).

1.6 Group Shape and Within Group Spatial Patterns

When food is distributed widely and at a low density, groups of animals should spread out in a rank formation as individuals should avoid foraging in the depleted swath behind another animal (Altmann, 1974).

Within the group, some positions are likely to be more advantageous than others (Krause, 1994). Central animals enjoy smaller domains of danger than peripheral animals (Hamilton, 1971). Individuals occupying safer central positions may be free to use riskier feeding techniques than those on the edge (Beauchamp, 2013), and may spend less time in vigilance. Central individuals may also be less vigilant because they face more competition (Blanchard et al., 2008).

Individual personality or temperament can also influence spatial patterns. “Shy” sheep grazed closer to their nearest neighbours than “bold” sheep (Sibbald, Erhard, McLeod, & Hooper, 2009). If temperament is heritable, then different groups of relatives, such as gelada OMUs, might have different spacing patterns.

1.7 Spatial Patterns in Selected Primates

1.7.1 Capuchin Monkeys (*Cebus* spp.).

Robinson (1981) studied a group of wedge-capped capuchin monkeys (*C. nigrivittatus*), which included a dominant male, 6-8 adult females, 2 young adult males, plus infants and juveniles. The group geometry of these capuchins was usually roughly circular, with similar width and length. Different individuals and demographic classes typically occupied certain positions within the group, although positions varied considerably. The dominant male and female tended to occupy the center front positions, while the other females were farther to the sides. The young adult and juvenile males tended to be at the front, and the juvenile females were at the rear.

Dominant white-faced capuchins (*C. capucinus*) occupied the desirable center front positions, while subordinates tended to take more peripheral positions in order to avoid the dominant animals (Hall & Fedigan, 1997). The amount of aggression an individual brown capuchin (*C. apella*) received predicted its spatial position within the group: monkeys that received more aggression were more likely to be on the edge of the group, and towards the rear (Janson, 1990). Brown capuchins foraging on the front periphery have a greater chance of discovering food, and a larger distance from its nearest neighbour is associated with a larger share for the first monkey to find the food (di Bitetti & Janson, 2001). The desirability of the center front position results from two factors: predation risk, which is higher at the edges and lower at the center of the group, and food, which is usually more abundant at the front of the group and becomes increasingly depleted towards the back (Hall & Fedigan, 1997). Dominant animals foraging behind the front periphery may benefit by allowing animals ahead of them to find food, and then displacing them from it (di Bitetti & Janson, 2001).

1.7.2 Woolly Monkeys.

In lowland woolly monkeys (*Lagothrix lagotricha poeppigii*), another New World primate, two social groups showed different spatial patterns (Schmitt & Di Fiore, 2015). In the larger group (n=26 individuals), adult males were found more often at the edge of the group, while juveniles were more often found at the center. In a smaller group (n=15) at the same site, there was no difference in demographic categories' probability of being on the edge. The larger group occupied a larger area, while individuals' distances to their nearest neighbours did not vary between the two groups.

1.7.3 Vervet Monkeys.

In Kenya, higher ranking female vervet monkeys (*Cercopithecus aethiops*) spent less time moving than did lower ranking females, while high ranking males moved more than low ranking males (Isbell & Young, 1993). Older and more dominant monkeys were more likely to initiate troop progressions (Struhsaker, 1967).

Larger groups of vervet monkeys enjoyed larger and higher quality territories, due to their ability to outcompete smaller groups (Cheney & Seyfarth, 1987). Members of larger groups spent more time in vigilance than those in smaller groups (Isbell & Young, 1993).

In South Africa, vervet monkeys (*Chlorocebus pygerthrus*) who were socially well-connected were more likely to occupy central positions where they were less exposed to predation (Josephs, 2015). At another site, males were found at the periphery or high in the canopy, more often than females (Baldellou & Henzi, 1992).

1.7.4 Macaques.

All macaque (*Macaca* spp.) species live in multi-male multi-female troops, in which females are philopatric while males disperse (Thierry, 2007). There is considerable variation in aggressiveness, with some species having steep dominance hierarchies, while others are more egalitarian.

Inter individual distances in Japanese macaques (*M. fuscata*) varied depending on behaviour: monkeys were farther apart when moving, closer together when resting or grooming, and intermediate distances apart when foraging (Sugiura, Shimooka, & Tsuji, 2011). Japanese macaques adjust their position relative to close neighbours, tending to prefer an intermediate number of neighbours within 20 m (Sugiura, Shimooka, & Tsuji, 2014). Male-female inter-individual distances were larger than female-female inter-individual distances (Otani, Sawada, & Hanya, 2014). Moor macaques (*M. maurus*) tended to be closer to their matrilineal relatives than to non-relatives when they were moving or resting/grooming, but not when they were foraging (Matsumura & Okamoto, 1997).

Japanese macaques sometimes form subgroups, especially in summer (Sugiura et al., 2011). Males regularly forage separately, more than 100 m from other group members, and low-ranking males are more often separate than dominant ones (Otani et al., 2014). Siberut macaques (*M. siberu*) did not form subgroups, and an individual’s position within the group was unrelated to its age-sex class (Richter, Gras, Hodges, & Ostner, 2015). This population may be free to spread out because they live on an island where predators are absent.

Among female long-tailed macaques (*M. fascicularis*), more dominant animals tended to be nearer to the front of the group, especially during travel, while females with clinging infants tended to be farther behind (van Noordwijk & van Schaik, 1987). Higher ranking females were more often in the safer central positions, while low ranking females were more often peripheral or in small subgroups while foraging (van Noordwijk & van Schaik, 1987). High ranking Japanese macaques were also more likely to initiate collective movements (Jacobs, Watanabe, & Petit, 2011)

1.7.5 Baboons.

Baboons (*Papio* spp.) are the sister taxon of the gelada, having a common ancestor between 7-3.5 million years ago (Jablonski, 2005). Like geladas, baboons are large, mostly terrestrial, cercopithecine monkeys. Most baboon species live in multi-male multi-female troops (Barrett & Henzi, 2008). The hamadryas baboon (*P. hamadryas*) lives in a multilevel society consisting of one-male multi-female groups that associate into higher levels such as bands and clans (Kummer, 1968; Schreier & Swedell, 2012b).

During troop progressions, yellow baboons (*P. cynocephalus*) usually proceeded in a random order, although there was some evidence that adult males were overrepresented at the front and rear during potentially dangerous situations (Altmann, 1979). Baboons tend to travel in a long file formation, and forage in a wide rank formation (Altmann, 1974). When the troop was moving, male yellow baboons were at the front more often than females, and higher ranking females were at the front more often than lower ranking females (Collins, 1984). Behaviour affects the spatial distribution of baboons within their troop. Yellow baboons had fewer neighbours within

25 m when moving than when stationary (Collins, 1984). In a desert population of chacma baboons, males were farther from other troop members than females, and separation increased for both sexes when the baboons spent more time in foraging habitat (Cowlishaw, 1999).

Busse (1984) found that chacma baboon females were more central when they were higher ranking or had dependent infants, while males were more central when they had been with the troop for a longer time. Similarly, in yellow baboons, higher ranking females and mothers with young infants were more central, and had more neighbours within 25 m, while pregnant females were more peripheral (Collins, 1984). Olive baboons (*P. anubis*) actively competed for central positions within the troop, and individuals that were more often in the center had higher levels of stress hormones (Tkaczynski et al., 2014). Among female chacma baboons, aggressive competition for a position close to other adult baboons was much more frequent than competition for food, and low ranking females faced a greater risk of predation than high ranking females (Ron, Henzi, & Motro, 1996).

Hamadryas baboons (*P. hamadryas*) deserves special mention here because their multilevel social system is unlike that of the other baboons, and somewhat similar to geladas. The smallest level of hamadryas baboon social organization is the one male unit (OMU), including an adult male and 1-9 females, and sometimes an additional young adult or young adult follower male (Kummer, 1968). Clans are groups of several associated OMUs, plus some solitary bachelor males, and bands are associations of two or more clans, totaling around 60 animals (Kummer, 1984). Hamadryas troops are defined as all the baboons that share a sleeping cliff; this may be hundreds of baboons in several bands.

Unlike gelada males, hamadryas males take over individual females, rather than entire OMUs, leading to female dispersal (Swedell, Saunders, Schreier, & Davis, 2011). Some hamadryas males begin their OMUs with a juvenile female, who can be as young as one year old (Kummer, 1968), (Pines, Saunders, & Swedell, 2011). Hamadryas OMUs are held together by the leader male's aggressive herding of his females, which causes the females to follow the leader male (Kummer, 1984).

Spatially, the hamadryas male is in front of his females while moving, and in the center while stationary (Kummer, 1968). Sometimes two OMUs will associate closely, with the two leader males occupying the front and rear positions during travel (Kummer, 1968). Bands are more likely to split up and forage as separate OMUs in habitats where food is less abundant, and more likely to stay together when a predator was heard the previous night (Schreier & Swedell, 2012a).

Young adult hamadryas males who have yet to acquire any females have two options: they can either be solitary, or they can join an OMU as a follower. Follower males are tolerated by the leader male, and are actually beneficial to the leader. Leader males that had a follower had longer tenures, controlled more females, and sired three times as many infants as leaders without a follower male (Chowdhury, Pines, Saunders, & Swedell, 2015). Follower males have a greater chance of taking over the females from their OMU, and they may gain inclusive fitness benefits if they are closely related to the leader (Pines et al., 2011).

A population of chacma baboons (*P. ursinus*) in South Africa's Drakensberg Mountains contained small groups similar to the OMUs found in hamadryas baboons (Byrne, Whiten, & Henzi, 1990). Food sources are dispersed for this population, so there is little contest competition and no need for females to form coalitions for agonistic support (Henzi, Lycett, & Weingrill, 1997). This lack of incentive for female philopatry, combined with the low risk of predation, allows the baboons to live in smaller groups (Barton, Byrne, & Whiten, 1996).

Guinea baboons (*P. papio*) have a highly variable social structure, different from both hamadryas and savanna baboons (Patzelt et al., 2011). A captive group formed groups similar to OMUs, but with some social interaction occurring between groups (Maestripieri, Mayhew, Carlson, Hoffman, & Radtke, 2006), and genetic analysis shows that males are the more philopatric sex, as in hamadryas baboons (Kopp, Fischer, Patzelt, Roos, & Zinner, 2015).

1.7.6 Geladas.

The gelada OMU is the main social unit as well as the reproductive unit (Dunbar & Dunbar, 1975). Bonds between related females hold the OMU together, and these relationships are stable over time (Dunbar, 1979). Grooming occurs only with other members of the same OMU; most grooming occurs within dyads who are typically a mother and daughter (Dunbar, 1984).

Although they are socially separate, gelada OMUs often overlap spatially, to the point that an observer cannot immediately determine where one OMU ends and the next begins (Crook, 1966). Snyder-Mackler, Beehner, and Bergman (2012) found that a leader male typically had at least one animal from outside the OMU, as close as the majority of his own females. Males rarely herd females, and female geladas may often range 50 m or more from their leader males while foraging without any response from the male (Dunbar & Dunbar, 1975). Sometimes females from one OMU will drive off another female who gets too close, and both leader males are likely to support their respective females (Dunbar & Dunbar, 1975).

Infants and juveniles will play with others outside their OMU (Crook, 1966). As juveniles become older, they may spend most of the day in juvenile groups, foraging and grooming together as well as playing, and larger male juveniles may associate with an all-male bachelor group (Dunbar & Dunbar, 1975). Young adult males leave their natal OMUs and either join a bachelor group or join another OMU as a follower male (Dunbar, 1984). All-male groups are usually associated with one band, although they may spend time with other bands, and membership is consistent (Crook, 1966; Dunbar & Dunbar, 1975).

Leader males are usually tolerant of other leader males, in contrast to the vigilance they show towards bachelor males (Bergman, 2010). Leader males from different OMUs sometimes acted collectively to drive away bachelor males (Pappano et al., 2012). Such cooperation also occurred in snub-nosed monkeys, another primate with a multilevel social system (Zuo-Fu et al., 2014). In geladas, spacing both between and within OMUs becomes smaller when bachelor males are near (Pappano et al., 2012).

Teams of two closely related units are likely the result of recent fission of one large unit, and bands may result from repeated fission over a long period of time (Dunbar, 1984). OMUs associate preferentially with certain other OMUs, and are more likely than chance to have particular other units as their nearest neighbours (Dunbar & Dunbar, 1975). Some pairs of units were found together much more often than others, and some bands were found in mixed band herds more often than others (Kawai et al., 1983). The time spent together by different OMUs was related to female genetic relatedness (Archie, Snyder-Mackler, Alberts, & Bergman, 2014).

(Kawai & Mori, 1979) studied inter individual distances and group cohesion within six gelada OMUs. They found that the mean inter individual distance among the adult members of an OMU was 8.8 m, or 7.7 m if follower males were excluded. Inter individual distances between females and other females, or between females and leader males were usually short. Distances from leader males to females were within 0-8 m 75.3 % of the time, and within 0-16 m 89.9 % of the time. Follower males were farther from the females than leader males were: distances from followers to females were 0-8 m 54.5 % of the time, and 0-16 m 74.1 % of the time. Juveniles were more than 60 m from adult members of their OMU about 60 % of the time. Geladas were closer together when their OMU was alone, than when they were in a herd with other OMUs. When a single OMU foraged alone, it stayed very close to the cliff, suggesting that large herds afford some protection against predation.

Spacing behaviour in geladas may also be affected by the presence of bachelor males, who could be considered social “predators” (Pappano et al., 2012). The same selfish herd grouping behaviours that protect animals against predators could also be protective against the threat of takeovers and potential infanticide by bachelor males. Individuals within OMUs moved closer together, and OMUs moved closer to other OMUs, when bachelor males were nearby (Pappano et al., 2012).

Much of the previous research on geladas has been conducted at sites in the Simien Mountains National Park, which experiences considerable pressure from surrounding human populations, especially overgrazing by livestock (African Wildlife Foundation & Ethiopian Wildlife Conservation Authority, 2015). Guassa is more ecologically intact, its tall-grass Afroalpine ecosystem having been preserved for centuries by the local community (Ashenafi & Leader-Williams, 2005). The diverse vegetation at Guassa is more representative of geladas' historical habitat, and the Guassa gelada population consumes a more varied diet than other populations in degraded habitats (Fashing, Nguyen, Venkataraman, & Kerby, 2014).

Chapter 2: Methods

2.1 The Study animal

Gelada monkeys (*Theropithecus gelada*) are large cercopithecine primates endemic to Ethiopia. They are the most terrestrial primate species, and rarely climb trees (Dunbar, 1984). Geladas have coats in various shades of brown, with darker fur on the limbs. The face is dark and hairless and the muzzle is shorter than in baboons (Ankel-Simons, 2000). Geladas are sexually dimorphic: females weigh about 11 kg and males weigh about 18.5 kg (C. J. Jolly, 2007). In addition to being larger, males can be distinguished from females by their larger canine teeth and manes or capes of long, dark hair on the back, shoulders, and head.

One of the gelada's most striking features is the hourglass-shaped patch of bare skin on the chest. In males, the colour of the patch signals male quality: leader males have redder chests than follower or bachelor males, and leader males with larger units have redder chests than those with smaller units (Bergman, Ho, & Beehner, 2009). This colouration can change dramatically in a few days, becoming paler when a leader male is replaced, or brighter when a male becomes a leader (Dunbar & Dunbar, 1975).

In females, the chest patch changes over the course of the reproductive cycle. During estrus, a "necklace" of raised beads or vesicles appears around the edge of the bare skin (Figure 2.1) (R. I. M. Dunbar & E. P. Dunbar, 1974b). Similar estrus beads may also appear on the bare paracallosal skin (above the ischial callosity), and on the lower abdomen.

Figure 2.1 Estrus beads are visible on the female on the right, but not on the female next to her.

2.1.1 Evolution and Range.

Theropithecus gelada is the sole surviving species of a formerly diverse genus (Jablonski, 2005). Its closest living relatives are the baboons (*Papio* spp.), with which they shared a common ancestor some 7-3.5 million years ago (Jablonski, 2005). Geladas have been known to hybridize with *Papio hamadryas* and *P. anubis* in captivity (C. Jolly, Woolley-Barker, Beyene, Disotell, & Phillips-Conroy, 1997; Markarjan, Isakov, & Kondakov, 1974) and possibly with *P. anubis* in the wild (R. I. M. Dunbar & E. P. Dunbar, 1974a).

Several subspecies of geladas are known. The geladas in the northern parts of Ethiopia (including the Simien Mountains National Park) are *Theropithecus gelada gelada*, while those found further south (from 9-12˚ north latitude, which includes

Guassa), are *T. g. obscurus* (Gippoliti, 2010). The most recently discovered population is south of the Great Rift Valley, in the Arsi highlands of the Bale region (A. Mori & Belay, 1990). These geladas are smaller and more golden in colour than those north of the valley, and are restricted to the cliff faces because humans have cultivated the grasslands of the plateau (A. Mori & Belay, 1990).

Geladas are endemic to Ethiopia and are found in the grasslands of the central plateaus between 1800 – 4400 m above sea level (Gippoliti & Hunter, 2008). Their range is limited by the availability of steep cliffs and gorges that serve as sleeping sites, and geladas seldom venture more than a few kilometers from these cliffs (Crook, 1966). The plateaus are dissected by deep gorges and rivers, making the geladas' habitat more heterogeneous than it might appear, and perhaps affecting the population structure (Gippoliti, 2010). Populations on isolated mountains showed differences in colouration (Crook, 1966).

2.1.2 Ecology, Habitat, and Diet.

Geladas are the only primate species to feed primarily on graminoid vegetation (grasses and sedges); they have evolved to cope with the low nutritional value of these plants (Dunbar, 1984). Geladas have a number of adaptations that allow them to thrive in their rather unique niche. Their hands are adapted for manual grazing, with highly opposable thumbs and a precise grip (Figure 2.2). Their elongated thumb and shortened index finger enable them to pluck individual blades of grass (Krentz, 1993). In this way, geladas can select only the highest quality green grass blades, in contrast to ungulates that harvest grass less precisely with their incisors (Iwamoto, 1993).

One challenge faced by folivorous animals is that most of the nutrients present in plant leaves are locked up behind the cellulose walls of plant cells. Large molars enable geladas to chew tough grasses into fine particles, damaging the cell walls so that nutrients can be absorbed more efficiently (Dunbar & Bose, 1991), (Venkataraman et al., 2014). Geladas also have some degree of hindgut fermentation, in which specialized bacteria break down cellulose, probably in the colon (Mau, Johann, Sliwa, Hummel, & Südekum, 2011). As a consequence of these specializations, gelada biomass is more than twice that of anubis baboons or vervet monkeys (459, 206, and 201 kg/km2 respectively) in the same environment (R. I. M. Dunbar & E. P. Dunbar, 1974).

To meet their nutritional needs on a relatively poor diet, geladas must spend a great deal of time foraging, especially at higher altitudes, ranging from 35.7 % of activity budget at 2300 m to 62.3 % at 3900 m (Iwamoto & Dunbar, 1983).

The Guassa gelada population feeds primarily on graminoids (56.8 % of the diet consists of various graminoid parts) but also consumes forbs (37.8 %), invertebrates (2.8 %) and other items (2.6 %) (Fashing et al., 2014). The better-known gelada population in the Simien Mountains National Park is even more dependent on grass (75.3 % to 97.3 % of feeding time spent eating grass), but the diet of this population has not been studied across the entire annual cycle (Iwamoto & Dunbar, 1983).

Figure 2.2 Manual grazing: Geladas spend a great deal of time in this upright position, either sitting or slowly shuffling forward without rising to the quadrupedal walking position. The highly opposable thumb and forefinger are used to pluck individual grass blades.

2.1.3 Social System.

Most cercopithecine primates live in cohesive social groups. Geladas can be found in unusually large herds that may contain up to 1000 individuals. Gelada have a four-tiered social organization that incorporates one-male units, teams, bands, and communities (Archie et al., 2014; Kawai et al., 1983).

The smallest social level is the one male unit (OMU) or reproductive unit. These units consist of 1-10 adult females, their infants and juvenile offspring, and a leader male who defends his females against rival males (Dunbar, 1984). About 25 % of OMUs also include one or more follower males (Nowak & Walker, 1999). All grooming occurs between members of the same unit, but units can overlap spatially (Johnson, Snyder-Mackler, Beehner, & Bergman, 2014).

Gelada females typically remain in their natal units, although some young adult females have occasionally been observed to transfer to a different group (Dunbar & Dunbar, 1975). Genetic analysis confirms this pattern; females within a unit are much more related than would be expected by chance, while leader and follower males are no more related to each other or to the females in their unit than to the community overall (Archie et al., 2014).

Bonds between females are strong enough to hold the OMU together after the death of the leader male (Dunbar & Dunbar, 1975). Females focus most of their grooming time on a single, closely-related, grooming partner, and rarely groom with any female who is not a close relative: mother, daughter, or sister (Dunbar, 1983a). The females within each OMU have a linear dominance hierarchy (Dunbar & Dunbar, 1977), (le Roux, Beehner, & Bergman, 2011). Female rank is inherited, with daughters ranking immediately below their mothers (le Roux et al., 2011). The leader male usually has one or two females that he grooms with much more than with the other females (Dunbar, 1983b). Unlike hamadryas baboons, gelada males rarely herd their females (Dunbar, 1983b).

Followers may be former leader males who were defeated by a rival and lost their dominant position, or else they may be young adults who are waiting for their chance to take over the leader male role. Follower males are tolerated by the leader male, and they may help the leader male to defend the unit against takeovers by other males outside the unit. Leader males have been found to have longer tenure as the leader when a follower male is present, and some follower males father offspring within the unit (Snyder-Mackler, Alberts, & Bergman, 2012).

The second level is the team, two units that have a close association. Teams may result from fission of a unit that became too large (Kawai et al., 1983). Only about one third of units belong to a team, so this level is optional (Archie et al., 2014).

The third level is the band, a group of units that are often, although not always, found together in the same herd. Units within the same band are found together in the same herd about 50 % of the time (Snyder-Mackler, Beehner, et al., 2012). Units within the same band share a core range where they spend most of their time, and so the band can be considered the ecological unit, similar to the multi-male multi-female troops found in many other primate species (Dunbar, 1984; Kawai et al., 1983).

The highest level, the community, includes the entire population that may interact over several years (Snyder-Mackler, Beehner, et al., 2012). Individual units can be readily identified because all members of a unit are always together, but identification of the higher levels of social organization is not obvious and requires long-term observation (Snyder-Mackler, Beehner, et al., 2012). Across all these levels of society, female members of units, teams, and bands that spent more time together, were found to be more closely related in a genetic analysis (Archie et al., 2014).

Given this multi-level structure, the herd therefore simply refers to a group of geladas found together at a given time and may include units from different bands, and need not include all members of any given band (Kawai et al., 1983). Herds usually contain several hundred individuals (Crook, 1966), (Dunbar, 1984). Geladas are tolerant of unfamiliar conspecifics (Bergman, 2010). The male's red chest patch may serve as a signal of condition or quality, allowing females and/or rival males to assess the fitness of a male they do not recognize as an individual (Bergman et al., 2009). The grass which geladas eat is both abundant and widely distributed, so there is no reason for geladas to defend territories (Willems & van Schaik, 2015).

2.1.4 Conservation Status.

Geladas are categorized by the IUCN as being of ‘Least Concern’ (Gippoliti & Hunter, 2008), although they face pressure from an increasing human population as well as from climate change. The Ethiopian highlands are densely populated and most of the land is under cultivation. Ethiopia’s human population is increasing rapidly and most people live as subsistence farmers. Only about 3 % of the original Afroalpine grassland ecosystem remains (Williams, Pol, Spawls, Shimelis, & Kelbessa, 2005).

Geladas occasionally come into conflict with famers over crop raiding. In the Simien Mountains, 47 % of households near the park reported serious damage to their barley crops, losing an average of 117 kg of grain per household (Yihune, Bekele, & Tefera, 2009). At Guassa, geladas were observed feeding on barley, the area’s main staple crop. They appeared to be eating the seeds of the ripe grain around the harvest time (observers did not follow the animals to fields in order to avoid conflict with the crop owners, so detailed observations were not possible). None of the data used in this study was collected while the geladas were feeding on crops.

Despite some conflict, many Ethiopians living near protected areas do value wildlife for various cultural reasons, as well as for tangible benefits such as jobs, infrastructure, and tourism revenues, and about 80 % believe that humans and wildlife can coexist (Tessema, Lilieholm, Ashenafi, & Leader-Williams, 2010). However, crop raiding does have a negative effect on both the farmers’ livelihoods and their attitudes to wildlife: about 15 % of farmers near the Simien Mountains National Park wanted the government to kill all the geladas (Yihune et al., 2009). At Guassa, an ecotourism initiative aims to promote conservation of wildlife and habitat, while bringing income into the local communities (Guassa Community Conservation Area; United Nations Development Programme, 2012).

Geladas were formerly hunted in some areas for the males' impressive manes, which the Oromo people used to make ceremonial clothing, but this no longer happens (Gippoliti & Hunter, 2008). Historically, in certain areas selective hunting of adult males affected sex ratios and led to larger OMUs and even some OMUs with young adult leader males (Crook, 1966).

Climate change is also a threat to Afro-alpine ecosystems. Geladas live in cool, wet climates that are found in the highlands at tropical latitudes. They are currently found at elevations ranging from roughly 1700 – 4200 m (Dunbar, 1998). The productivity of vegetation is affected by temperature, which is in turn affected by altitude: high temperatures lead to desiccation of the grass in the dry season, while very low temperatures reduce growth rates (Sinha, 2004). Geladas prefer to consume green grass, which is more nutritious, rather than dry grass (Iwamoto, 1993). When the productivity of the grass is too low, grazing animals such as geladas must travel farther each day, and spend more time foraging (Dunbar, 1992a). Since the monkeys have a limited amount of time available, they are only able to survive at elevations where there is sufficient grass to meet their nutritional requirements in the time available (Dunbar, 1992a).

Anthropogenic climate change has resulted in changes to the distributions of numerous species, with increases in the minimum, maximum, and mean latitude and/or altitude where those species are found (Newman, Anand, Henry, Hunt, & Gedalof, 2011). The ranges of many plant species in the Ethiopian highlands are expected to decrease in size and move to higher altitudes (Mekasha, Nigatu, Tesfaye, & Duncan, 2013). Climate change could result in geladas being restricted to small areas at the peaks, reducing the population and putting the species at risk of extinction (Dunbar, 1998).

2.2 About the Site

Research was conducted at the Menz-Guassa Community Conservation Area in the central highlands of Ethiopia. The site is in the North Shewa zone of Amhara Regional State, 265 km northeast of Addis Ababa (Ashenafi, Leader-Williams, & Coulson, 2012). The site is located on the Guassa Plateau at the edge of the Great Rift Valley and has an Afroalpine tall-grass ecosystem (Fashing, Nguyen, & Fashing, 2010). Some parts of the valley edge consist of sheer cliffs that serve as sleeping sites and refuges for the geladas.

Guassa is one of the largest intact areas of Afroalpine tall-grass habitat remaining, at 111 km2 (Fashing et al., 2014). The dominant vegetation communities include *Festuca* grassland, *Euryops-Festuca* grassland, *Helichrysum-Festuca* grassland, *Euryops-Alchemilla* shrubland, and Erica heathland (Ashenafi, Coulson, Sillero-Zubiri, & Leader-Williams, 2005). The three most abundant plant species are *Festuca macrophylla*, *Thymus schimperi*, and *Alchemilla abyssinica* (Fashing et al., 2014). Another notable plant species is the giant lobelia (*Lobelia rynchopetalum*) (Fashing et al., 2014). Some photos of the geladas' habitat at Guassa are presented in Figure 2.3.

Figure 2.3 Gelada habitat at Guassa. Top left: short grass grazed by livestock, with cultivated fields visible in the background. Top right: long grass and shrubs, with giant lobelia. Bottom right: long grass with few shrubs. Bottom left: dry hilltop with grass, shrubs, and bare rock

The Ethiopian highlands are home to a number of mammal species. Besides geladas, the fauna at Guassa includes duikers, klipspringers, and hares. A variety of rodent species are present (Ashenafi et al., 2012). The Ethiopian wolf is endemic to Ethiopia and is listed as Endangered by the IUCN (Marino & Sillero-Zubiri, 2013). The wolves' diet consists mainly of rodents, but they occasionally take larger prey including sheep, antelope, and hares (Sillero-Zubiri & Gottelli, 1995). Ethiopian wolves commonly forage among grazing geladas, and the approach of a wolf seldom causes geladas to flee (Venkataraman, Kerby, Nguyen, & Ashenafi, 2015). The wolves experience increased foraging success when they are among geladas, possibly because the monkeys flush out rodents, or because the monkeys (which are harmless to rodents) impede the rodents' ability to detect the wolves (Venkataraman et al., 2015). Other carnivores also found at Guassa include spotted hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*), and servals (*Leptailurus serval*), as well as the African Wolf (*Canis aureus lupaster*) (Fashing et al., 2014), (Rueness et al., 2011).

Another interesting species found in this ecosystem is the tapeworm *Taenia serialis*, whose indeterminate (immature) life stage causes cysts or coenuri on geladas (Nguyen et al., 2015), (Schneider-Crease, Snyder-Mackler, Jarvey, & Bergman, 2013). Almost one third of adult geladas at Guassa suffered from this condition, which resulted in increased mortality and decreased reproductive rates for affected individuals (Nguyen et al., 2015).

Guassa has been managed for over four hundred years under an indigenous common property resource management system called *Qero*, which prohibits the cultivation of crops in the area, and restricts livestock grazing and the harvesting of grass

(*Festuca* spp.) which is used for thatched roofs (Ashenafi & Leader-Williams, 2005). The community management system was designed to preserve the grass for human use, but it has also had the effect of conserving habitat for wildlife (Ashenafi et al., 2012). Community management is still a feature of the area, and in recent years there has been an increasing focus on conservation and the development of ecotourism (United Nations Development Programme, 2012).

The climate of the North Shewa region has three main seasons: a short rainy season from February to May (*Belg*), a long rainy season from July to October (*Kiremt*), and a dry season from October to February (*Bega*) (Rosell, 2011). Guassa receives about 1650 mm of precipitation annually, over half of which falls during the two months of July and August (Fashing et al., 2014). Guassa experiences considerable diurnal variation in temperature, with mild days and cold nights (Ashenafi et al., 2012). Mean monthly high and low temperatures were 17.8 and 4.3˚C respectively (Fashing et al., 2014).

The subjects of this study belonged to the population of wild gelada monkeys that have been studied since December 2005 by Drs Peter Fashing and Nga Nguyen (Fashing et al., 2010). The study animals were members of the Steelers Band, which contains about 220 individuals (Nguyen et al., 2015). The animals were well habituated to human observers and could be approached to within 1-3 m without causing them to change their behaviour in response. The subjects of my study could be recognized individually by natural characteristics (such as facial features, injuries, and parasitic cysts, as well as by their age and size). They were not artificially marked or handled in any way.

2.3 Study Animals

Nine one-male units (OMU) were chosen for study. They ranged in size from 4 to 9 adult and young adult animals, and from 1 to 8 adult and young adult females (Table 1). Juveniles were often not close to their natal unit, instead playing or foraging with juvenile peer groups, where they may spend much of the day (Dunbar & Dunbar, 1975). The intent of the study was to examine spatial patterns in cohesive groups of geladas, within the larger herd, so juveniles were omitted from data collection because they did not always remain in a cohesive group with the rest of the OMU; in addition it would be impractical to locate them during follows when they could potentially be hundreds of meters from the adult members of the OMU. All studied animals were categorized as belonging to one of four demographic classes: adult female (n = 37), young adult female (n = 8), leader male (n = 9), or follower male (n = 5). Females were considered to be adults from the time of their first pregnancy, and young adult from their first observed menstruation until their first pregnancy. All leader males were adults. Young adult males were closer in size to adult males than to adult females, and their manes and canine teeth resembled more closely those of adult males than they did juvenile males (see Subadult stage 2 in (Dunbar & Dunbar, 1975)). Three of the five follower males were young adults (one in R unit and two in G). The other two follower males were older, former leader males (in D and T OMUs) (Nguyen et al., 2015).

The composition of the units is summarized in Table 2.4. None of the studied animals changed from one demographic class to another during the within-group data collection, and none transferred into or out of the studied units. One animal disappeared during this period (an adult female from S group, her infant as well as another infant from the same unit were presumed to have been captured by a predator; the S group therefore had 9 animals for most of the study and only 8 at the end).

Table 2.4 Size and demographic composition of the nine OMUs that were sampled for this study.

OMU	Number of study animals	Adult Females	Follower Males	Young adult females
A	6	5	0	0
D	9	5	1 old	2
G	4	1	2 young adult	0
K	4	3	0	0
L	9	6	0	2
P	4	2	0	1
R	7	3	1 young adult	2
S	9 (8 after one died)	7 (6 after one died)	0	1
T	7	5	1 old	0
Total	59	37	5	8

2.4 Data collection

The data analyzed in this thesis were collected on 64 days over the period 03 Oct 2013 to 28 Jan 2014. Focal follows were done on a single OMU at a time and were 60 min in duration. A total of 171 follows was conducted on the study OMUs (range 11 – 25 follows per unit, mean 9). Follows were distributed across three time blocks: morning (starting before 11:00), noon (starting 11:00 to 13:30), and afternoon (starting after 13:30). An effort was made to collect equal numbers of follows for each OMU and for each time block. Table 2.5 shows how follows were distributed across OMUs and time blocks. The minutes of usable data refers to the time period when interpolation was possible. Interpolated positions could only be calculated when there was a GPS point before and after that time, for every animal in the OMU. This restriction meant that there was a period at the beginning and end of every follow where GPS points existed for only some of the animals, so those periods could not be used. Larger OMUs lost more time during this process because more time was required to locate and identify a larger number of individuals. The following section discusses the interpolation process in more detail.

Table 2.5 Number of follows and minutes of usable data collected for each OMU in each time block

	A (n=6)	D (n=9)	G (n=4)	K (n=4)	L (n=9)	P (n=4)	R (n=7)	S (n= 8/9)	T (n=7)
AM (before 11:00)									
minutes	274	84	345	554	75	195	318	118	498
follows	7	5	7	8	5	3	6	6	9
NOON (11:00 - 13:30)									
minutes	228	49	394	448	87	318	341	244	181
follows	6	5	8	9	6	5	8	6	5
PM (after 13:30)									
minutes	341	61	304	511	87	103	340	169	459
follows	8	8	5	8	4	3	6	6	9

During each follow, I recorded the locations of all adult and young adult members of the focal unit as frequently as possible, constrained by my ability to locate all group members and reach their location. Follows were terminated if the animals became unavailable for at least 15 minutes (on steep terrain such as the sleeping cliff, when travelling too fast for observers to keep up, or when foraging in barley fields on private property where observers were not welcome).

To collect each data point, the GPS receiver was held directly above the animal. As it could take up to ten seconds to acquire a reliable reading, points reflect the animal's position at the beginning of the 10 seconds and were not changed if the animal happened to move away during that time. A high precision GPS receiver (MobileMapper 120 from Spectra Precision), with sub-meter accuracy (Spectra Precision, 2013) was used to minimize spatial error.

After an initial habituation period (3-4 weeks; data points collected during habituation were not used in any analysis), most animals did not react to the GPS data collection by flinching, looking at the observer, or moving away. There were a few exceptions, and the procedure was modified to avoid disturbing the less habituated animals. Often it was possible to take a point behind an animal just after it moved away (taking care not to cause it to move away). This worked well during travel or when animals moved a few meters between feeding sites. These points were taken less than ten seconds after the animal left the location. When it was not feasible to take a point above the animal or behind it, the point could be offset by 1-4 m (usually 1 or 2 m). Distance was estimated visually and the bearing from the GPS point to the animal was measured using a magnetic compass. Offsets were also occasionally used for other animals that were close to a timid subject, or when steep terrain made it difficult to get close to the monkeys.

Along with the spatial coordinates, each GPS point included the date and time, the ID of the individual monkey, and its behaviour.

2.5 Projection and Interpolation

The GPS points collected in the field could not be used directly in the analysis. Some processing was required to obtain ‘snapshots’, simultaneous estimates of the position of every animal in a particular OMU at a particular time. Figure 2.6 shows an overview of the process used to generate the snapshots, and further details are given below.

The first step in the process was to convert the coordinates of the GPS points from decimal degrees to UTM (UTM zone 37 N, WGS 1984) using the Project Tool in ArcMap (ESRI, 2013). The UTM projection has the useful property that its coordinates are in meters, allowing simple calculation of distances between two points. Where points were offset from an animal, I recorded my distance (estimated, usually 1-3 m) and bearing (observed using a magnetic compass) from the animal. The GPS points were corrected in R to move the point in the correct distance and direction.

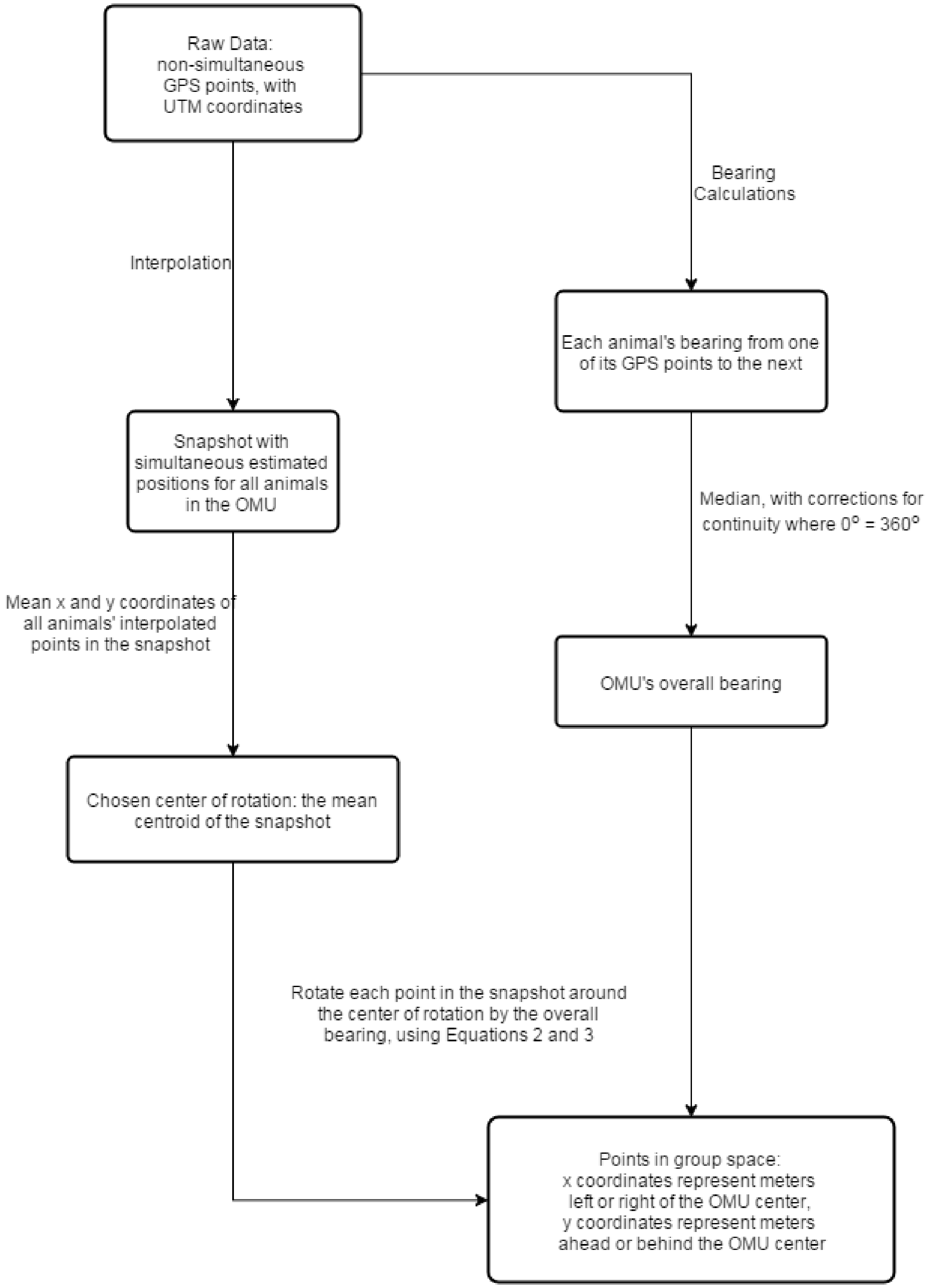

Figure 2.6 Overview of the process used to create snapshots with simultaneous positions for each animal, and to shift the snapshots into a standardized frame of reference. Steps are described below in greater detail.

As GPS points were collected by a single observer, it was not possible to record the positions of individual animals at a single moment. To estimate the position of all animals during a single moment in time, I made use of linear interpolation. This method relies on knowing the position of an animal at two sequential time points, and estimating an animal's position between these points based on straight line travel and a constant speed (Figures 2.7, 2.8, and 2.9). Interpolation was therefore used to create 1 minute "snapshots", each containing simultaneous estimated positions for all the animals in the OMU. The calculations described below were performed in R (R Core Team, 2013).

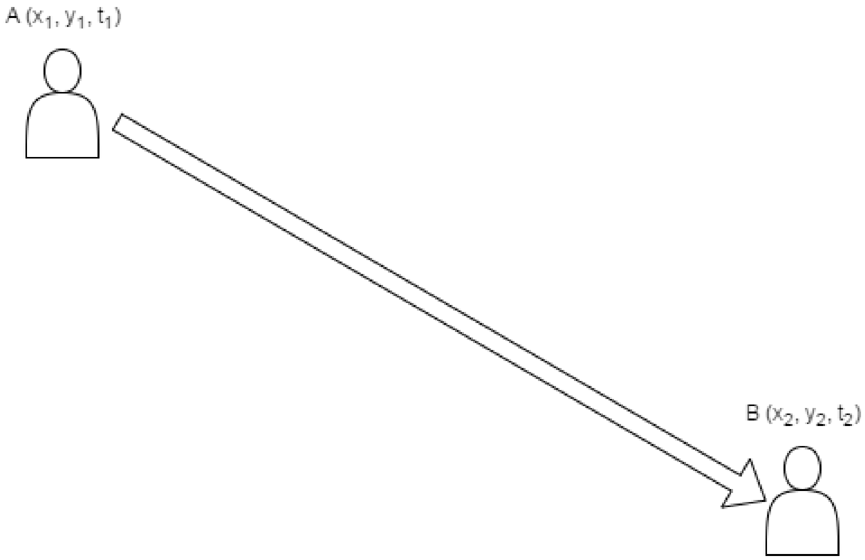

Figure 2.7 The interpolation process: Interpolation requires two GPS points, one before and one after the interpolated time. GPS points include spatial coordinates (in meters east and north, relative to the southwest corner of the UTM zone), and each point also includes the time. The points are marked on this diagram as A and B, with their coordinates (x1, y1, t1) and (x2, y2, t2); these represent the same animal’s positions at two consecutive GPS points. We want to estimate the animal’s spatial position at ti, a time between t1 and t2. The intermediate position was estimated using linear interpolation. Note that the animal’s actual route from A to B is unknown: it could have changed its speed and/or direction during its journey from A to B. Since no data points were recorded between A and B, the interpolation process requires the assumptions that the animal travelled in a straight line from A to B, and that it moved at a constant rate of speed.

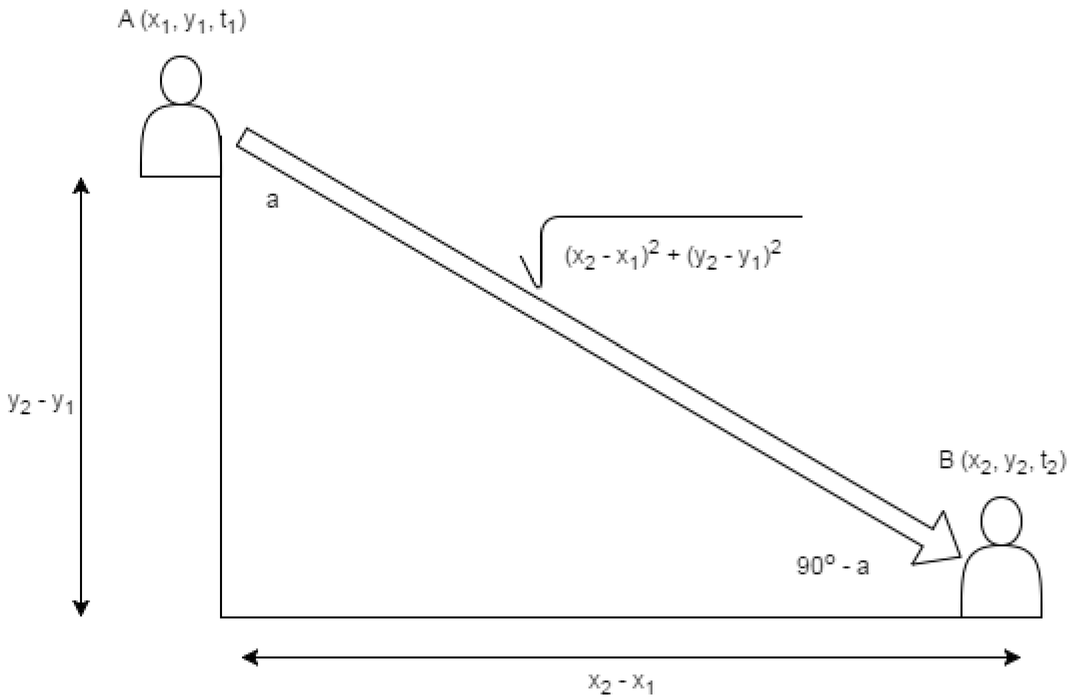

Figure 2.8 The interpolation process continued: Using the x and y coordinates of points A and B, we can create a right triangle. The length of the vertical side is y2 – y1, and the length of the horizontal side is x2 – x1. The length of the hypotenuse is found using the Pythagorean Theorem. The angle a can be calculated using the sine law, now that all the sides and one of the angles are known, ant the third angle must be 90˚ - a. At this point, all the sides and angles of this triangle are known.

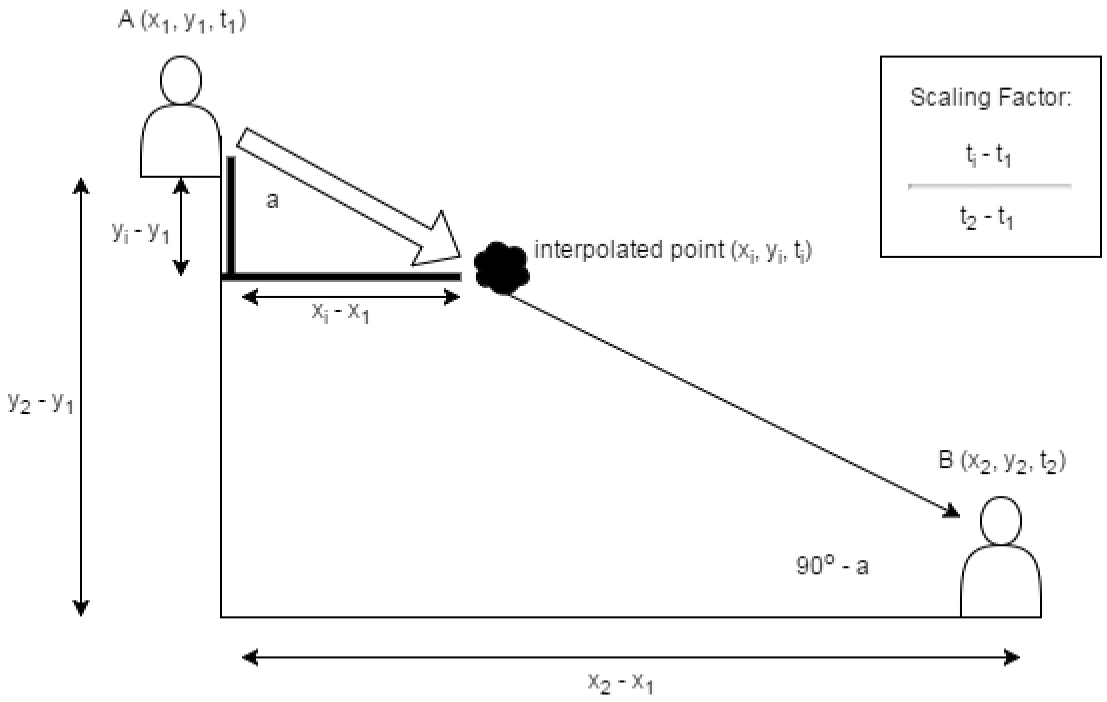

Figure 2.9 The interpolation process continued: Now that all the sides and angles are known, a triangle of the same shape can be constructed in any size, by multiplying the sides by a scaling factor and keeping the angles unchanged. The scaling factor is calculated using the difference in time between the two points. Recall that ti is the interpolated time, which can be any time between t1 and t2. The scaling factor is calculated as the ratio of the time elapsed between the interpolation time and the initial time, divided by the time elapsed between the final time and the initial time. The scaling factor will be between zero and one. The lengths of the horizontal and vertical sides of the triangle are multiplied by the scaling factor, to make a new triangle that is smaller than the first one, but the same shape. For this small triangle, we know the horizontal and vertical sides, and we know the coordinates of the initial point (x1, y1), so we can calculate the x and y coordinates of the interpolated position.

2.5.1 Directions of Travel.

At each snapshot the direction of travel was calculated for each animal and for the OMU overall. For each animal, the bearing was calculated using the same two GPS points that were used for interpolation, as shown in Figure 2.10. Calculations for the bearing are shown in Equation 2.11.

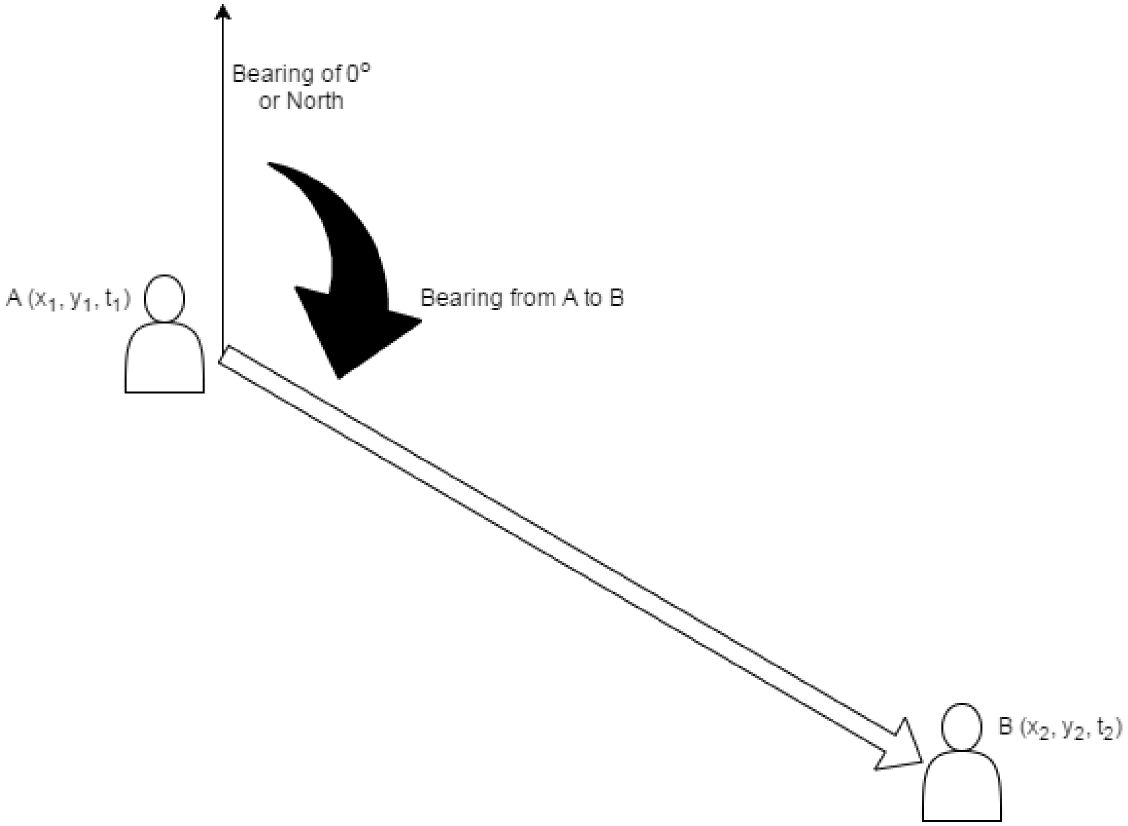

Figure 2.10 Individual travel direction: The animal travelled from its GPS point A to its GPS point B. Its direction of travel was the bearing from A to B.

Equation 2.11 Calculation of travel bearing for individual animal

$$\textit{Bearing from A to B} = 90^{\circ} - \arctan\left(\frac{y_2 - y_1}{x_2 - x_1}\right)$$

Equation 1 gives a bearing between 0˚ and 180˚. The code to calculate bearings included a conditional statement so that if the animal moved in a westerly direction (x2 < x1), 180˚ was added to the bearing, giving values between 0˚ and 360˚. Conditional statements were also used to handle three special cases where Equation 1 would not produce the correct bearing. If the animal moved due north or south (x1 = x2), Equation 1 would require division by zero, so these cases were corrected to either 0˚ (if y2 > y1), or

180˚ (if y2 < y1). Equation 1 would also produce the same result (90˚) whether the animal moved due east or due west (y1 = y2). Cases when the animal moved due west (y1 = y2 and x2 > x1) were corrected by the conditional statement to 270˚, instead of 90˚. The other unusual case was the situation where the animal's GPS point fell exactly at the interpolated time.

The group's overall direction of travel was calculated as the median of all the individual animal bearings in the group at each time point. The median bearing was chosen instead of the mean because it is less susceptible to outliers. In the case where most of the animals moved in roughly the same direction, but one moved in a very different direction, the median is a better reflection of the actions of the majority. Calculating the median bearing of the group presents a problem, as the individual angles are circular in nature and can cause errors in calculating the median if individuals bearings vary across the 0 and 360 degrees line (Figure 2.12). For, example the median of two individuals traveling at 45 degrees and 315 degrees is 180. To solve this problem I identified snapshots which encountered this continuity or wrap-around issue.

Cases that would encounter the continuity problem described in Figure 2.12 could be identified because they had the largest bearing 270˚ or more, and the smallest bearing 90˚ or less. These cases could be fixed as described in Figure 2.13, by converting the bearings from a scale of 0˚ to 360˚, to a scale of -180˚ to +180˚. Using these new values, the median bearing would correctly represent the group's direction. The median group bearing in these cases, was then transformed back to be comparable to the snapshots in which continuity was not an issue. If the group's median bearing resulted in a negative value, 360˚ was added to that value to give a positive bearing that was consistent with the other group bearings.

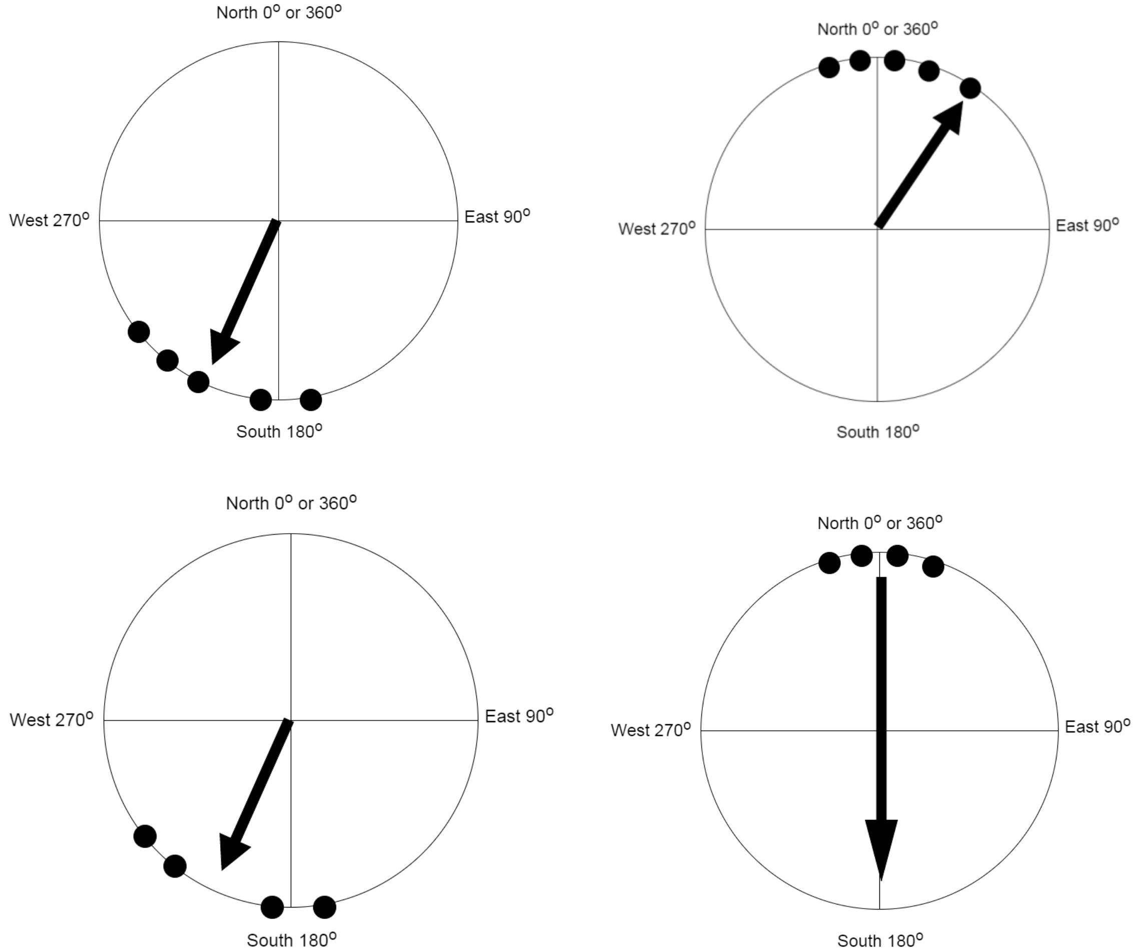

Figure 2.12 Calculating group bearings (arrows) from the individual bearings (black dots): In the two left figures, simply calculating the median of all the individual bearings produces a median group bearing that is a reasonable representation of the group's direction, for groups containing an odd or even number of animals.. In the top right figure, simply calculating the median bearing does not account for the fact that bearings of 0˚ and 360˚ are the same; the bearings include three small values (maybe 5˚ to 35˚) and two large ones (maybe 350˚ and 355˚), and the median is 35˚, not representative of the group's average direction. With an odd number of animals, this problem can become even worse, as in the lower right figure. All animals were moving in a northerly direction, but the median bearing is actually south.

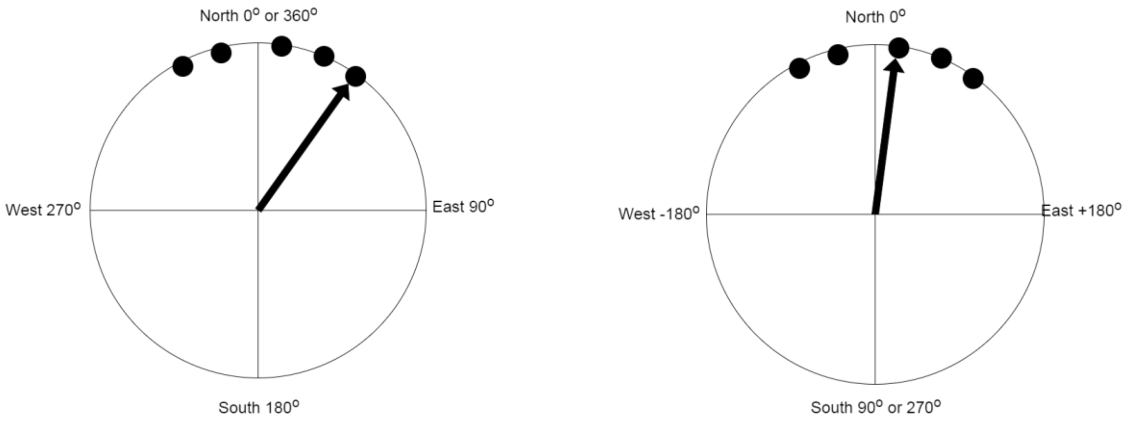

Figure 2.13 Correcting for continuity: When individual animal bearings included values both east and west of north, bearings were converted from a range of 0˚ to 360˚, to a range of -180˚ to +180˚. On the 0˚ to 360˚ scale, the median bearing did not reflect the group's overall bearing (left figure). In the -180˚ to +180˚ scale, the median of all the animal bearings gave a reasonable indication of the group's bearing (right figure). In this example, the median was a positive value, but if the median happened to lie between -180˚ and 0˚, then 360˚ was added to it to give a positive value that was comparable with the other group bearings.

2.5.2 Rotation and Group Space.

The group bearings were used to rotate each snapshot so that the median direction of travel was a bearing of 0˚. Rotation into group space made the different snapshots more comparable, by making the x and y coordinates more meaningful. In the original interpolated points, the x and y coordinates represented each animal's position on the surface of the Earth. In the rotated points, each animal's x-coordinate represented its distance left or right of the mean center of the group, and its y-coordinate represented its position ahead or behind the mean center of the group, with all the directions being relative to the group's direction of travel. The formulae in Equations 2.14 and 2.15 were applied to each animal's interpolated position in each snapshot to rotate the snapshot, as shown in Figure 2.16. These equations preserved animals' relative positions, while changing the frame of reference.

Since the rotation equations involved rotation around a chosen center point. I chose to rotate animal points around the group's center. The center was defined as the point whose x-coordinate was the mean of the individual animals' x-coordinates, and the center's y-coordinate was the mean of the animals' y-coordinates. It should be noted that the choice of the rotation center did not affect any of the five metrics used in the models (for individuals: nearest neighbour distance, median inter-individual distance, and distance ahead or behind the group's median; for OMUs: area and length/width ratio). A different center of rotation could have been used, such as using the median x and y coordinates, or even the origin of the UTM zone, without affecting the results.

Equations 2.14 and 2.15: Rotation of a point. The coordinates of the initial point (x, y) are rotated by the group bearing (angle A) to generate a new point (x', y') that has been rotated around the origin.

$$x' = x\cos(A) - y\sin(A)$$

$$y' = x\sin(A) + y\cos(A)$$

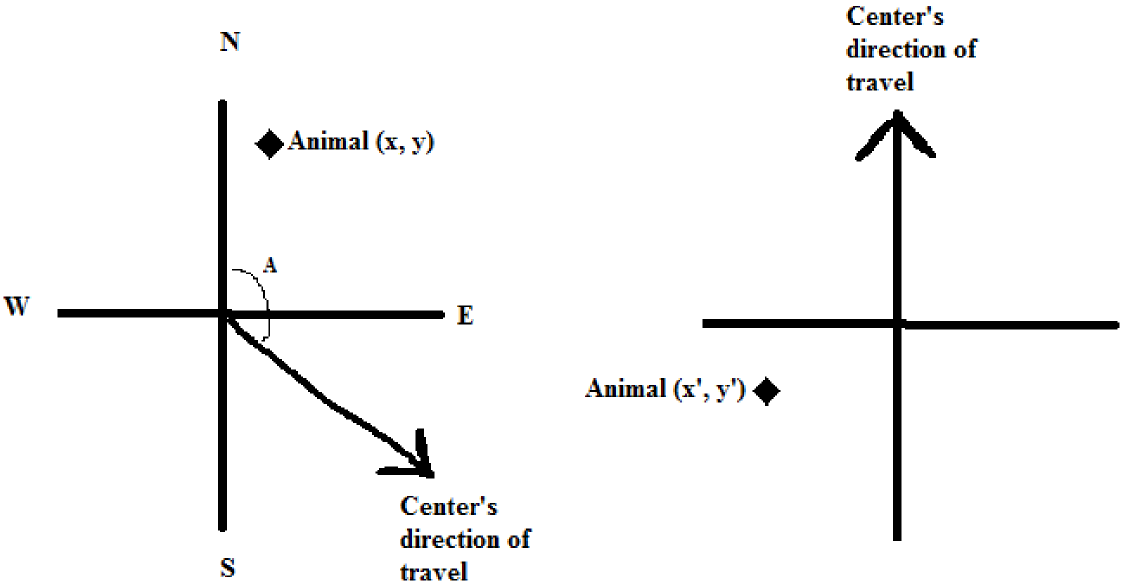

Figure 2.16: Rotation of snapshots: To standardize all animals' positions relative to the OMU, the group bearing of the OMU (angle A) was set as the zero direction and the animals' points were rotated by the angle A. The formulae to rotate the animal’s point (x, y) by the group’s bearing A, to produce the new point (x’, y’), are shown in Equations 2 and 3.

2.6 Autocorrelation and Independence

In order to determine the independence of interpolated points prior to statistical analysis, I estimated the extent of autocorrelation, using the acf function in R, to determine the time intervals at which the animal’s positions could be considered to be independent. The magnitude of autocorrelation was measured within each animal’s trajectory (using the 1-minute interpolated points) during each follow, for three parameters: travel speed, and the animal’s x and y distances from the mean. For each trajectory, the first time point was recorded at which there was no significant autocorrelation (at 95% significance level, calculated as in Equation 2.17).

Equation 2.17: Calculation of after how many minutes there ceased to be significant autocorrelation within an animal’s trajectory. The qnorm function in R returns the quantile of the inverse cumulative distribution function, and is used here to set the desired significance level.

$$\frac{qnorm\left(\frac{1 + 0.95}{2}\right)}{\sqrt{length\ of\ follow\ in\ minutes}}$$

Table 2.18 shows the distribution of the times when autocorrelation disappeared. Less than 1% of locations were significantly autocorrelated after 15 minutes for both speed and position. Statistical analyses were therefore conducted on a subset of the interpolated positions, where subsequent points were separated by 15 min. This generated 2726 points for 59 animals and 453 points for analyses at the level of the group.

Table 2.18 Distribution of times taken for significant autocorrelation to disappear in travel speed, and the animal's x and y coordinates relative to the group center. Intervals of 15 minutes showed no significant autocorrelation in more than 99% of the 943 animal trajectories, for all three variables.

	Median	75th percentile	90th percentile	95th percentile	99th percentile	Maximum
Travel Speed	4	5	8	10	14.6	21
X-Coordinate	4	5	7	8	11.6	16
Y-Coordinate	3	4	5	7	10.6	16

2.7 Models

I constructed five models, using each animal's inter-individual distance, nearest neighbour distance, and position near the front or back of the group, to determine which variables were related to both the area occupied by each OMU and its spatial structure.

The area occupied by each OMU was estimated by the area of the 1 standard deviation directional distribution ellipse around the animals. Some representative ellipses are shown in Figure 2.19. The ellipses were calculated in ArcGIS using the "directional distribution" tool (ESRI, 2013). The tool determines the center of the group of points, using the mean of the points' x and y coordinates. It then calculates the distance of each point from the center, in both the x and y dimensions. The lengths of the two axes of the ellipse are derived from the standard deviations of the x and y distances from the center to the points, and the ellipse is rotated so that its long axis is parallel to the long axis through the group of points. If the points are normally distributed in space, then about 68% of the points will lie within one standard distance of the center (ESRI, 2013).

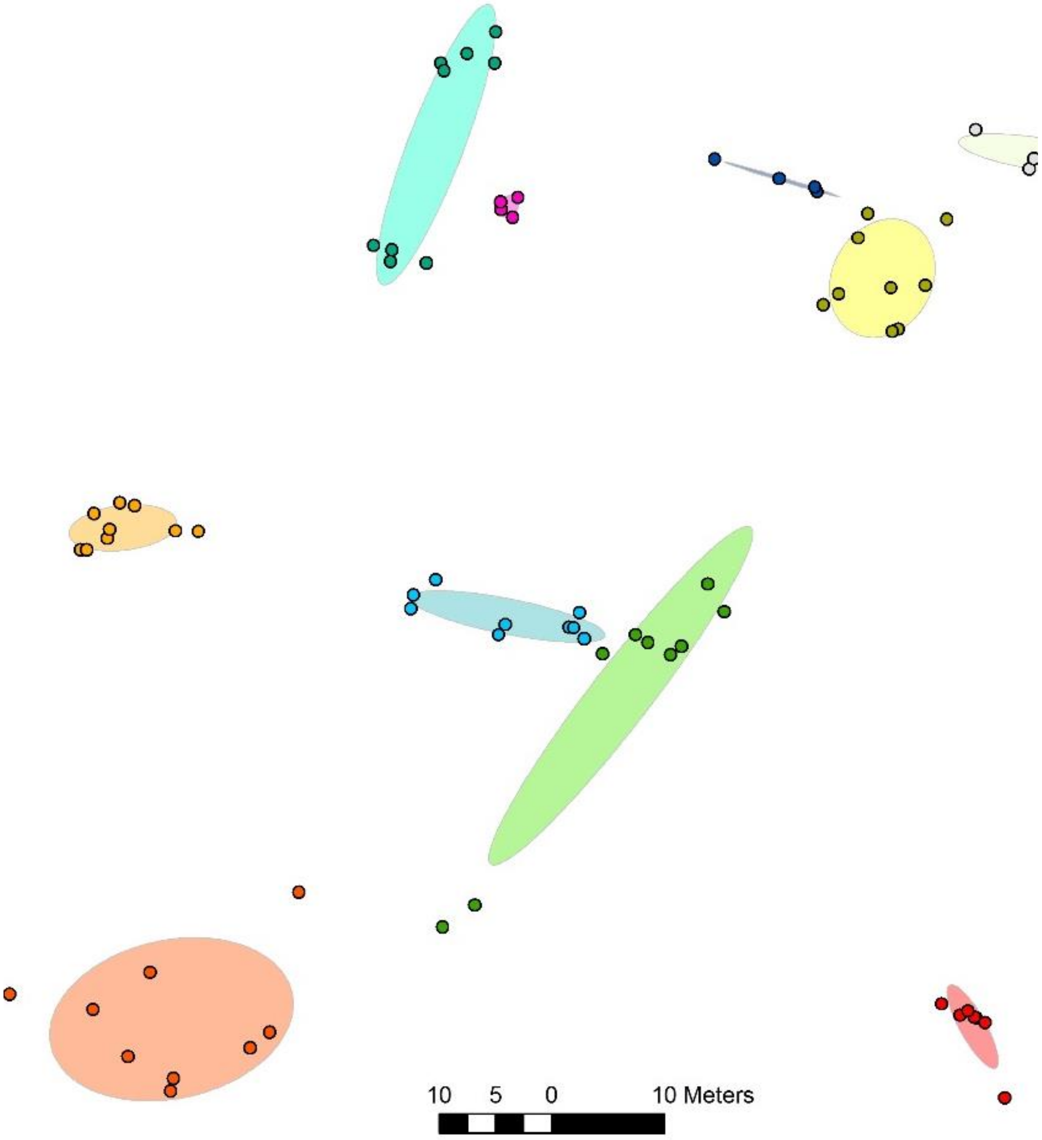

Figure 2.19 Representative standard deviation ellipses around gelada positions. Each colour represents one OMU at a particular time point.

The shape of each OMU was described in terms of the ratio of its length and width. The interpolated positions were rotated so that the direction of travel was parallel to the y-axis, so length was the largest y-value minus the smallest y-value. Width was calculated similarly on the x-axis, which was the axis perpendicular to the direction of travel. Larger ratios of length/width indicated groups that were stretched along the direction of travel. A ratio of 1 indicated a round or square configuration, and a ratio less than 1 indicated that the group's width was greater than its length.

Inter-individual distances (IID) were calculated for each animal at each time. The animal's distance to each of its neighbours was calculated, and the median of these distances was the animal's IID. Nearest neighbour distance (NND) was the distance to the animal's closest neighbour. Distance ahead or behind the group center was derived from each animal's y-coordinate, where the median y-coordinate of group members was set to zero. Positive values indicated that the animal was ahead of the median, while negative values indicated that the animal was behind the median. Lateral distance from the center line was the absolute value of the individual's x-coordinate. Left and right were not differentiated; animals on the far left or right had large distances from the center line, while those close to the center line had small values.

These models included independent variables that described the environment, behaviour of the animals, and attributes of the OMU and the individual animal. Environmental variables included distance from the sleeping cliff, elevation and slope of the terrain, and a vegetation index derived from satellite imagery (NDVI). Environmental variables were only included in the OMU models (area and ratio). Behavioural variables included the proportion of the group that was foraging, and travel speed (the individual's speed in individual models, and the median speed in OMU models). For individual models, the individual's behaviour at its previous GPS point was included in addition to the group's proportion foraging. Attributes of the OMU included size (number of study animals), the presence of a follower male, and the presence of at least one female in estrus. Demographic category (adult female, leader male, young adult female, or follower male) was an attribute of individual monkeys. None of the study animals changed from one class to another during the study period.

2.8 Statistical analysis

The data contained repeated measures of the same individuals, and those individuals were clustered within OMUs, so mixed effects models were used to account for these patterns. The identity of each OMU was included as a random effect in all models. In models of individual IID, NND, and distance ahead/behind, a random effect of individual nested within OMU was included. In some models the random effects were not significant but they were retained anyway to reflect the structure of the data (Barr, Levy, Scheepers, & Tily, 2013). Models were constructed using the lme4 package for R (Bates, Maechler, Bolker, & Walker, 2014).

Some independent variables were categorical with more than two levels, including the demographic category and individual behaviour at the previous GPS point. When the multilevel models showed significant effects for these categorical variables, pairwise comparisons were performed using the glht function with Tukey adjustment of p-values for multiple comparisons, from the “multcomp” package for R (Hothorn, Bretz, & Westfall, 2008). These pairwise comparisons were based on the multilevel model and compared the different levels of the factor to each other, while controlling for the other fixed and random effects in the model.

2.8.1 Individual Behaviour.

At each GPS point, the animal’s behaviour was recorded as foraging, moving, social, or resting. Foraging was any activity related to obtaining or consuming food, including behaviors such as plucking grass blades, chewing, digging for underground items, searching the ground for food, or slowly walking with frequent pauses to pick food. Shuffling in an upright position from one feeding site to the next was also considered foraging. Moving included any movement with a loping or running gait, or walking without foraging. Walking while chewing and/or gathering food was placed into the foraging category. Social behaviour was usually allogrooming, but also included autogrooming when the animal’s attention was directed at the body part being groomed for at least three seconds (a brief scratch while the animal continued to forage did not qualify). Other social interactions with others, including play, sexual behaviour, and aggression, also fell into this category. Resting animals were stationary and relaxed, with eyes closed or gazing into the distance.

Behaviour was not recorded between GPS points, so behaviour at the interpolated points was not known. However, each interpolated point had an associated GPS point that recorded the animal’s behaviour a few minutes before, and these behaviours were used in the models. Individual behaviour was a factor only in the individual models.

2.8.2 Foraging Intensity.

Foraging intensity of the group that was foraging was defined as the number of animals foraging at their GPS points before the interpolated time, plus the number foraging after the interpolated time, divided by twice the group size. It represents the proportion of the group that was foraging at the interpolated time. Foraging intensity was used to describe the behaviour of the group as a whole. This was especially important in the group models, where individual behaviour would not be meaningful. Foraging intensity was also included in addition to individual behaviour in the individual models.

2.8.3 Travel Speed.

The travel speed was calculated using the distance and time between each animal's GPS points before and after interpolation. Each individual's speed was used in the individual models, and the median of all unit members' speeds was used in the group models. Speed was reported in km/h. The observed speeds were limited by the observer's walking pace; geladas can run faster but they were not habituated to humans running after them.

2.8.4 Demographic Category.

The animals were divided into four demographic categories. Adult females had been pregnant at least once. Young adult females had had their first estrus cycle but had not yet become pregnant; they were generally smaller than adult females. Leader males were all large, healthy-looking, adult males. Follower males fell into two categories: young adults who were smaller than adult males, with less developed manes, and older followers, who had been leader males and then been overtaken by younger, stronger males. Due to the small numbers, the two types of follower males were not separated in the analysis.

2.8.5 Landsat 8 Data and Vegetation Index.

Satellite images of the study area were obtained from available Landsat 8 data (United States Geological Survey, 2014). I used images taken on 04-Dec-2014 (Path 168, Row 53). The study period was from October 2013 through January 2014 but the Landsat images from that period were not used because they had more cloud cover.

Landsat 8 data includes 11 different bands, or images recording different wavelengths of the electromagnetic spectrum (United States Geological Survey). The bands used in this study were blue, green, red, and near-infrared (bands 2, 3, 4, and 5; 0.45-0.51 µm, 0.53-0.59 µm, 0.64-0.67 µm, and 0.85-0.88 µm respectively) which have a resolution of 30 m. I used the panchromatic band (band 8, 0.50-0.68 µm) to improve the resolution of the other bands to produce sharper images. Each band by itself appeared as a black and white image indicating the amount of electromagnetic radiation reflected at the wavelengths of the band. The image from each band was then clipped to the extent of the study area (about 8.5 km from north to south and 5.4 km from east to west), using the Clip tool in ArcGIS.

Two colour images were prepared using the Composite Bands tool from ArcMap: a true colour image from the red, green, and blue bands, and a false colour image from the near-IR, red, and green bands. The resolution of these images was improved using the pan-sharpen tool and the panchromatic band so that the new images had 15 m resolution.

The false colour image was used to estimate the amount of green vegetation present at each animal’s position. Green growing plants absorb red light while reflecting near infrared light. Bare earth has similar reflectance in both bands. The difference between the red and infrared reflectance will therefore be higher in areas with more vegetation, and lower in areas with more bare earth (Gao, 2009). NDVI has been found to be correlated with net primary productivity in grassland environments (Box, Holben, & Kalb; Paruelo, Epstein, Lauenroth, & Burke, 1997; Wang, Rich, Price, & Kettle, 2005), and with leaf area index (Carlson & Ripley, 1997). NDVI is widely used as a proxy for

Since the satellite data was from a different year than the gelada data, the NDVI values can only be considered an estimate of the amount of vegetation present at different locations; however, the patterns should be broadly similar across different years (i.e. areas with more vegetation in 2014 due to springs, good soil, or topography, should be the same areas that had more vegetation in 2013). NDVI responds more strongly to seasonal variation than to interannual variation in rainfall (Richard & Poccard, 1998).

The NDVI tool in ArcGIS was used to calculate the normalized difference vegetation index (NDVI), using the formula in Equation 2.20, and the value of the NDVI raster at the animals' positions was added to the interpolated animal points using the Extract Values to Points tool (ESRI, 2013). Figure 2.21 shows the NDVI values.

Equation 2.20: NDVI, an estimate of the amount of green vegetation, was calculated from the red and infrared reflectance in the satellite data

$$NDVI = \frac{Infrared\ Reflectance - Red\ Reflectance}{Infrared\ Reflectance + \ Red\ Reflectance}$$

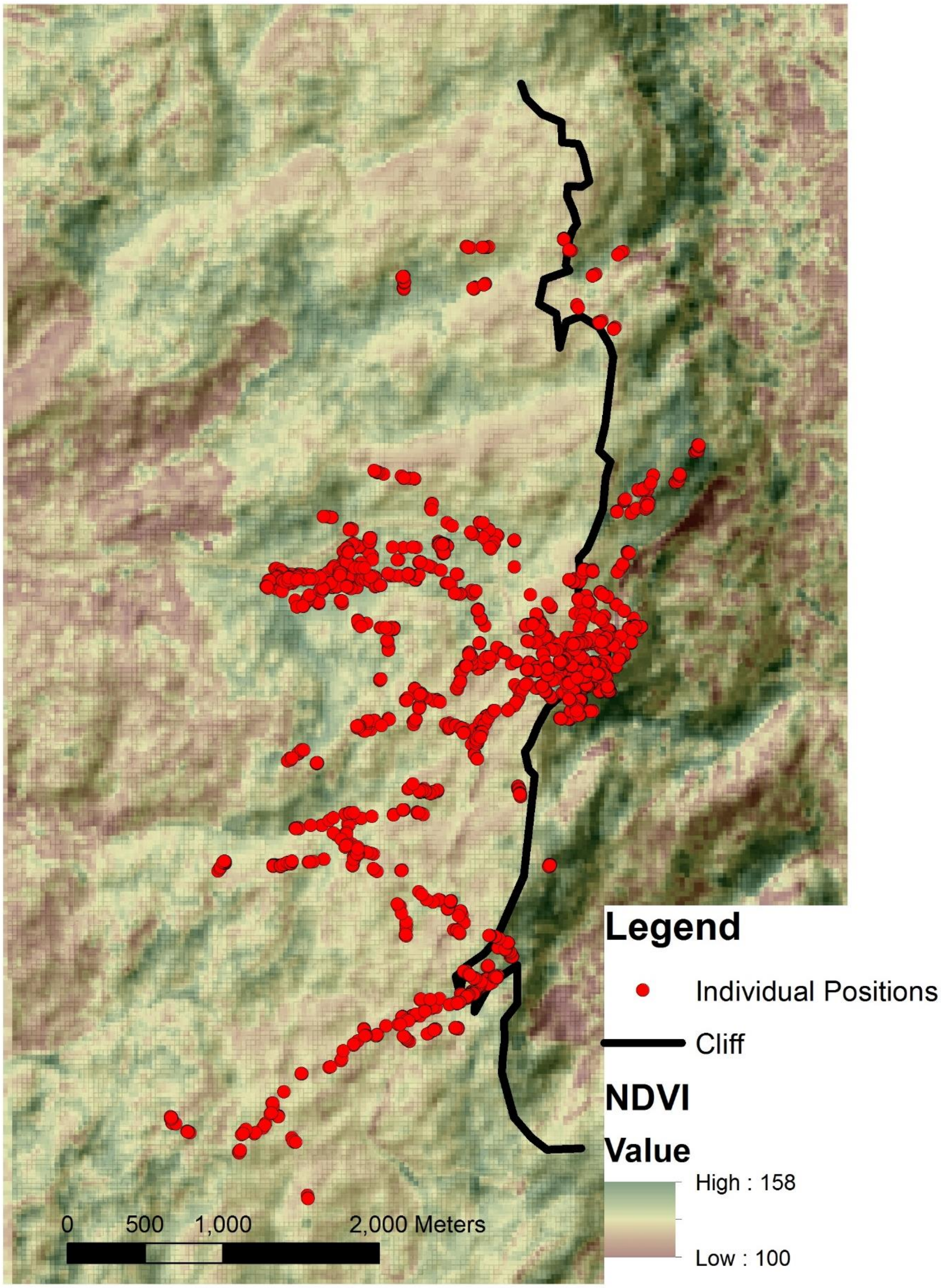

Figure 2.21 NDVI values indicate the amount of green vegetation.

2.8.6 Elevation and Slope.

The ASTER digital elevation model for the study area was obtained from the USGS Earth Explorer website (NASA Land Processes Distributed Active Archive Center (LP DAAC), 2011). Applying the Slope tool in ArcMap's Spatial Analyst toolbox to the DEM created a raster image showing the slope of the terrain. Elevation and slope values were added to each interpolated individual position using the "extract values to points" tool. The median of all the individual values for each time point was calculated in R, and those values were used in the OMU models. Gelada positions were recorded at elevations from 3201 m to 3530 m above sea level, and on slopes from 0˚ to 65˚. Figure 2.22 shows the elevations at Guassa, and Figure 2.23 shows the slopes of the terrain.

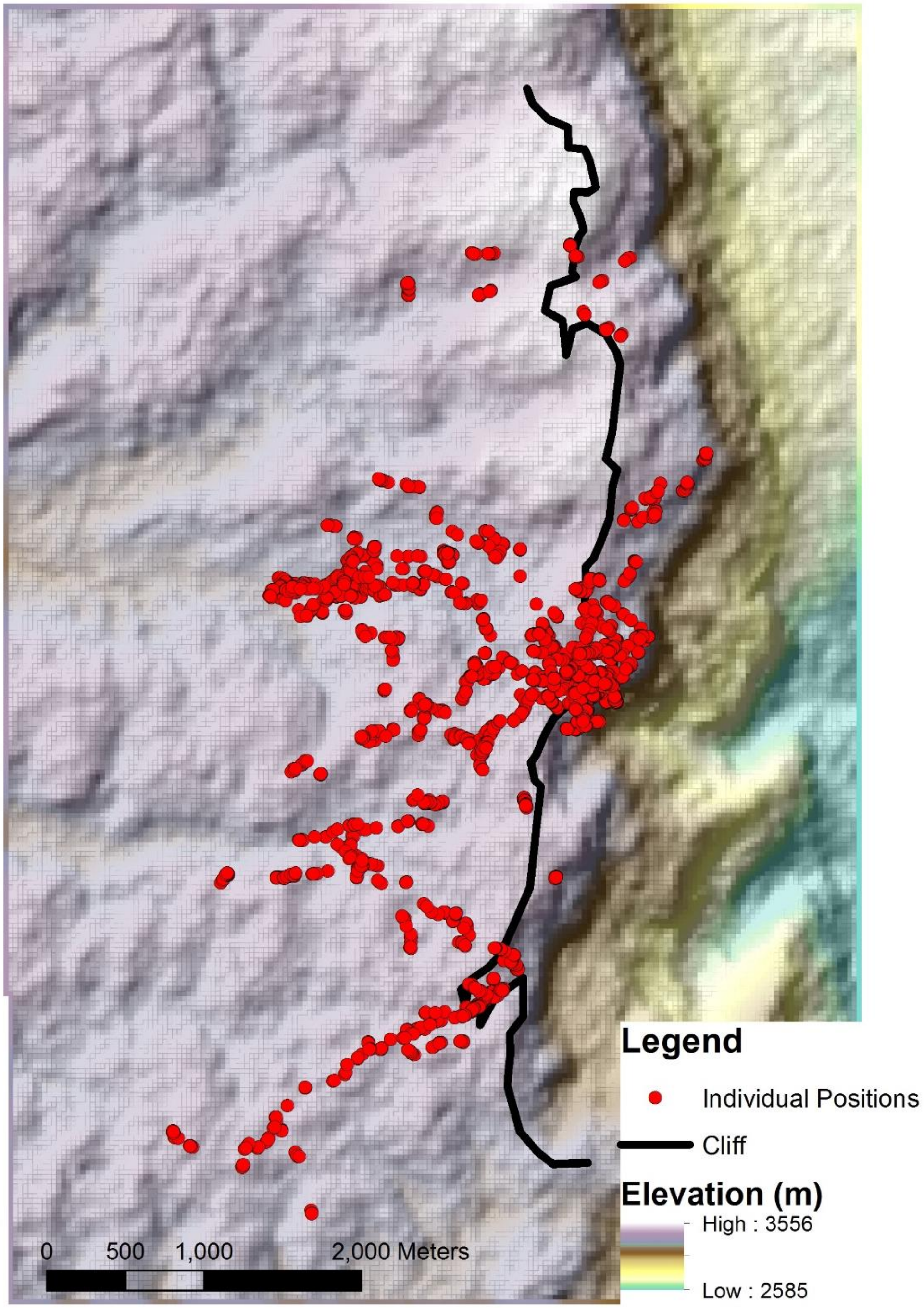

Figure 2.22 Elevation at Guassa

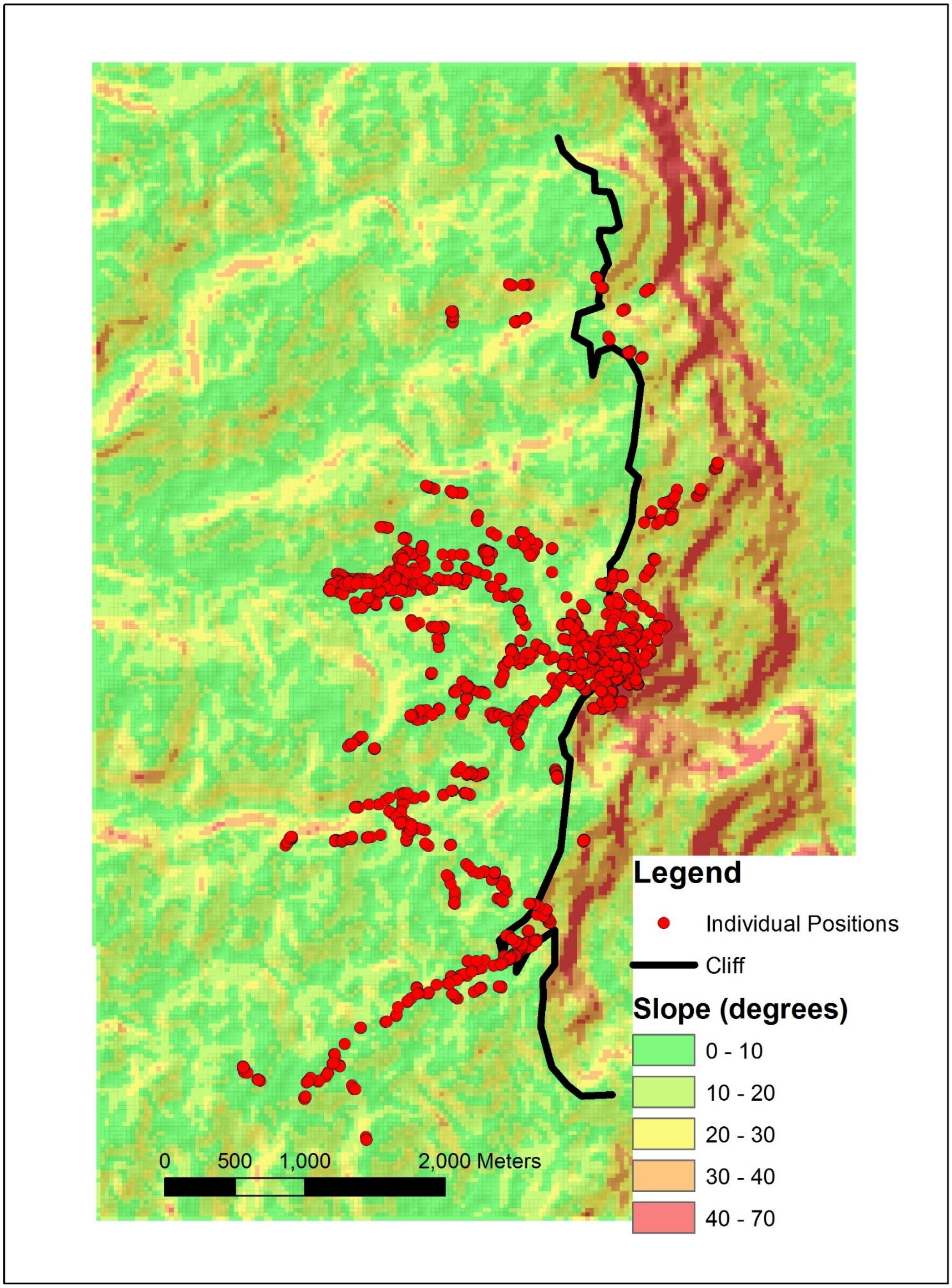

Figure 2.23 Slope of the terrain was included as a variable in the OMU models.

2.8.7 Aspect and the Cliff Edge.

The edge of the Guassa Plateau has two distinct levels, delineated by the upper and lower cliff edges (Figure 2.24). At the upper cliff edge the relatively flat plateau drops off into a steep slope with grass and shrubs. People can walk on the slope and geladas can forage. Lower down, the slope reaches the lower cliff edge which is a true cliff in many places. Much of the area below the lower cliff edge is dangerously steep for humans, although there are trails in some places used by people and their livestock. The geladas sleep on small ledges on steep rocky cliffs below the lower edge. Since geladas use the cliff as a refuge, their distance from the cliff might affect their behaviour.

Applying the “Aspect” tool created an image showing the aspect, or the direction the slope faces, at each point. The edge of the Great Rift Valley can be clearly seen in the aspect image (Figure 2.25). A line was drawn freehand along the upper cliff edge (using the aspect raster layer) to define the top of the cliff. The distance to the cliff line was calculated for each of the interpolated gelada points using the “Near” tool in ArcGIS (ESRI, 2013). The median distance to the cliff edge of all the animals at each time point was used in the OMU models. Gelada positions were recorded up to 2024 m from the upper cliff edge.

Figure 2.24 Cliffs and gorges where the edge of the Guassa Plateau drops off towards the Great Rift Valley. Top left, and top and bottom right photos show the contrast between the grassy slopes of the upper cliff and the steep rocky cliffs of the lower cliff. Lower left image shows the view down one of the gorges, looking towards the fields below.

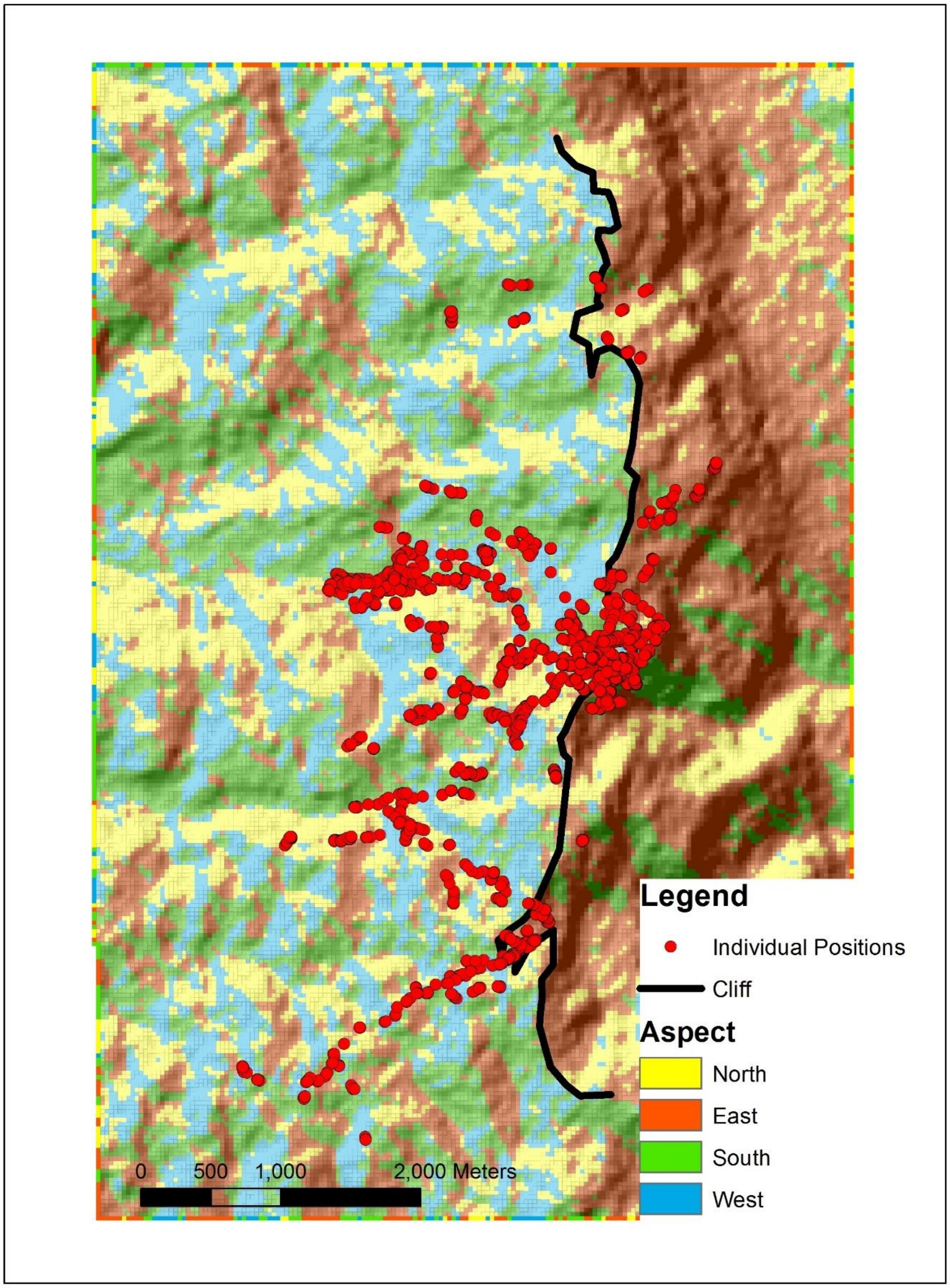

Figure 2.25 Aspect: the top of the upper cliff, where the plateau begins to slope down into the Great Rift Valley, could be identified using the aspect values. To the east of the cliff line, the terrain slopes steeply down to the east. To the west of the cliff line, the Guassa plateau slopes gradually westwards, and the plateau is dissected by valleys that run from east to west.

Chapter 3: Results

3.1 Size and shape of OMUs

To determine which demographic, behavioural, and environmental factors were related to the shape and area of gelada OMUs, I created two linear mixed effects models (LMM), one with the length/width ratio as the dependent variable (Table 3.1), and the other with the area of the OMU (estimated by the 1-standard deviation directional distance ellipse) as the dependent variable (Table 3.2). Both models included fixed effects of group size (number of adult and young adult animals), the presence or absence of a follower male, whether any of the females was in estrus, the proportion of the OMU that was foraging, and the speed of travel (the median of all the individual speeds). Additional fixed effects described the environment, including the amount of green vegetation present (NDVI), the geladas' distance from the upper cliff edge, the elevation above sea level, and the slope of the terrain. The random effect of OMU was included in each model. There was no random effect of individual in these models because the response variable pertained to the whole OMU. Each value of the response variable came from one OMU at one time point (N=453).

Table 3.1 The fixed effects of predictor variables on the length/width ratio of gelada OMUs. Ratio was log transformed. N=453.

Parameters	Estimate	Std. Error	t value	p value
Group Size	0.0611	0.0222	2.7550	0.0061
Follower Male Present	0.0885	0.0843	1.0500	0.2945
Estrous Female Present	0.1241	0.0928	1.3370	0.1818
Proportion Foraging	0.2243	0.2033	1.1040	0.2704
Speed (km/h)	0.9969	0.1031	9.6660	< 2E-16
NDVI	-0.0006	0.0083	-0.0690	0.9454
Distance to Cliff (m)	-0.2752	0.0880	-3.1280	0.0019
Elevation (m)	0.0006	0.0013	0.4660	0.6413
Slope (percent)	-0.0010	0.0043	-0.2300	0.8180
β	-2.0130	4.8520	-0.4150	0.6785

The LMM did not differ significantly from the LM (LR test, X2= 0.0, P= 1.0). Shaded rows indicate that the variable was significant in the model ($p < 0.05$).

Table 3.2 The fixed effects of predictor variables on the area occupied by gelada OMUs (log transformed). N=453.

Parameters	Estimate	Std. Error	t value	p value
Group Size	0.4667	0.0595	7.8490	2.89E-05
Follower Male Present	0.2944	0.2391	1.2310	0.2544
Estrous Female Present	-0.1549	0.1400	-1.1060	0.2692
Proportion Foraging	0.5020	0.2954	1.6990	0.0900
Speed(km/h)	1.6550	0.1495	11.0650	< 2E-16
NDVI	-0.0258	0.0121	-2.1220	0.0344
Distance to Cliff (m)	0.6497	0.1299	5.0030	8.10E-07
Elevation (m)	0.0030	0.0019	1.5770	0.1156
Slope (percent)	0.0053	0.0062	0.8550	0.3928
β	-6.8420	7.1260	-0.9600	0.3375

The LMM differed significantly from the linear model (LR test, X2 = 8.503, P = 0.0035). Shaded rows indicate that the variable was significant in the model ($p < 0.05$).

In the aggregate, gelada OMUs were longer in the direction of travel than they were wide (Figure 3.3, Table 3.4). OMUs with more animals were longer (greater length/width ratio) than those with fewer animals. OMUs with more animals also occupied larger areas. The effect of group size appeared to be more pronounced for area than for the length/width ratio, indicating that there was an increase in width as well as length (Figure 3.5).

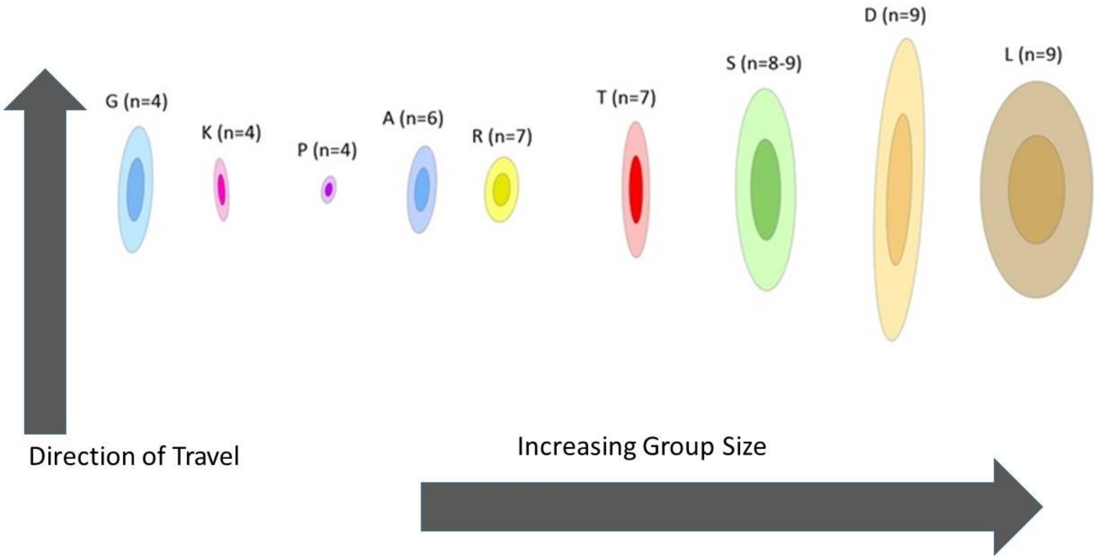

Figure 3.3 The aggregate shape of gelada OMUs. Arrow points in direction of travel. Directional distribution ellipses were calculated to show the shape of each of the nine OMUs. The ellipses were calculated from the independent individual position estimates in group space. The group space positions were relative to the mean centroid of all the individual positions at each time point; y coordinates represented the animal's distance ahead or behind the center, and x coordinates represented its distance left or right of the center. All the individual positions for each OMU, for all the independent time points, were overlaid. From the combined positions across time, directional distribution ellipses were calculated using the "directional distribution" tool in ArcGIS (ESRI, 2013). The lengths of the ellipse's axes are determined from the standard deviations of the x and y coordinates. The larger ellipses used 2 standard deviations, and the smaller ellipses used 1 standard deviation. All ellipses are drawn to the same scale.

Table 3.4 The relation between the length and width of gelada OMUs. Length was specified as parallel to the direction of travel, while width was perpendicular to length. N=453 time points.

	Number of time Points	Percentage
Length > Width	354	78
Width > Length	99	22
Length > 2x Width	232	51
Width > 2x Length	35	8

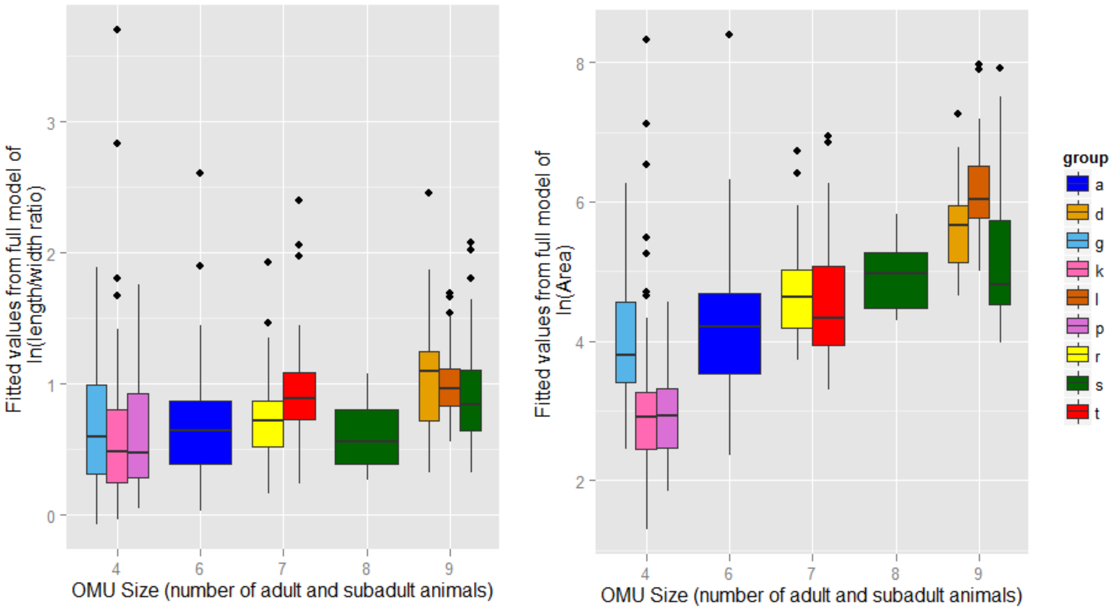

Figure 3.5 The relationship between OMU size and (a) shape and (b) area occupied. Larger OMUs were more elongated in the direction of travel and occupied larger areas as they moved. Boxes show 25th to 75th percentile, with horizontal line for the median. Whiskers show 95% CI of median, and points show data points outside this range.

OMUs also covered more area and were more elongated at faster travel speeds (Tables 3.1 and 3.2, Figure 3.6). Travel speeds were usually slow, and were limited by the observer’s walking pace since geladas were not habituated to humans running after them.

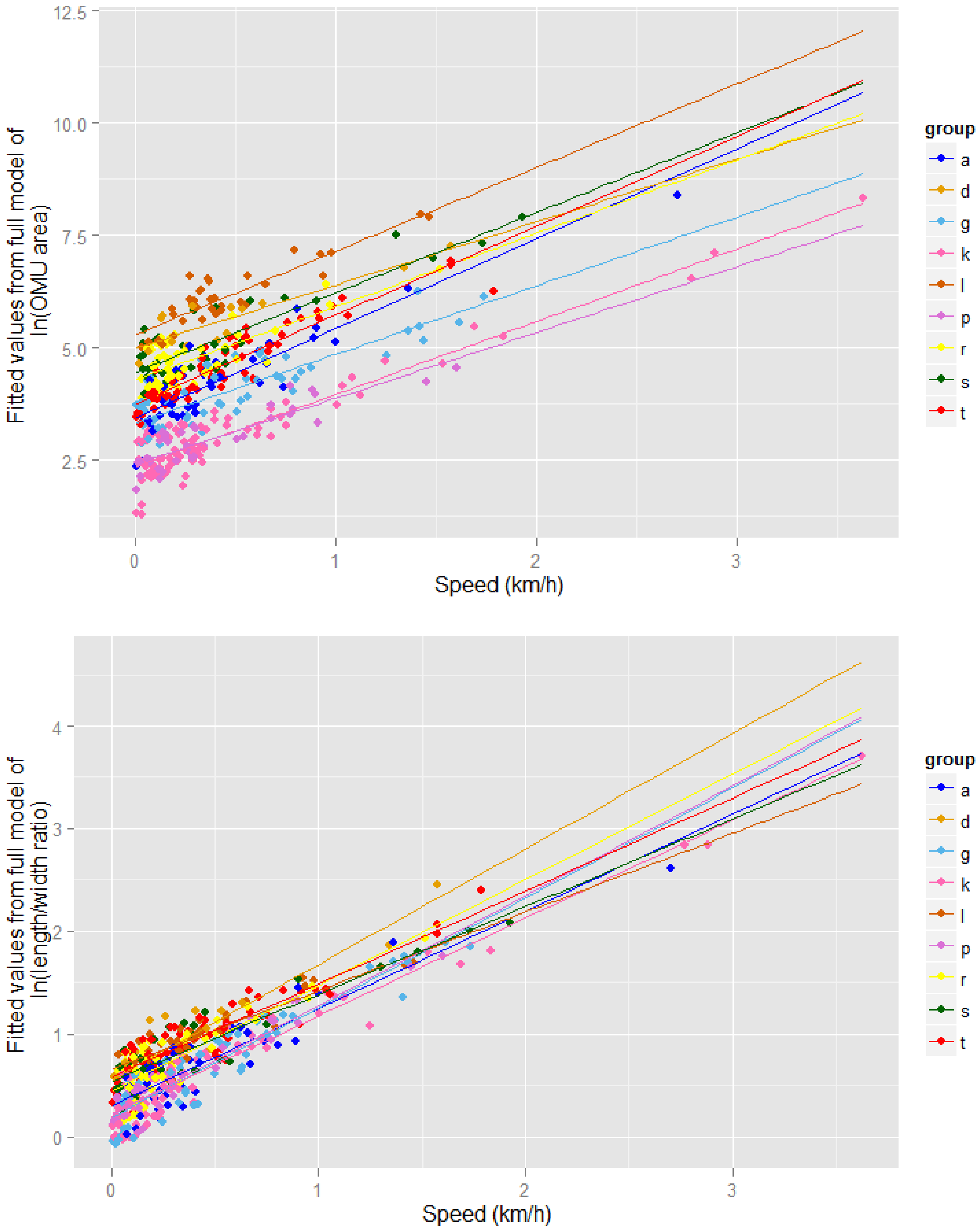

Figure 3.6 Travel speed and the size and shape of gelada OMUs. The figures are generated from the fitted values for area and shape in the full models.

There was no support for the prediction that units would contract when they were away from the safety of the cliff. The results indicate that OMUs became less elongated and increasingly widely spread the further they were from the cliff (Tables 3.1 and 3.2, Figure 3.7).

Lastly, the area covered by the OMU decreased with increasing amounts of green vegetation (Table 3.2, Figure 3.8).

Figure 3.7 The effect of the distance from the cliff on the area covered by, and the relative shape of, OMUs. The figures are generated from the fitted values for area and shape in the full models.

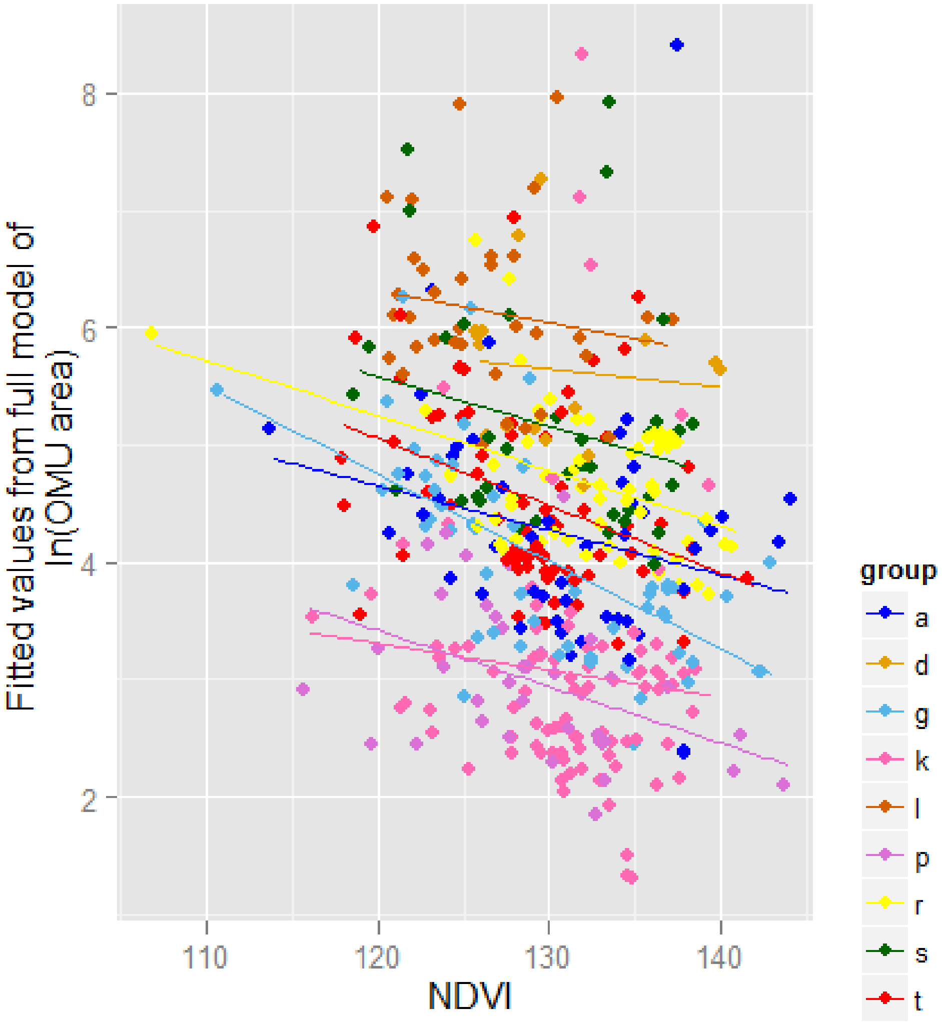

Figure 3.8 The relationship between NDVI and the area covered by OMUs: OMUs occupied a smaller area when there was more green vegetation). The figure is generated from the fitted values for area in the full model.

3.2 Structure within OMU

To determine which factors were related to an individual gelada's position relative to the other members of its OMU, I created four models. The first response variable was the individual's distance ahead or behind the median, relative to the group's direction of travel, which served to indicate whether the animal was more often at the front or back of the group. The second was the individual's lateral distance from the center line, perpendicular to the direction of travel. The third was inter individual distance (IID), the animal's median distance to each of its neighbours at that time, which served as a measure of group cohesion. IID also should be larger for peripheral animals than for those at the center of the group. The fourth response variable was the animal's distance from its nearest neighbour. IID was somewhat correlated with NND, especially in OMUs with fewer animals (Figure 3.9).

All four models included fixed effects related to the individual and to the OMU. The individual level fixed effects were the animal's demographic category, its behaviour at its previous GPS point, and its speed. The OMU level fixed effects were the proportion of the OMU that was foraging, the group size (number of adult and young adult animals), whether the OMU had a follower male, and whether any of the females was in estrus.

The random effects of individual identity nested within OMU were included in each model. OMU. Each value of the response variable came from one individual at one time point.

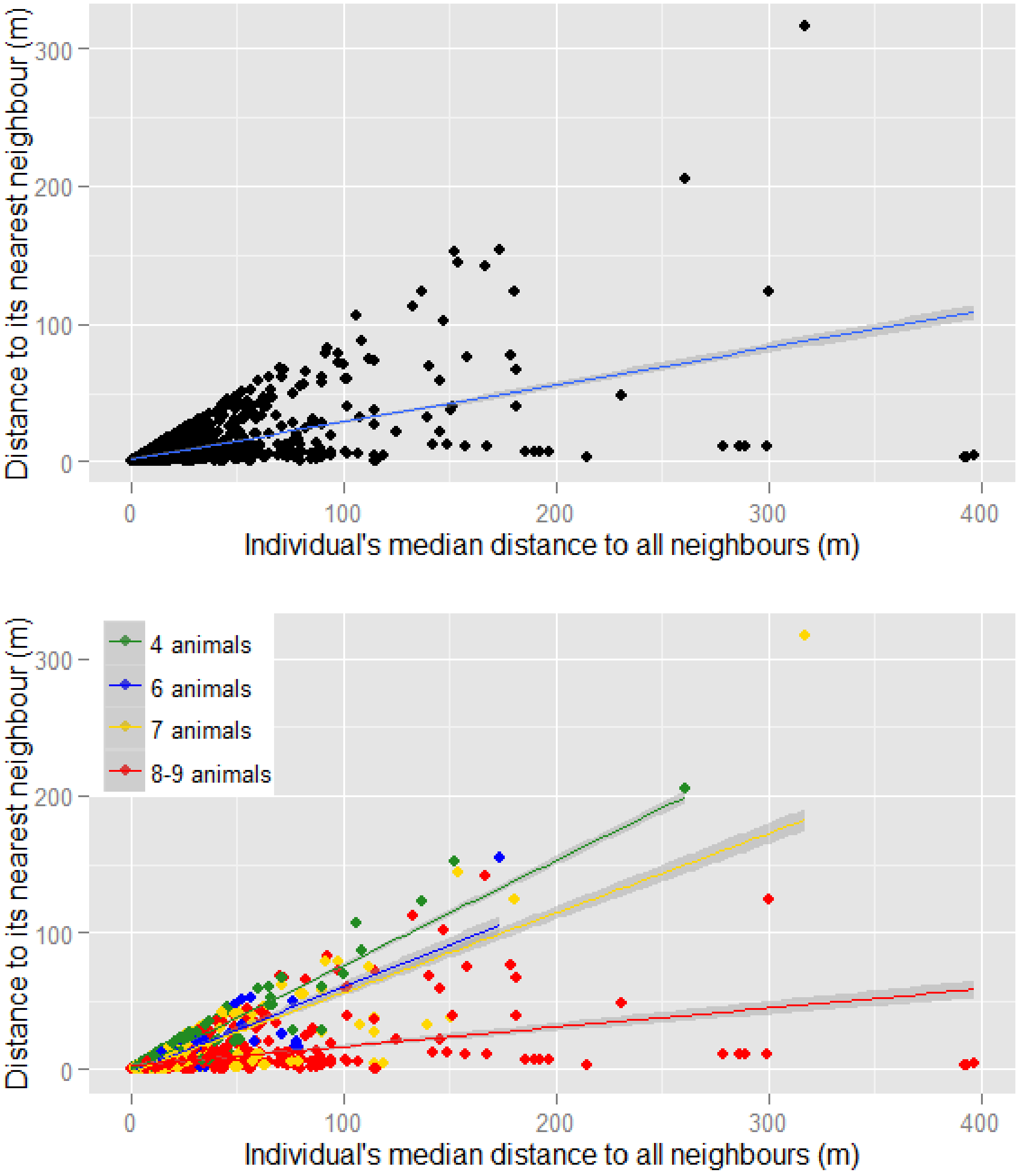

Figure 3.9 Top: Individual geladas' distances from their nearest neighbours were correlated with their median distance to all neighbours (linear model, r-squared = 0.35). Bottom: The correlation was stronger in smaller OMUs.

Tables 3.10, 3.11, 3.12, and 3.13 show the coefficients of the coefficients of the multilevel models for individual distance ahead or behind relative to the median, distance from the center line, inter-individual distance, and nearest neighbour distance (the individual models), which were calculated from 2726 individual interpolated positions, at the same independent time points as used for the OMU models. All the response variables were log transformed, with the exception of individual distance ahead or behind. All models used random intercepts; similar models with random slopes failed to converge.

Table 3.10 Multilevel model of effects of predictor variables on an individual's distance ahead or behind the median. Log transformation was not required for this variable.

	Estimate	Std. Error	t value	p value
Individual Level Fixed Effects				
Demographic Category (relative to Adult Female)				
Follower Male	1.0211	3.1264	0.3270	0.7464
Leader Male	6.0994	2.3006	2.6510	0.0128
Young Adult Female	-2.5845	2.5766	-1.0030	0.3221
Behaviour at previous GPS point (relative to Foraging)				
Resting	-5.5946	3.6361	-1.5390	0.1240
Social	-8.3258	2.5228	-3.3000	0.0010
Traveling	4.0858	1.8725	2.1820	0.0292
Speed (km/h)	-11.9908	1.3376	-8.9650	< 2E-16
OMU Level Fixed Effects				
Proportion Foraging	-9.7152	3.2028	-3.0330	0.0024
Group Size	-0.7438	0.4472	-1.6630	0.1052
Follower Male Present	3.0047	1.7511	1.7160	0.0960
Estrous Female Present	2.8712	1.2838	2.2370	0.0254
β	11.9380	4.4306	2.6940	0.0084

The LMM differed significantly from the linear model (LR test, X2 = 7.69, p = 0.02135).

Shaded rows indicate that the variable was significant in the model ($p < 0.05$).

Table 3.11 Multilevel model of effects of predictor variables on an individual's distance from the center line (log transformed)

	Estimate	Std. Error	t value	p value
Individual-level fixed effects				
Demographic Category				
Follower Male	9.3990	0.0934	1.0070	0.3141
Leader Male	-9.5080	0.0667	-0.1420	0.8867
Young Adult Female	3.4060	0.0841	0.4050	0.6856
Individual Behaviour (relative to foraging)				
Resting	6.8560	0.1516	0.4520	0.6511
Social/Grooming	2.9570	0.1054	0.2810	0.7791
Traveling	2.2220	0.0781	0.2840	0.7762
Speed (km/h)	4.9700	0.0561	8.8560	< 2e-16
OMU-level fixed effects				
Proportion Foraging	3.3310	0.1348	2.4710	0.0135
Group Size	1.7030	0.0415	4.1050	0.0018
Follower Male Present	8.5960	0.1745	0.0050	0.9962
Estrous Female Present	-1.4570	0.0550	-2.6480	0.0081
β	-0.8614	0.3150	-2.7350	0.0154

The LMM was significantly different from the linear model (LR test, X2 = 77.278, p <2E-16). Shaded rows indicate that the variable was significant in the model ($p < 0.05$).

Table 3.12 Multilevel model of effects of predictor variables on individuals' IID (log transformed)

	Estimate	Std. Error	t value	p value
Individual Level Fixed Effects				
Demographic Category (relative to Adult Female)				
Follower Male	0.0366	0.0638	0.5730	0.5667
Leader Male	-0.0533	0.0456	-1.1690	0.2425
Young Adult Female	0.0657	0.0575	1.1410	0.2539
Behaviour (relative to Foraging)				
Resting	-0.0702	0.1035	-0.6780	0.4978
Social/Grooming	-0.3105	0.0720	-4.3130	6.70E-06
Traveling	0.3551	0.0534	6.6520	4.80E-12
Speed (km/h)	0.9347	0.0383	24.3810	< 2e-16
OMU Level Fixed Effects				
Proportion Foraging	0.1853	0.0921	2.0120	0.0443
Group Size	0.1712	0.0323	5.3090	0.0004
Follower Male Present	0.1138	0.1370	0.8310	0.4292
Estrous Female Present	0.0226	0.0376	0.6010	0.5480
β	0.3627	0.2406	1.5080	0.1560

The LMM differed significantly from the linear model (LR test, X2 = 96.00, $p < 2.2e-16$). Shaded rows indicate that the variable was significant in the model ($p < 0.05$).

Table 3.13 Multilevel model of effects of predictor variables on individuals' NND (log transformed)

	Estimate	Std. Error	t value	p value
Individual Level Fixed Effects				
Demographic Category (relative to Adult Female)				
Follower Male	0.1585	0.0882	1.7960	0.0802
Leader Male	-0.0816	0.0629	-1.2970	0.2019
Young Adult Female	0.0384	0.0770	0.4990	0.6193
Behaviour at previous GPS point (relative to Foraging)				
Resting	0.0517	0.1272	0.4060	0.6847
Social	-0.7118	0.0884	-8.0510	1.11E-15
Traveling	0.3164	0.0656	4.8250	1.48E-06
Speed (km/h)	0.8653	0.0470	18.4080	< 2E-16
OMU Level Fixed Effects				
Proportion Foraging	0.4092	0.1129	3.6230	2.96E-04
Group Size	0.0289	0.0355	0.8150	0.4393
Follower Male Present	0.0964	0.1493	0.6450	0.5402
Estrous Female Present	-0.0721	0.0461	-1.5650	0.1176
β	0.2545	0.2688	0.9470	0.3647

The LMM differed significantly from the LM (LR test, X22 = 63.12, p = 1.97e-14).

Shaded rows indicate that the variable was significant in the model ($p < 0.05$).

3.2.1 Demographic Factors.

IID was significantly related to group size, but NND was not (Figure 3.14). When OMUs contained more individuals, geladas spread out so that individuals could maintain the same amount of distance to their nearest neighbours. They did not squeeze closer together to maintain their distance to all members of the group. Animals in larger OMUs were farther from the center line of the group perpendicular to the direction of travel (Figure 3.15), but were not farther ahead or behind the median.

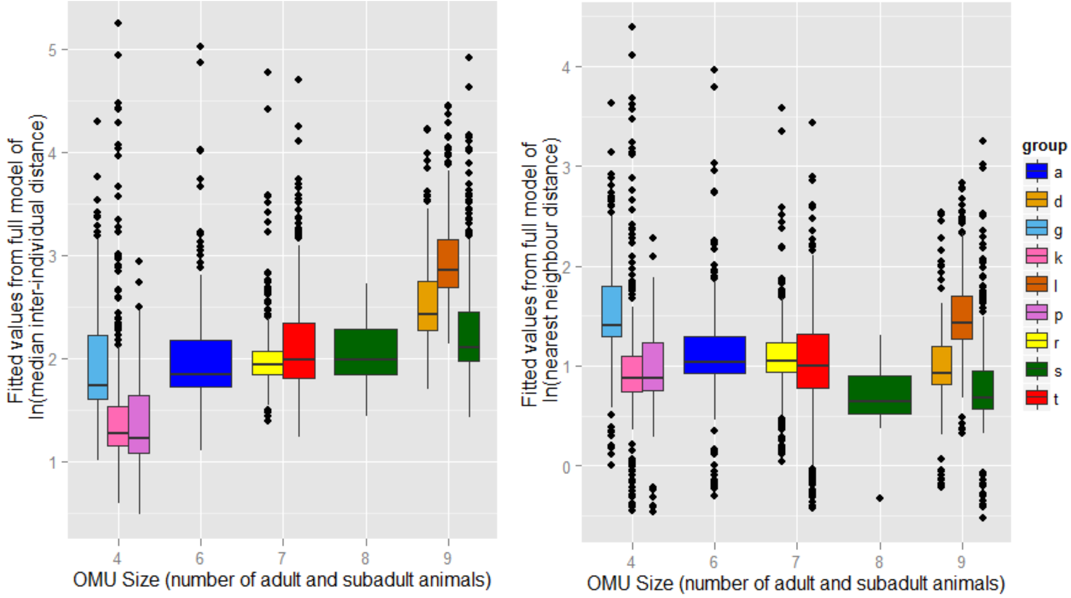

Figure 3.14 Group Size: Members of larger OMUs had larger median inter individual distances (left), but group size was unrelated to an individual's distance from its nearest neighbour (right). Boxes show 25th to 75th percentile, with horizontal line for the median. Whiskers show 95% CI of median, and points show data points outside this range.

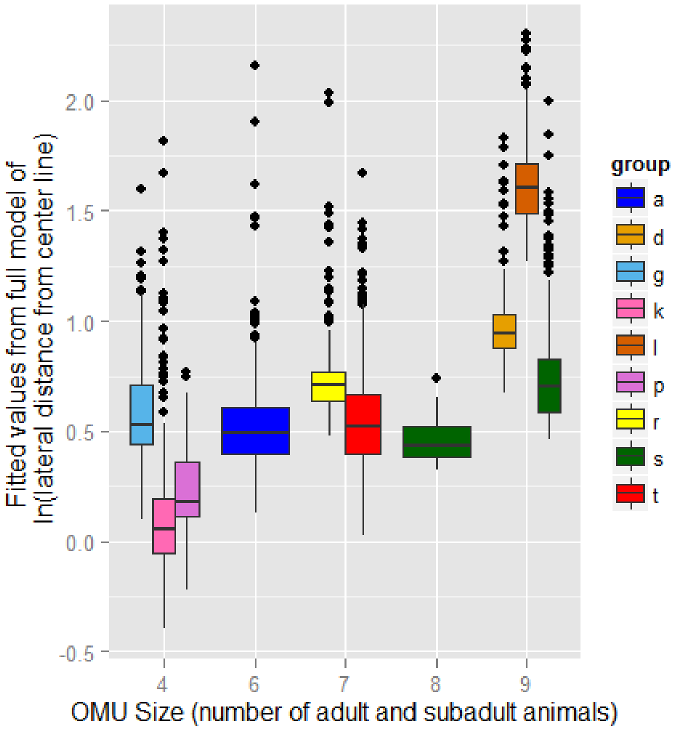

Figure 3.15 Lateral distance: geladas were farther from the center line in OMUs that contained more individuals. Boxes show 25th to 75th percentile, with horizontal line for the median. Whiskers show 95% CI of median, and points show data points outside this range.

Leader males were farther ahead (or less far behind) than females (Figure 3.15, Table 3.16). Follower males were slightly farther ahead (or less far behind) than females, but the effect was not significant. There was no significant difference between demographic categories in their median inter-individual distances, their nearest neighbour distances, or their distances from the center line. Follower males were slightly farther from their nearest neighbours, but the effect was not significant. Follower males were also farther ahead than females, but the effect was not significant.

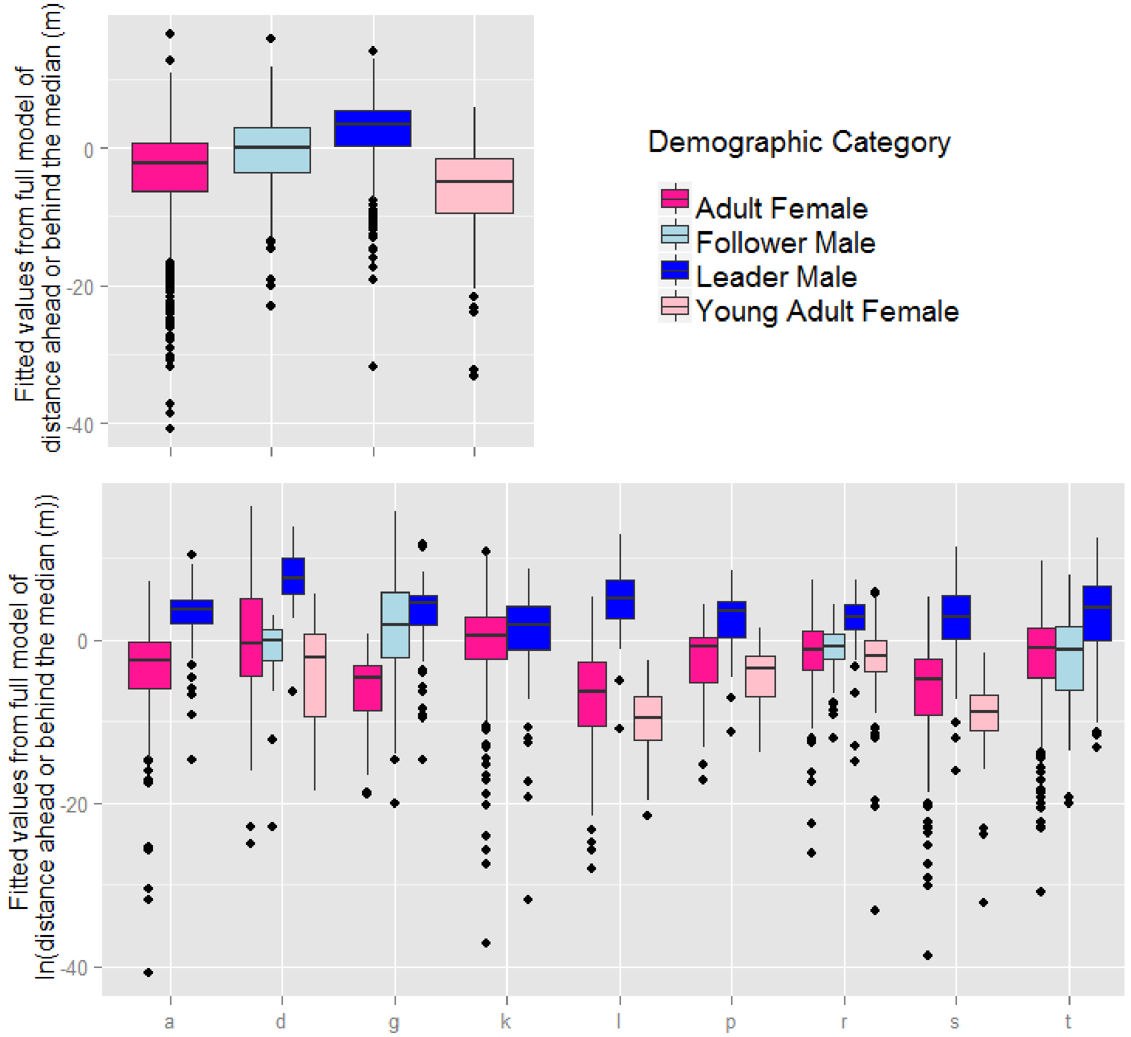

Figure 3.16 Leader males were significantly farther towards the front of the group than adult or young adult females (top). The difference can be seen across all OMUs (bottom). Boxes show 25th to 75th percentile, with horizontal line for the median. Whiskers show 95% CI of median, and points show data points outside this range.

Table 3.17 Pairwise comparisons of demographic categories. Comparisons were performed using the “glht” package for R, and were based on the multilevel models. (AF = adult female, YF = young adult female, LM = leader male, and FM = follower male)

	Estimate	Std. Error	z value	p value
Distance ahead or behind the median				
FM - AF	1.021	3.126	0.327	0.987
LM - AF	6.099	2.301	2.651	0.038
YF - AF	-2.585	2.577	-1.003	0.738
LM - FM	5.078	3.508	1.448	0.457
YF - FM	-3.606	3.766	-0.957	0.765
YF - LM	-8.684	3.158	-2.750	0.0286
Distance from the center line (log transformed)				
FM - AF	0.0940	0.0934	1.0070	0.7360
LM - AF	-0.0095	0.0667	-0.1420	0.9990
YF - AF	0.0341	0.0841	0.4050	0.9760
LM - FM	-0.1035	0.1027	-1.0080	0.7350
YF - FM	-0.0599	0.1171	-0.5120	0.9540
YF - LM	0.0436	0.0983	0.4430	0.9690

Table 3.17 Continued: Pairwise comparisons of demographic categories

	Estimate	Std. Error	z value	p value
IID (log transformed)				
FM - AF	0.037	0.064	0.573	0.937
LM - AF	-0.053	0.046	-1.169	0.635
YF - AF	0.066	0.058	1.141	0.653
LM - FM	-0.090	0.070	-1.281	0.563
YF - FM	0.029	0.080	0.363	0.983
YF - LM	0.119	0.067	1.771	0.277
NND (log transformed)				
FM - AF	0.158	0.088	1.796	0.265
LM - AF	-0.082	0.063	-1.297	0.553
YF - AF	0.038	0.077	0.499	0.957
LM - FM	-0.240	0.097	-2.473	0.061
YF - FM	-0.120	0.109	-1.100	0.679
YF - LM	0.120	0.091	1.322	0.537

3.2.2 Estrus.

When at least one female in the OMU was in estrus, all individuals were farther ahead (or less far behind), and closer to the center line (Figure 3.17). IID and NND were not affected.

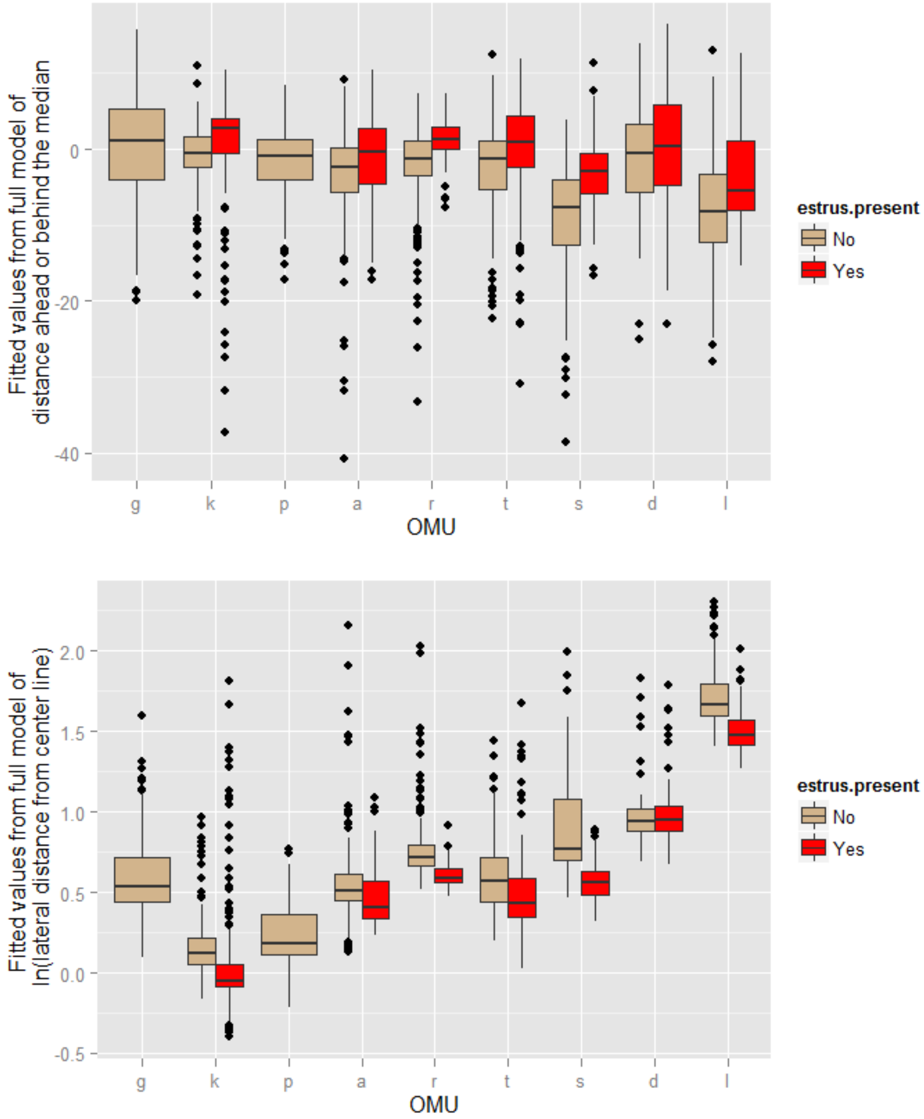

Figure 3.18 Geladas were less far behind (top), and less far from the center line (bottom), when a member of the OMU was in estrus. Boxes show 25th to 75th percentile, with horizontal line for the median. Whiskers show 95% CI of median, and points show data points outside this range.

3.2.3 Behaviour.

Foraging was the most common behaviour, accounting for over 75% of data points (Table 3.18). Since data collection deliberately focused on periods when the geladas were actively foraging and moving, these values cannot be considered to represent the overall activity budget. The foraging and travel categories were overrepresented, while social and rest behaviours were underrepresented, relative to the animals' behaviour over the entire day.

Individual behaviour affected geladas' position within the OMU (Figure 3.19). Animals that were moving at their previous GPS point were farther ahead and farther apart (greater IID and NND). Those that were socializing were farther behind, and had smaller IID and NND. Individual behaviour at the animal's previous GPS point was included in the individual models. The fixed effect of behaviour was significant in all three individual models, so pairwise comparisons were performed (Table 3.20). The general pattern was for monkeys that were moving to have larger IID, NND, and to be farther to the front of the group, while those that were socializing tended to have smaller IID, NND, and were farther to the back of the group. Foraging and resting fell in between these extremes. Individual behaviour was not related to geladas' distances from the center line.

Table 3.19 Distribution of different behaviour categories during follows

Behaviour	Number of Data Points	Percentage of Data Points
Forage	2049	75.2
Travel	373	13.7
Social	222	8.1
Rest	82	3.0
Total	2726	100

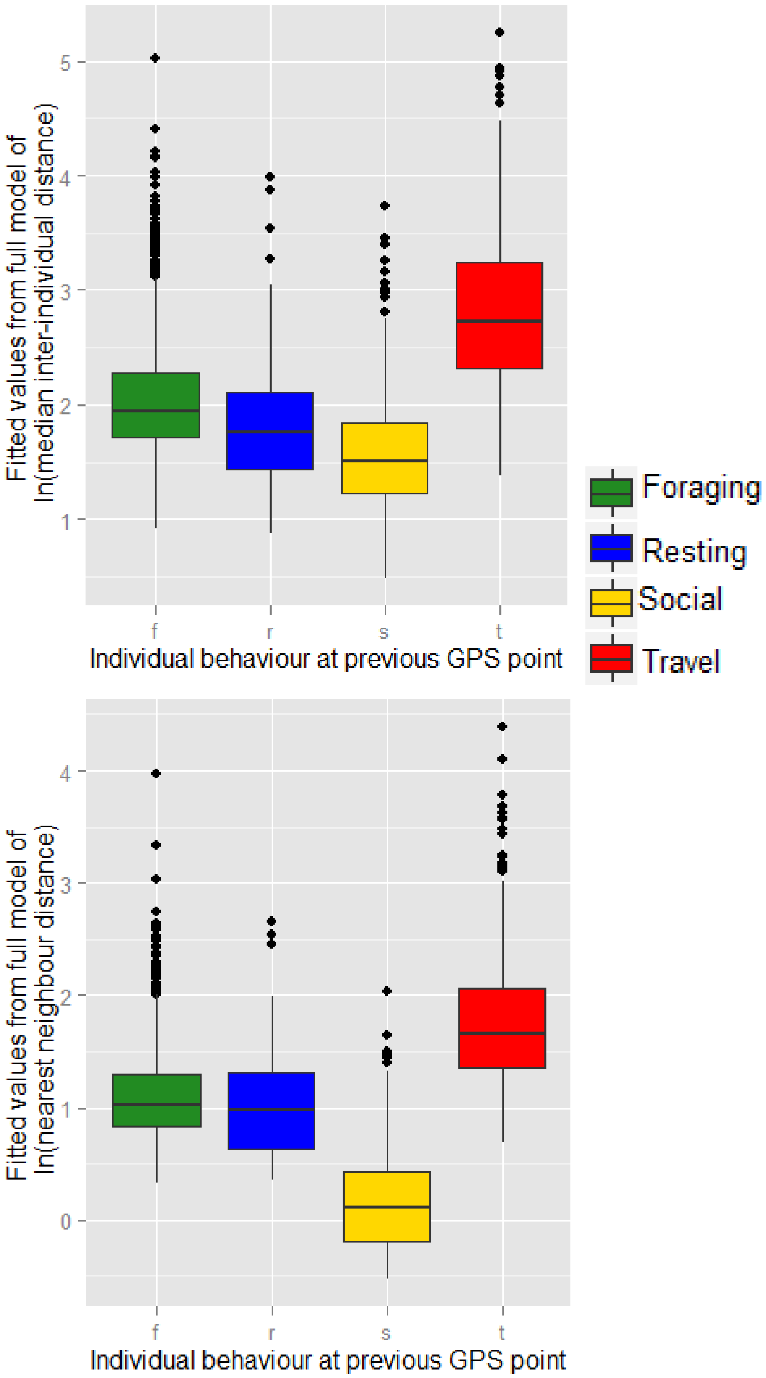

Figure 3.20 Geladas were farthest apart during travel (red), and closest together during social behaviour (yellow). This pattern was observed in both median inter individual distance (top) and nearest neighbour distance (bottom). Boxes show 25th to 75th percentile, with horizontal line for the median. Whiskers show 95% CI of median, and points show data points outside this range.

Table 3.21 Pairwise comparisons of individual behaviour categories. Comparisons were performed using the “glht” package for R, and were based on the multilevel models above.

	Estimate	Std. Error	z value	p value
Distance ahead or behind the median (m)				
Rest - Forage	-5.595	3.636	-1.539	0.399
Social - Forage	-8.326	2.523	-3.300	0.005
Travel - Forage	4.086	1.873	2.182	0.120
Social - Rest	-2.731	3.858	-0.708	0.888
Travel - Rest	9.680	3.802	2.546	0.050
Travel - Social	12.412	2.779	4.467	< 0.001
Distance from the center line (log transformed)				
Rest – Forage	0.0686	0.1516	0.4520	0.9670
Social - Forage	0.0296	0.1054	0.2810	0.9920
Travel - Forage	0.0222	0.0781	0.2840	0.9920
Social - Rest	-0.0390	0.1610	-0.2420	0.9950
Travel - Rest	-0.0463	0.1586	-0.2920	0.9910
Travel - Social	-0.0074	0.1162	-0.0630	1.0000

Table 3.21 Continued: Pairwise comparisons of behaviour categories

	Estimate	Std. Error	z value	p value
IID (log transformed)				
Rest - Forage	-0.070	0.104	-0.678	0.900
Social - Forage	-0.310	0.072	-4.313	<0.001
Travel - Forage	0.355	0.053	6.652	<0.001
Social - Rest	-0.240	0.110	-2.185	0.119
Travel - Rest	0.425	0.108	3.926	<0.001
Travel - Social	0.666	0.079	8.383	<0.001
NND (log transformed)				
Rest - Forage	0.052	0.127	0.406	0.976
Social - Forage	-0.712	0.088	-8.051	<0.001
Travel - Forage	0.316	0.066	4.825	<0.001
Social - Rest	-0.763	0.135	-5.649	<0.001
Travel - Rest	0.265	0.133	1.989	0.181
Travel - Social	1.028	0.097	10.547	<0.001

Shaded rows indicate comparisons where one demographic category was significantly different from another ($p < 0.05$).

Unsurprisingly, individual behaviour was related to the two group-level measures of behaviour: speed and proportion foraging (Figure 3.21). Travel speed of individuals that were foraging or travelling at their previous GPS point decreased with the proportion of the OMU that was foraging. For individuals that were socializing or resting, the trend was in the opposite direction.

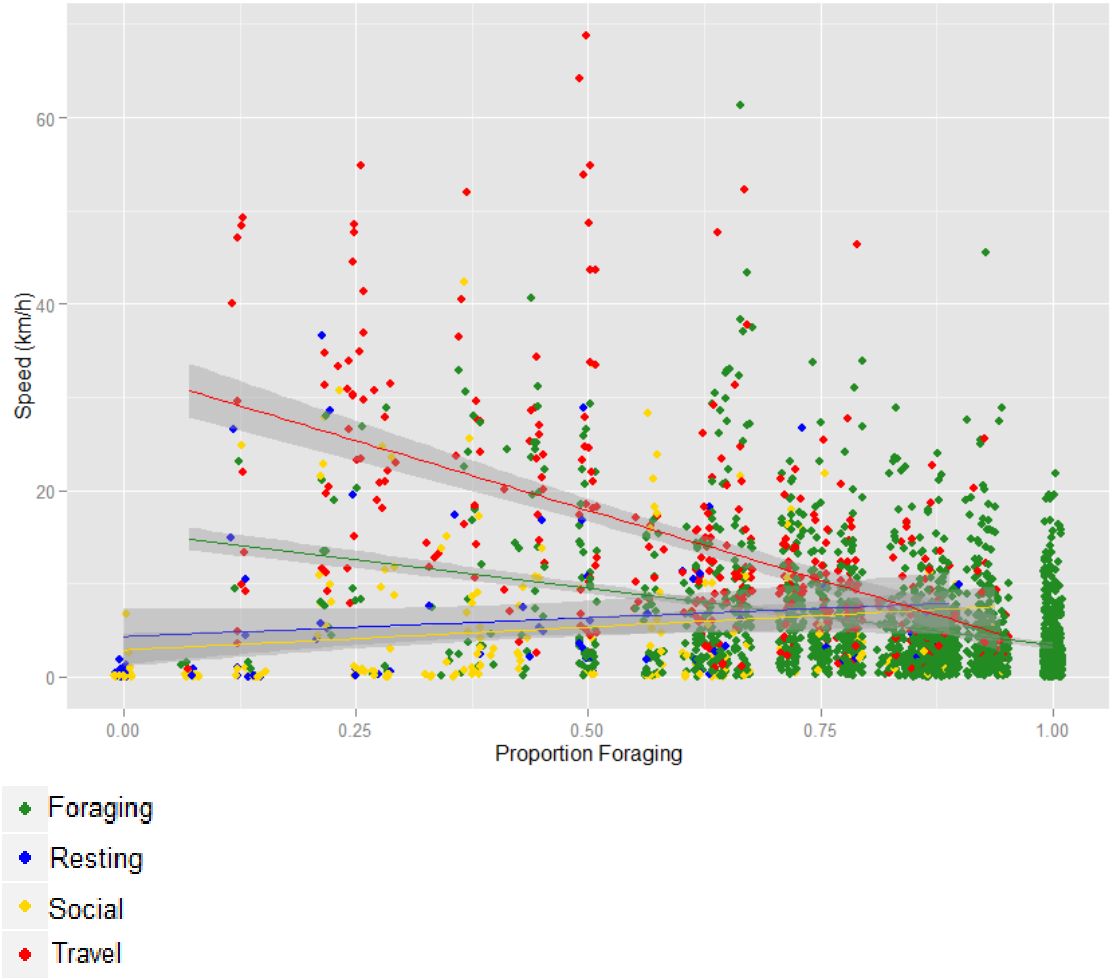

Figure 3.22 Individual and OMU level behaviour

3.2.4 Individual Speed.

In all models, travel speed was very significant (Figure 3.22). Geladas were farther apart when they were moving faster, as shown by the increased IID, NND, and lateral distance from the center line. They were also farther behind.

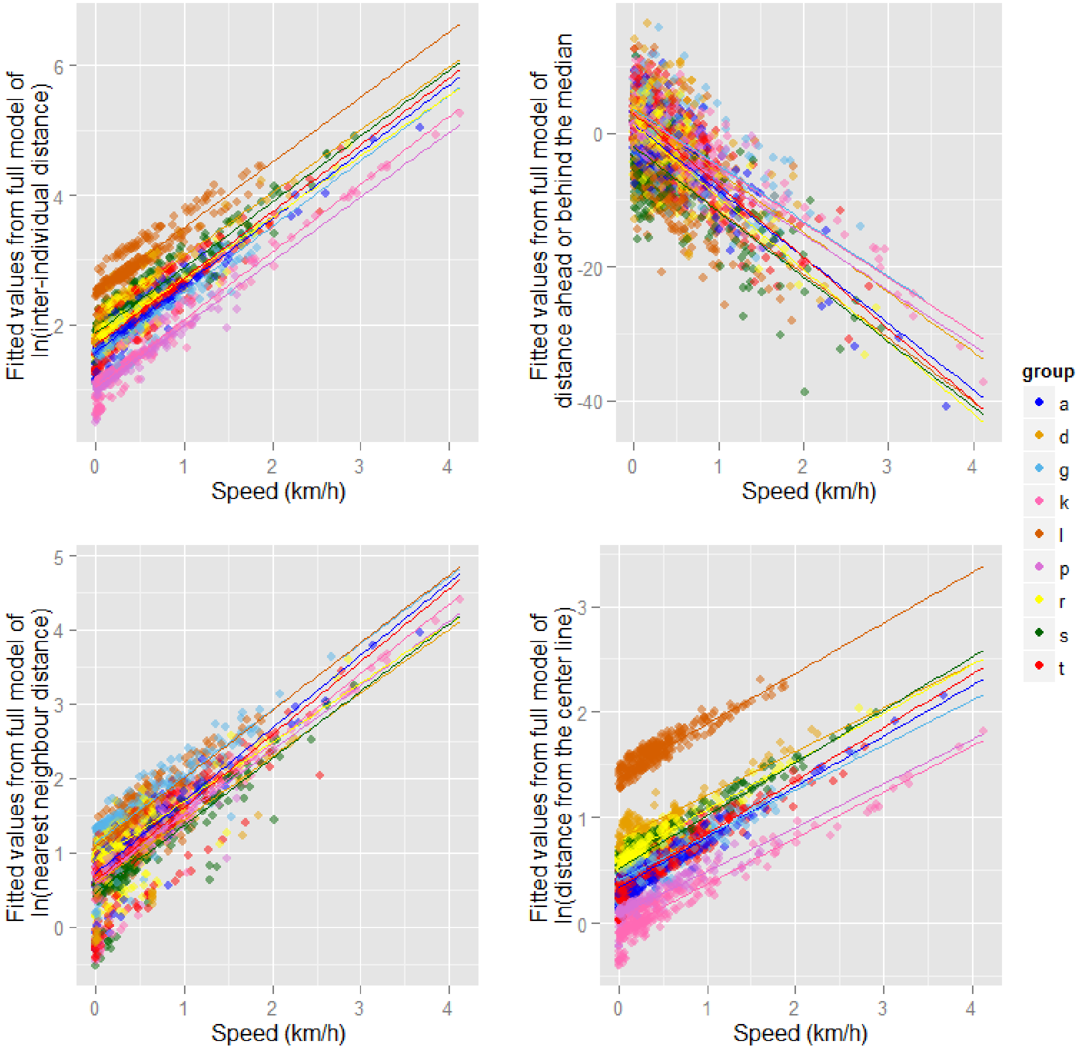

Figure 3.23 Travel speed was highly significant in all models. Individual monkeys that were moving faster had larger IID (top left), NND (bottom left), and distance from the center line (bottom right), and were farther behind the center of the OMU (top right).

3.2.5 Proportion Foraging.

The proportion of the OMU that was foraging was also related to all four metrics of individual behaviour (Figure 3.23). When more animals were foraging, geladas were farther ahead, farther from the center line, and had larger IID and NND.

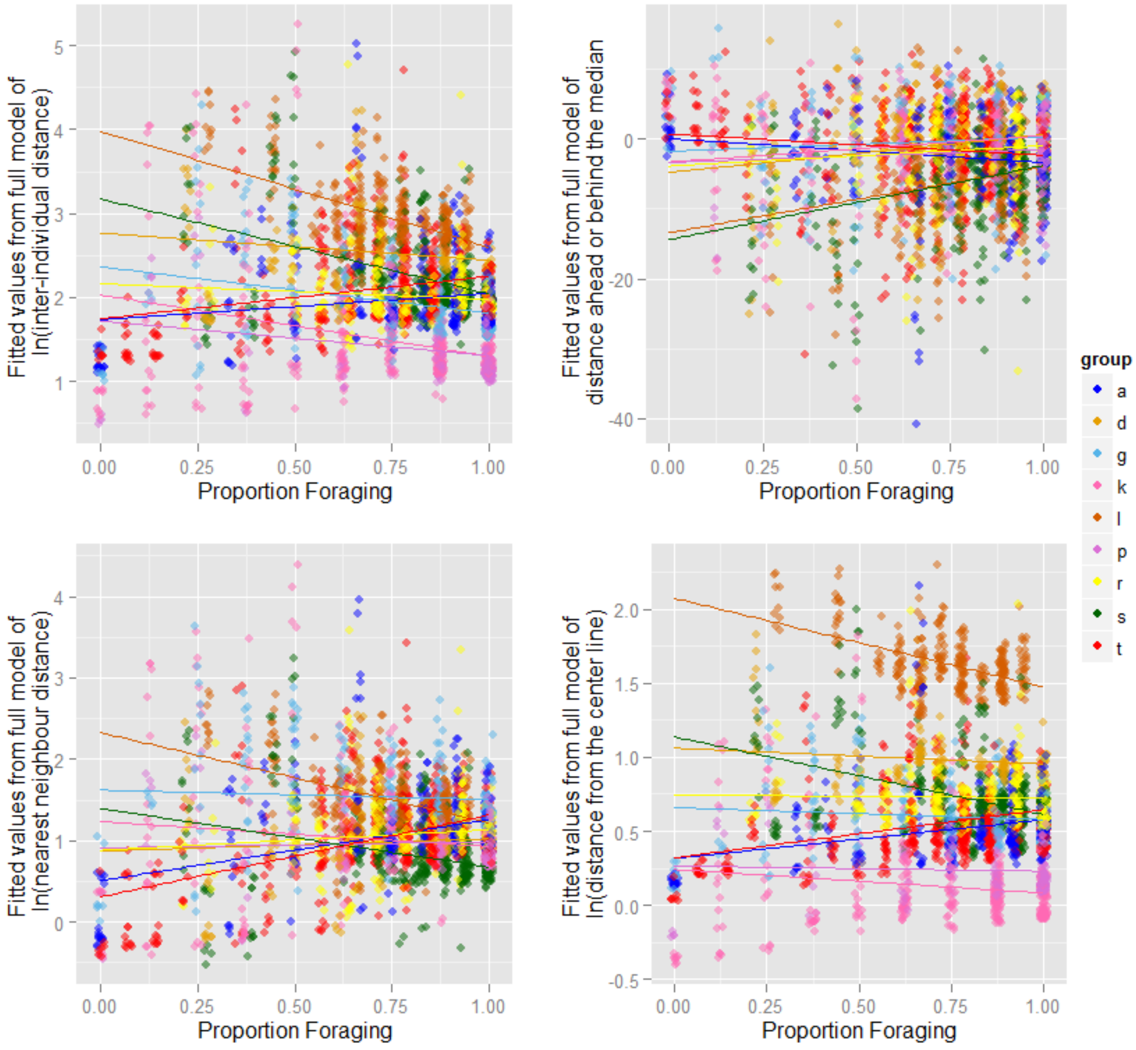

Figure 3.24 When a greater proportion of the OMU was foraging, geladas had larger IID (top left) and NND (bottom left), and were farther ahead (top right) and farther from the center line (bottom right)

3.3 Random Effects

Likelihood ratio tests were used to determine whether OMUs, or individuals, differed significantly from each other. These models included only random effects; no fixed effects were included. Even where random effects were not significant, they were retained in further models to best reflect the structure of the data (Barr et al., 2013). Table 3.24 shows the results of these comparisons. Four of the five metrics were significantly different for different OMUs, and the fifth was close ($p < 0.06$). After considering the effect of OMU, individuals had significantly different distances ahead or behind the median. There was no evidence that IID or NND were different for different animals.

Table 3.25 Random effects: For each of the six dependent variables, a model containing the random effect(s) listed was compared to a simpler comparison model, using a likelihood ratio test. All models were compared to the mean-only model. For the three individual-level dependent variables, comparisons were also made between models with random effects of both individual and OMU, as opposed to models with only the random effect of OMU.

	Random Effect(s)	Comparison Model	Chi-Squared	p value
Length/Width Ratio				
	OMU	Mean only	3.6256	0.0589
Area				
	OMU	Mean only	119.95	<2.2E-16
Distance from the Center Line				
	OMU	Mean only	244.63	<2.2E-16
	Individual within OMU	Mean only	244.63	<2.2E-16
	Individual within OMU	OMU only	0	1
Inter-Individual Distance				
	OMU	Mean only	431.53	<2.2E-16
	Individual within OMU	Mean only	431.53	<2.2E-16
	Individual within OMU	OMU only	0	1
Nearest Neighbour Distance				
	OMU	Mean only	79.456	<2.2E-16
	Individual within OMU	Mean only	80.895	<2.2E-16
	Individual within OMU	OMU only	1.4388	0.2303

Table 3.25 Continued: Random effects

	Random Effect(s)	Comparison Model	Chi-squared	p value
Distance ahead/behind				
	OMU	Mean only	5.2419	0.02205
	Individual within OMU	Mean only	19.862	4.86E-05
	Individual within OMU	OMU only	14.62	1.315E-4

Shaded rows indicate comparisons where one demographic category was significantly different from another ($p < 0.05$).

Chapter 4: Discussion

4.1 OMU Shape

Altmann (1974) predicted that savanna baboons should travel in a rank (perpendicular to the direction of travel) “whenever there is an advantage to remaining in a group and the group is foraging on slowly renewing resources that are of low overall density in the home range and that are not locally abundant”. To forage efficiently under such conditions, an animal should not forage in the wake of others. If animals avoid being behind others, the result will be that the group spreads out along a broad front that is wider along an axis that is perpendicular to the direction of travel. Baboon troops have been found to spread out in a broad front, with dominant animals occupying central positions (Dostie et al., in press). In contrast, my results indicate that the formation described by gelada OMUs, being more spread along the direction of travel, was closer in shape to a file.

One possible reason why gelada OMUs were long, rather than wide, is that OMUs were almost always found in the company of other OMUs, rather than ranging independently like troops of most cercopithecine monkeys. This suggests that the spatial structure of OMUs might be a consequence of the constraints imposed by adjacent OMUs. Geladas spend much of their foraging time in a seated position, either stationary or shuffling slowly in the seated position, using short bouts of quadrupedal walking to reach a new food supply (Wrangham, 1980). Given Altmann’s argument, the recent depletion of resources coupled to the presence of other OMUs, suggests that some directions of movement should be more likely than others. Walking perpendicular to the direction of travel would mean walking into another OMU, and would take the animal farther from its own OMU. Walking forward would either take the individual into fresh territory, or take it close to other members of its own OMU. Approaching members of its own OMU is safer than approaching strangers because intra-unit relationships are well defined, with a clear dominance hierarchy that reduces the potential for conflict.

It is more likely, however, that the absence of a rank formation can be explained by the fact that, unlike savanna baboons, geladas generally forage on abundant and evenly distributed graminoids (Jablonski, 2005). Fashing et al. (2014) found that graminoid plants (grasses and sedges) covered almost 30% of the ground at Guassa, and were found in over 73% of vegetation plots, and that these plants comprised 56.8% of the geladas' diet. The geladas were sometimes observed to return to the same areas on consecutive days, suggesting that they had not fully depleted the grass on their first visit. This being so, we can conclude that the primary driver of the modal formation adopted by OMUs is the proximity of other OMUs on either side and reflects their repulsive influence.

4.2 Correlates of shape

OMUs were longer relative to their width when they were travelling faster, when they were closer to the cliffs, and when they had more members. Paths may have structured movement while travelling, or the longer shape may have resulted from stragglers falling far behind the rest of their OMU (or alternatively from individuals rushing far ahead of the rest). The shape of the OMU during rapid travel was probably influenced by the terrain and the monkeys' preference for easier travel routes. The study site includes many linear features that afford convenient travel routes, including paths made by humans as well as watercourses and geological features. Travel in single file along these linear features accounts for some cases where OMUs were longer in the direction of travel. However, paths could not fully explain the long shape of the OMUs because geladas spent most of the observation time foraging across open grassland, where their movements were not constrained by paths.

OMUs may have been longer closer to the sleeping cliff because geladas were more likely to be travelling, either travelling away from the cliff in the morning or towards the cliff in the afternoon. Geladas usually spend the beginning and end of their day grooming and resting near the cliff, but my data collection procedure attempted to avoid these stationary periods. The first follow of the day therefore usually began when the herd began to move away from the cliff, and afternoon data collection ceased when the geladas were at, or almost at, the cliff edge.

The increased length of larger OMUs must stem, in part at least, simply from the inevitable fact that, given avoidance of other OMUs, a larger number of animals must generate a longer line than a smaller group. Consequently, larger OMUs to occupied more space. This suggests that geladas preferred to maintain their distance from the other members of the OMU, rather than maintaining their distance to all members of the OMU, or to a key individual such as the leader male.

OMUs also occupied larger areas when they were travelling faster. This could result from the animals being spread out along a path, particularly if the path curved. Perhaps geladas were less concerned about being far from their group members during travel. If the focus was on reaching a destination, rather than on social interactions, it may not have been important to stay close to familiar individuals.

Interpolation error could also have contributed to making the OMU areas larger at faster speeds. Since data collection was limited by the observer’s walking speed, faster travel speeds may have had coarser temporal resolution due to the time required to walk from one animal to the next.

Nevertheless, modal global shape can emerge from a variety of configurations of OMU members – they might be evenly distributed along the long axis or clustered in one or other way – that is not discernible in the length/width ratio.

4.3 Individual Distance Ahead or Behind the Median

Geladas tended to be farther towards the rear of the OMU when they were travelling faster. The finding that individuals being farther behind when travelling faster is related to the OMU being longer when travelling faster. The number of individuals ahead and behind the median must be identical. If the mean distance ahead or behind the median moves towards the rear, then that means that the individuals behind the median are farther behind, than the individuals ahead of the median are ahead. Therefore, it appears that the OMU is longer during faster travel because some stragglers are falling behind.

Geladas also tended to be farther behind when a greater proportion of the OMU was foraging. This could indicate an interaction effect between the proportion of the group that was foraging and travel speed, which relates to behaviour. When a high proportion of the group was foraging, the overall behaviour mode was foraging. When the proportion foraging was low, the animals could be either travelling or grooming, and these two modes could be distinguished by the speed.

The behaviour of individual geladas at their previous GPS point was also related to their position towards the front or rear within the OMU. Individuals that were travelling were farther ahead than those that were resting or socializing, and individuals that were foraging were farther ahead than those that were socializing. Two trends could contribute to these results. First, when most of the group was engaged in the same behaviour, that behaviour would be related to the behaviour described by the speed and proportion foraging metrics. For instance, when all the animals were travelling, each individual's behaviour would be travelling, and the speed would be high, and the proportion foraging would be low. In this situation, the model predicts that each individual should be farther ahead because its speed is high, farther ahead because the proportion foraging is low, and farther behind because the individual is travelling. It is possible that these effects cancel each other out.

Second, when the OMU members were performing different behaviours, there could be a real effect of behaviour on individuals' position within the group. Animals that were travelling might end up in forward positions because they started walking first, while those that stayed behind resting or socializing would start to move later, and end up at the rear of the group. Foraging individuals were farther ahead of those that were socializing because socializing is a stationary behaviour, while foraging usually involves some movement, so foraging animals would pull ahead of those that were socializing.

4.4 Lateral Distance from the Center Line

This metric represented the individual’s distance from the center line of the group, perpendicular to the direction of travel (regardless of the individual’s position near the front or back of the group). Larger average distances from the center line indicated more of a broad front shape, with less overlap in the travel paths of different individuals. Smaller distances indicated more overlap, potentially forcing monkeys to forage in a depleted zone immediately behind another monkey.

Another cause of variation in distance from the center line would be a difference between peripheral and central animals. In fact there was no tendency for certain individuals or demographic categories to be closer or farther from the center line. This suggests that geladas’ distance from the center was related more to the situation, rather than to something intrinsic to individual animals.

4.5 Individual Distance from All Other OMU Members (Inter-Individual Distance)

Inter-individual distance (IID) was larger when OMUs contained more animals. It appears that geladas living in larger OMUs spread out, rather than squeezing closer together to stay close to the entire group, or to a certain focal individual such as the leader male. Animals foraging too close together would interfere with each other’s foraging, so maintaining a suitable separation would help geladas to feed efficiently. It is also possible that females in larger OMUs are less closely related, genetically and/or socially, to some of the other females in the group. Geladas might prefer to keep their distance from less-related group members, or from more dominant animals, and these effects might be more pronounced in a larger group.

IID was also related to the geladas' behaviour. Faster travel speeds and a greater proportion of the group foraging were both associated with larger IID. Individuals that were travelling at their previous GPS point were farther from other group members than those engaged in any other behaviour. Geladas were closer together during social behaviour than when they were foraging. These results are similar to the results from the OMU area model because the two metrics both relate to the average distance between individual geladas.

The difference is that the OMU area is a measure of the average distance between all members of the group, while the IID model considers whether individuals' average distance from the other members of their group. By considering individuals' distances, it is possible to determine whether demographic category, and the random effect of individual variation, affect geladas' positions within the OMU. Smaller IIDs indicate more central animals that tend to stay close to the others, while large IIDs indicate a tendency to be farther away, and thus closer to the edge of the group. In fact, there was no evidence that IID varied between demographic categories. Considering the random effects, IID differed significantly between OMUs, but did not differ between individuals after controlling for the effect of OMU. IID was related to group size, behaviour, and OMU identity, but not to specific individuals or demographic categories.

4.6 Nearest Neighbour Distance (NND)

Most of the patterns observed for NND were similar to those for IID, and the two metrics were somewhat correlated. Group size was related to IID but not to NND. The correlation between IID and NND was greater in smaller groups. The similarity reflects the fact that the whole group was usually engaged in similar behaviours, and experiencing similar environmental and social conditions, at the same time. The factors that affect the focal animal's distance from its nearest neighbour, are simultaneously affecting its group members' distances from their nearest neighbours, contributing to IID and to the area of the group.

Behavioural factors were related to an individual's proximity to its nearest neighbour. Individuals were closest to their nearest neighbours during social behaviour, and farthest during travel, with foraging being intermediate. Faster travel speeds and a greater proportion foraging were associated with geladas being farther apart.

There was no difference in NND between demographic categories, or between different individuals within each OMU. This metric did not distinguish the identity of the nearest neighbours, so it is unclear whether geladas were consistently closer to certain individuals. This consistency between different individuals and demographic categories might indicate that a range of nearest neighbour distances are acceptable to geladas, and so the variation within individuals is greater than the variation between individuals. Most of the habitat at Guassa consists of open grassland, where visibility is good. The difference between being, say, 4 m from your neighbour, rather than 6 m, might not be important to geladas.

4.7 Effects of sex and reproductive status on spacing

Leader males tended to be farther forward than adult or young adult females. Follower males were between leader males and females, and not significantly different from either. Leader males might position themselves at the front because they are choosing the direction the OMU will take, but a front position does not necessarily indicate leadership or decision-making. Positioning himself at the front might also be adaptive for a leader male if the herd encounters a predator, and his position at the front enables the leader male, as the largest and strongest animal in the group, to protect his offspring from the predator.

Another possibility is that males require more food because they are larger. Larger animal species tend to have larger day ranges (Carbone, Cowlishaw, Isaac, & Rowcliffe, 2005). Perhaps male geladas have a longer optimal day range than the smaller females and juveniles, although obviously their actual day range must be acceptable for all demographic categories. Such a difference might mean that males are ready to move on sooner than females, and so find themselves at the front.

When OMUs included a female in estrus, individual animals were less likely to fall behind, as well as being less likely to be far from the center line of the group. This relationship could result if estrous females altered their behaviour to stay near the male, with the male tended to be near the front. Perhaps the leader male was more vigilant, or more inclined to herd stragglers, when one of his females was fertile. Gelada females in an OMU tend to have synchronized estrus cycles (Dunbar, 1980), so it is quite possible that many data points that had at least one estrous female, actually had more than one.

4.8 Conclusions

Gelada OMUs were usually longer in the direction of travel, than in the perpendicular direction. OMUs were larger in area and longer in shape when the group was travelling faster, or contained more individuals. Distance from the cliff edge was the most important environmental variable: OMUs were larger and wider when they were farther from the cliff. OMUs also occupied smaller areas when there was more green vegetation available.

Average inter-individual distances were greater in OMUs containing more animals, but nearest neighbour distances were not affected by group size. Individual geladas varied significantly in terms of their positions near the front or back of the group, their distances from their nearest neighbours, and their median inter individual distances. Leader males tended to be farther ahead than females. Individuals that were travelling at their previous GPS point were farther ahead, while those that were socializing were farther behind. Animals that were travelling were also farther apart, while those that were socializing were closer together.

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