THE UNIVERSITY
of LIVERPOOL

Ecological Determinants of Gelada Ranging Patterns

(*Theropithecus Gelada*)

Thesis submitted in accordance with the requirements of the
University of Liverpool for the degree of Doctor in Philosophy.

Chadden Piers Hunter

July 2001

ABSTRACT

Ecological Determinants of Gelada Ranging Patterns
(*Theropithecus Gelada*)

The foraging ecology of a band of gelada monkeys (*Theropithecus gelada*) was studied in the field at Sankaber, Ethiopia, for 14 months. The field site is at high altitude (3300m) and experiences severe variation in climatic and vegetational conditions across distinct wet and dry seasons and between different microhabitats. Gelada live in a complex fission/fusion social system and occupy a unique environmental niche as the world's only graminivorous primate species. Research was directed towards examining the ecological parameters affecting the gelada's group-level behavioural ecology. The nature and distribution of gelada food resources was found to be a more complex and influential selective force than previously acknowledged.

Gelada ranging behaviour varied in relation to spatial and temporal variation in food availability and specific small scale weather patterns, but not in relation to the distribution of sleeping sites, refuges or water sources. Group size and day journey length covaried significantly between seasons and months and the strength of the correlation between the two variables was determined by levels of food availability. The rate at which the main gelada study band underwent fission or fusion correlated to the degree in which food was patchily distributed but not direct levels of food availability. Distribution of food sources varied significantly between habitats as did levels of visibility. Gelada alarm and flight response rates were found to correlate more strongly to levels of visibility under 10 metres within each habitat than mean levels of visibility per se.

Both males and females spent significantly more time feeding, (and feeding on subterranean food items specifically) in the dry season, resulting in a slightly higher mean daily calorific intake than in the wet season. It is suggested that the dry season does not represent a 'nutritional bottleneck' to the gelada as previously thought, but does constitute a period of increased energy requirements due to seasonal variation in lactation and thermoregulation demands.

ACKNOWLEDGEMENTS

In completing this PhD I owe many people a great deal of gratitude. Without their kind and generous help the fieldwork and thesis writing would not have been possible.

My parents, Louise Hunter and Gorol Dimo, have been an unwavering source of love and encouragement throughout my education, and this PhD is in no small way dedicated to their emotional investment and support. My father also provided the substantial financial backing which made the whole thing possible.

I am deeply grateful to my supervisor, Prof. Robin Dunbar, whose earlier work inspired me to study gelada in the first place and who remained forever positive and supportive through a project that many supervisors would discard as a logistical nightmare. Robin was blessed with an uncanny knack of always saying the right thing at the right time, and I would have given up in despair on a number of occasions if it were not for his kind, insightful and optimistic coaching.

In Ethiopia, the Biology Department of Addis Ababa University kindly sponsored me as a Visiting Researcher. Permission to conduct fieldwork in the Simen Mountains National Park was granted by the Ethiopian Wildlife and Conservation Organisation (EWCO) and the Agriculture Bureau of Amhara National Regional State, and would have been impossible without the cooperation and help of the Simen Mountains National Park Staff. Invaluable local support was provided Gelaye Tsega and his family, most notably Mulualem Gelaye, who faithfully stuck it out as my Right Hand Man in the Simen Mts. through the harshest and sometimes dangerous conditions.

In Liverpool, I am indebted to my friend and colleague, John Lycett, for his logistical and moral support which got me through some of the darkest moments of the adventure; Russell Hill for kindly and patiently guiding me through the statistical jungle; Simon Chu for his steady hand in helping tidy up at the finish line; Katy Parry, Nicola Koyama and Suzanne Shultz for proof-reading; and a large number of close friends without whose encouragement and good cheer I would have lost sight of the light at the end of the tunnel. I hope I get to thank you all personally.

CONTENTS

Ecological Determinants of Gelada Ranging Patterns
(*Theropithecus Gelada*)

Chapter 1: Introduction

Chapter 2: Methods

Chapter 3: Study Site and Population

Chapter 4: Factors affecting home range use and habitat selectivity

Chapter 5: Food Availability and Feeding Behaviour

Chapter 6: Group dynamics and spatial patterns

Chapter 7: Predation Risk and Alarm Responses

Chapter 8: Discussion

LIST OF FIGURES

CHAPTER THREE

CHAPTER FOUR

CHAPTER FIVE

CHAPTER SIX

CHAPTER SEVEN

LIST OF TABLES

CHAPTER TWO

CHAPTER THREE

CHAPTER FOUR

CHAPTER FIVE

CHAPTER SIX

CHAPTER SEVEN

CHAPTER ONE

Introduction

1.1 Theoretical background

Over the past few decades a large body of research has been devoted to the causes and consequences of group living in primates (e.g. Crook & Gartlan, 1966; Kummer, 1971; Altmann, S. 1974; Wrangham, 1980; Terborgh, 1983; van Schaik & van Hooff, 1983; van Schaik, 1989). A number of studies have suggested that competition for, and defence of, food resources represents the main ecological factor underlying the advantage of forming stable groups (e.g. Cheney & Seyfarth, 1987; Robinson, 1988; Wrangham, 1980, 1983; Isbell, 1991), while other researchers have considered predation pressure to be the primary factor promoting group living among primates (e.g. Alexander, 1974; de Ruiter, 1986; Isbell, 1994; Cowlishaw, 1997a,b; Hill & Dunbar, 1998). Although debate continues on the relative importance of each factor in the *evolution* of primate group formation, it is generally accepted that both factors may operate simultaneously on the current ecology of a primate group. For instance, predation pressure might force primates into group living, but the patterns of competition for resources within the group might be the primary force determining its internal social structure (Terborgh, 1983; van Schaik & van Hooff, 1983; van Schaik, 1989; Barton & Whiten, 1993; Houston *et al.*, 1993).This thesis represents an attempt to examine the influence of these two key ecological factors on the group level behavioural ecology of gelada (*Theropithecus gelada*) in the Simien Mountains of Ethiopia.

Food acquisition and predation risk have also been invoked when investigating the determinants of group size among primates. Larger primate groups are assumed to have a lower risk of predation (Cowlishaw, 1999) and it has thus been suggested that predation risk is a key factor determining the lower limit to group size (van Schaik, 1983; Dunbar, 1988). On the other hand, larger groups have been shown to spend more time foraging and/or travelling, indicating a relationship between group size and food exploitation (Waser, 1977; van Schaik *et al.*, 1983; de Ruiter, 1986; Steenbeek & van Schaik, 2001). Therefore, the levels of competition for food facing group members are believed to determine the upper limit to possible group size (Dunbar, 1996). Indeed, de Ruiter (1986) demonstrated that larger groups of wedgecapped Capuchin monkeys (*Cebus Olivaceus*) held an advantage in terms of predation risk but smaller groups held an advantage due to lower intergroup food competition. Moreover, it is thought to be scramble-type competition for food within groups that underlies the commonly found positive relationship between group size and day journey length (Stacey, 1986; Wrangham *et al.*, 1993; Gaynor, 1994; but see Henzi *et al.*, 1997a). Accordingly, as group size increases so too does within-group feeding competition which requires more time to be devoted to foraging (Waser, 1977; Terborgh & Janson, 1986). In turn, temporal investments in feeding can only increase to an extent constrained by the requirements of other crucial activities, such as resting and social activities (Dunbar, 1992). In line with this, Dunbar (1996) has suggested that the maximum permissible group size for *Papio* baboons is influenced by climatic variables acting, via resource availability, on time-budget constraints. Concurrently, if minimal permissible group size is dictated by levels of predation risk then optimal group size is expected to arise out of a trade-off between the costs of feeding competition and the benefits of predator avoidance (e.g. Pulliam & Curaco, 1984; Terbough & Janson, 1986; van Schaik, 1989; Hill & Lee, 1998, Hill, 1999).

One particular focal point of recent primate socioecological models has been the recognition of different forms of feeding competition and their effect on social relationships (Janson & van Schaik, 1987; van Schaik, 1989). For instance, indirect or 'scramble' competition among members of a primate group is thought to limit the size of the group but not place any major constraint on the nature of social relationships within it. In contrast, the existence of direct or 'contest' competition within a group is assumed to promote strategic alliances among kin (Janson, 2000). For example, in a cross species comparison of squirrel monkeys, Mitchell *et al.* (1991) were able to show that when competition for food was most intense and patches of food were easier to defend, the species was more likely to be female-bonded. This scenario highlights the fact that the style of the feeding competition is thought to be based on the size and distribution of appropriate food patches (Terborgh, 1983; Terborgh & Janson, 1986).

Although the theoretical models of primate socioecology outlined above focus on the key components of predator avoidance and food acquisition, both factors have proven very problematic to demonstrate in field research (see Fraser & Huntingford, 1986 for a review). Without excellent observation conditions actual food intake is difficult to measure under field conditions (Byrne *et al.*, 1993) and is often hindered by the complex and diverse diet exhibited by primates (Whiten *et al.*, 1991). As each plant-food species will contain different combinations of nutrients and indigestible material this has made it difficult to gain a detailed assessment of the influence of nutritional constraints on broader patterns of primate socioecology (but see Altmann, 1991; Wrangham *et al*, 1991; Barton 1992; Byrne *et al*., 1993). Similarly, predators of primates are typically cryptic, predator-prey relationships are poorly understood and actual predation is rarely observed (Cheney & Wrangham, 1987; Isbell, 1994). Nonetheless, Cowlishaw (1997a) was able to show that, although neither factor was directly quantifiable, the trade-off between diminishing predation risk and enhancing food acquisition was manifest in the way a baboon troop used different habitat types.

A number of primate studies have found cross-species comparisons useful in elucidating connections between ecology and behaviour (Crook & Aldrich-Blake, 1968; Gartlan & Brain, 1968; Altmann, 1974; Hladik, 1977; Dunbar, 1993). Given that different *Papio* baboon populations experience great variation in habitat, group size and environmental conditions, they have proven one of the most rewarding taxa of primates for analysing and testing the aforementioned patterns in cross population studies (see Barton *et al*., 1992; Dunbar, 1992, 1993, 1996; Hill, 1999).

1.2 *Theropithecus gelada*

Gelada 'baboons'[1] are an exceptional species with which to examine the influence of ecological conditions on the nature of group living in primates. They are highly terrestrial and easy to observe, while their social structure and ecological niche are unique amongst primates (Crook, 1966). More specifically, in light of the theoretical framework discussed in this introductory chapter, gelada experience a number of

---

[1] Although, given the divergence of their social system and ecological niche from *Papio spp*. their reclassification outside the *Papio* genus appears justified (Groves, 1993)(see also Section 2.2).

relatively extreme parameters in terms of group formation and resource distribution. For example, gelada form unusually large foraging groups which are remarkably flexible in their day to day size and composition (Ohsawa, 1979). These large associations are a key feature of gelada society yet the factors affecting foraging decisions made at the group level are poorly understood. This represented an important area in which to focus the current field study, since although family-units (see below) provide the context for social and reproductive behaviours, group-level patterns provide the context for understanding the influence of ecological factors on the foraging, movement and dynamics of gelada groups.

Aided by excellent observation conditions, early field studies tended to focus on the social and behavioural aspects of the gelada socioecology, and extensive descriptions can be found in Dunbar and Dunbar (1975), Kawai (1979) and Dunbar (1984). In summary, the basic component of the gelada social structure is the one-male unit, which consist of one reproductive male and an average of four (but up to ten) reproductive females and their young, and has been described in great detail elsewhere (Mori, 1979; Dunbar, 1979a, 1983a,b,c). Gelada units that share a common home range typically forage together and are called a 'band' (see Kawai *et al.*, 1983), while bands, or parts-there-of, often join to form large but labile multi-band foraging herds numbering many hundred individuals. Although a number of other primate species' social structures are based on one-male reproductive units (see Dunbar, 1988 for a review), gelada, along with hamadryas baboons (*Papio hamadryas*), are unique in that one-male units typically join in a hierarchical arrangement forming the large multi-unit associations (Dunbar, 1983d). However, comparatively little is known about all higher levels of gelada association, which range from individual units travelling alone to mixed-band herds numbering over 850 animals.

In terms of past field studies, gelada are unusual among the primate taxa in that earlier researchers were able to adopt a somewhat 'top-down' perspective and concentrate on the fine-grained details of individual behaviour and social relations. In contrast, relatively less fieldwork has focused on 'bottom-up' ecological constraints on the gelada group as a whole. This research in this study will aim therefore to focus on the latter. More specifically, the investigation was begun with four broad questions in mind:

1). How does the spatio-temporal distribution of resources influence gelada ranging behaviour?
2). How does seasonality affect the gelada's foraging ecology and do they experience a dry-season nutritional shortage?
3). What factors determine the patterns of gelada group fission and fusion?
4). Do gelada show a behavioural response to variation in predation risk?

These general questions will guide the thesis and each touches on a respective theme of the individual data analysis chapters 4 through 7. The background theory behind each of these chapters will now be outlined in turn below.

1.3 Habitat use and feeding ecology

A relatively rich body of literature exists on the ecological determinants of foraging ecology and group movement in *Papio* baboons, and how the influence of these factors may vary in time and space (Altmann & Altmann, 1970; Barton *et al.*, 1992;

see Hill, 1999 for a review). For example, temperature and rainfall are often cited as fundamental ecological components that can influence a primate's movements either directly, through adverse climatic conditions and temporary water sources, or more often indirectly by affecting growth of the animal's resource base (Bronikowski & Altmann, 1996). A number of studies have also demonstrated the importance of water sources in dictating day journey lengths and directions (Altmann & Altmann, 1970; Sigg & Stolba, 1981; Hamilton, 1986; Brain, 1990; Barton *et al.*, 1992), while others have noted that the distribution of sleeping sites appears to influence the spatial preference of baboons (Altmann, 1979; Post, 1978; Barton *et al.*, 1992). Nonetheless, the ways in which a group of primates utilises the space around it is thought to be primarily influenced by the distribution of their food sources (Altmann, 1974; Barton *et al.*, 1992), and diet is commonly examined as an intervening variable between a primates environment and its population density, abundance and social organisation (e.g. Crook and Gartland, 1966; Altmann, S. 1974; Wrangham, 1979, 1987; Byrne *et al.*, 1993).

Gelada ranging behaviour is assumed to be influenced by similar factors to those outlined above. However, little has been documented about variations in their day ranging or how these patterns are underpinned by the distribution of their resources. The key aim of Chapter 4, therefore, will be to elucidate these patterns. For example, while it is generally agreed that the most important factor influencing primate ranging behaviour and habitat use is the spatial and temporal distribution of food (Davidge, 1978; Anderson, 1981a; Dunbar, 1988) gelada represent a somewhat unique example amongst the primates, since their diet is highly specialised towards graminivorousness (grass-eating) and the short grasses on which they graze are assumed to be predominant throughout their environment (Crook, 1966; Crook & Aldrich-Blake, 1968; Dunbar, 1977; Iwamoto, 1979). Implicit in these studies is the assumption that the gelada's environment is relatively uniform and resources are evenly distributed, therefore exerting a minimal influence on day-to-day ranging patterns (Iwamoto, 1979). An aim within Chapter 4 will be to test this assumption.

Crook (1966) suggested that the contrast in social systems between gelada and other *Papio* baboons was a function of the difference between respective environments in terms of food availability, predation pressure and the characteristics of secure sleeping sites and refuges. Furthermore, a number of early studies proposed that the essence of hamadryas and gelada social structure (i.e. one-male units that fuse into larger groups when possible) is a shared adaptation to an arid, or at least seasonally arid, environment (Crook & Gartlan, 1966; Crook, 1970; Jolly, 1970; Eisenberg *et al.*, 1972). Dunbar and Dunbar (1975) brought this hypothesis into question; firstly by pointing out that despite surface similarities between the one-male units of gelada and hamadryas, striking differences existed in the social organisation within the units (see also Kummer, 1971). Secondly, they noted that until more detailed ecological research was conducted, it was difficult to presuppose variations in the resource base or quality of the gelada's habitat. Furthermore, since their resource base is thought to be widely and evenly dispersed it is thought to represent the extreme low end of food 'patchiness'. This is a crucial aspect of gelada ecology to follow up since much of the theory underlying foraging ecology is based on the concept of the size and distribution of 'patches' (Charnov, 1976; Stephens & Krebs, 1986) and the nature of feeding competition in particular is thought to be directly influenced by the level of 'patchiness' of a resource (Zahavi, 1971; Wrangham, 1980). Hence, Chapter 4 will begin the analytical component of the thesis by focusing on how the spatiotemporal distribution of resources influence the ranging patterns of gelada.

As mentioned, the Gelada's diet is one of the most specialised of all primate species, with monocotyledon grasses accounting for over 90% of their total intake (Dunbar, 1977; Iwamoto, 1975). Unlike their frugivorous relatives (baboons and macaques), gelada must face the problems resulting from such a folivorous diet, in which the majority of nutrients are held in the indigestible cell walls of the foliage. Ruminant folivores (e.g. cows) deal with this problem by utilising microbial fauna in the forestomach, whereas non-ruminant folivores (e.g. equines, geese) rely on hind-gut fermentation (Chivers & Hladik, 1980). While gelada are clearly non-ruminants, very little is known of their digestive micro-fauna (Iwamoto, 1993a). It has been suggested that they deal with this specialisation for a high cellulose graminivorous diet chiefly by bulk feeding and thorough mastication of the food (Dunbar & Bose, 1991), for which they have smaller incisors and larger molars than the other frugivorous *Papio* baboon species (Teaford, 1993). Through the gelada's need for bulk feeding, their dietary specialisation will necessarily influence time budget and ranging patterns, and thus carries important consequences for all social and reproductive behaviours (Iwamoto, 1975). Indeed, gelada spend more time feeding than any other herbivorous primate (Iwamoto, 1993b).

But the gelada's foraging problems do not end there. One of the key features of gelada environment is the extreme seasonality associated with rainfall. This carries emphatic consequences for their chief food source, short green grasses, which grow in abundance for roughly 6 months of the year (May-October) but are desiccated severely during the dry season. The gelada's heavy dependence on grasses is also reflected in the fact that band size appears to be determined by the amount of green grass in that band's home range (Dunbar & Dunbar, 1975). However, the Dunbar's (1975) vegetational data were based on one set of dry season transects (recorded in January 1972) and the distinct wet and dry seasons of the Ethiopian highlands lead to extensive seasonal desiccation of the green grasses eaten by gelada. This transition also results in a dietary shift to more subterranean food resources during the dry months between December and May, and the relative importance of levels of grass coverage during this time might therefore be diminished. Hence the gelada's ability to exploit underground food sources successfully appears to be a crucial element to their foraging ecology, although little actual data are available. It is also not clear whether this dietary shift represents a seasonal, 'nutritional bottleneck' as implied by Crook (1966), since very little is known about fluctuations in food availability within the gelada's environment. Struhsaker (1967) pointed out that roots and rhizomes represent a highly nutritious dry season food source for vervet monkeys (*Ceropithecus aethiops*) in a savannah environment, and Iwamoto (1979) found no evidence to suggest food shortage was ever a factor in gelada mortality. The implications of seasonal shifts in gelada foraging ecology and nutrient intake represent the focus of Chapter 5, and will be driven by the testing of Crook's (1966) hypothesis that the dry season constitutes a period of food paucity for the gelada.

1.4 Ranging patterns and predation risk

An important component of Crook's (1966) original thesis was that seasonal deficiencies in the resource base underpin the tendency for gelada bands to split into smaller groups during the dry season. However, very little is known about the actual nature of this variations in group size, namely the mechanism of fission and fusion of gelada groups. A number of studies have examined the factors effecting fission of primate groups (Stolz & Saayman, 1970; Nash, 1976; Dittus, 1987; Hamilton & Bulger, 1993; Gaynor; 1994; Henzi *et al*, 1997b), while a smaller number have described cases of group fusion (Altmann, 1980; Isbell, 1991; Hawkins, 1999). Some authors have posited that social and not ecological factors are the determinants of primate group fission or fusion (Chagnon, 1975; Malik, *et al*, 1985). For example, Henzi *et al* (1997a) concluded that troop fission, at least for mountain baboons (*P. chacma*), is not exacerbated by predation or inefficient foraging, but by the limited time available for individuals to service social relationships as troop size increases. However, it is important to make the distinction between one-off fission or fusion events, of which the above studies relate, and a true fission-fusion social organisation.

True fission-fusion systems, in which subgroups vary frequently in size and composition, are rare among primates but spider monkeys (*Ateles spp.*) and chimpanzees (*Pan troglodytes*) are two species that do not form spatially cohesive social groups. In order to test the ecological factors underlying the fission-fusion system of spider monkeys, Robbins *et al* (1991) used a cross-species comparison. They point out that gibbons (e.g. *Hylobates muelleri*) and spider monkeys (e.g. *Ateles geoffrroyi*), share very similar diets, morphologies, locomotor styles, body sizes and life histories, yet display markedly different social organisations. Gibbons remain in long-term territorial monogamous pairs, while spider monkeys exhibit a fission-fusion style social system in which subgroups change size and composition frequently. Because spider monkeys and gibbons show similar group size only when the distribution of their food patches is equivalent, the difference appears to lie in the fact that gibbon food patches are usually more evenly distributed (gibbons: food patches/ha, CV = 55.3%; spider monkeys: food patches/ha, CV = 85.6%). Thus, the fission-fusion nature of spider monkey social organisation appears to be driven by seasonal, ecological (as apposed to social) constraints. Similarly, Doran (1997) found that lowland rainforest chimpanzees (*Pan troglodytes verus*) of Täi were significantly smaller and less mixed in the height of the dry season. Chapman *et al* (1995) were able to show that both spider monkeys and chimpanzees (at Kibale, Uganda) congregate into larger sub-groups when food sources are plentiful and evenly distributed, but reduce their subgroup size when food is scarcer and more patchy in space. Smaller groups deplete patches relatively slowly and therefore reduce travel costs. However, when larger patch size allows larger groups, spider monkeys may gain more from decreased predation risk, while it is suggested that chimpanzees might be subject to some additional social costs and benefits (Chapman *et al*, 1995; Doran, 1997).

The issues facing gelada are somewhat different. Firstly, the overall size of the foraging group is of little immediate social relevance to individual gelada as their relationships are confined to the unit. Increased herd size therefore, poses little or no constraint on social time. Furthermore, the flexibility of the gelada system enables foraging groups to split and rejoin on a much finer temporal scale than that suggested by Crook (1966). A primary aim of Chapter 6 will therefore be to test the hypothesis that the gelada fission-fusion system is responding to shorter term variation in ecological parameters, as apposed to Crook's longer-term (seasonal) changes.

If the nature of the gelada fission-fusion system is based on a pattern of spatial or temporal resource distribution it implies some level of feeding competition. Given that grazers such as gelada are not expected to experience contest competition for food (Crook & Aldrich-Blake, 1968; Wittenberger, 1981; Thouless, 1990), it is interesting that they exhibit such a strong matriarchal social system. A number of primate studies have endorsed the idea that stable hierarchical relationships among females, such as those manifest in the gelada one-male units, are the result of contest competition for food (Janson, 1985; van Noordwijk & van Schaik, 1987; Mitchell *et al.*, 1991; Gore, 1993), and more recent models, outlined above, have shown that females are more likely to be philopatric and form stable coalitions when ecological conditions promote within-group contest competition (Barton *et al.*, 1996). Some authors however, have noted that within-group competition is not always clear in primate field studies (Janson & van Schaik, 1987) or may occur only seasonally, when food availability is lowest (Post, 1978). Barton (1993) made the important observation that it might not be lower levels of food availability per se, driving higher feeding competition during the dry season, but the degree to which that food is clumped (see also Barton & Whiten, 1993).

Although feeding competition has proven extremely difficult to discern among grazers (Appleby, 1983; Thouless, 1990), a number of points suggest it might be worth investigating in gelada. Firstly, Iwamoto (1978) has shown that gelada band size and population density are largely affected by the primary production of their habitat, despite levels of consumption efficiency being maintained well below those considered critical. Secondly, Wrangham (1976) noted that gelada showed preference for certain grass species and individuals appeared to avoid eating from previously used feeding sites, citing these observations as evidence for low levels of grazing competition within the herd. Simply the tendency for gelada to form very large foraging herds raises implications in terms of feeding competition since competition, regardless of form, increases with the number of group members (Janson & van Schaik, 1987; Barton and Whiten, 1993). Furthermore, Kawai and Mori (1979) suggest that gelada may have social units integrated at the smallest physical spacing among all primate species and note that units put great effort into maintaining spatial integrity within the larger herd.

It has also been noted that feeding competition may operate through numerous mechanisms and has proved very difficult to measure in field studies (Janson & van Schaik, 1987). Thouless (1990) identified feeding competition in grazing red deer (*Cervus elaphus*), existing as a passive process by which subordinates not only avoided conflict with more dominant individuals, but fed at significantly slower rates the nearer they were to an animal able to displace them, whether a displacement occurred or not. In this way, the cost to the 'aggressor' is minimal but lower ranking individuals may be forced to shift some investment from feeding effort to social vigilance. Barton (1993) demonstrated that even very low levels of supplanting among *Papio* baboons can result in and maintain differentials in foraging success between individuals. This is especially pertinent to gelada, although their feeding ecology appears closer to that of many non-primate grazing herbivores. For example, American bison cows (*Bison bison*) form linear hierarchies in which more dominant individuals gain advantages in feeding efficiency even though aggressive interactions between cows are almost non-existent (Rutberg, 1986), and Appleby (1983) was able to show higher levels of feeding displacement among red deer only in winter when food availability was lowest. Thus subordinates suffer reduced food intakes even when feeding on scramble type foods (e.g. capuchins, Robinson, 1981; red deer, Thouless, 1990). In light of the studies outlined above, the traditional dichotomy between scramble and contest competition appears somewhat simplistic, especially for large mammals such as primates with complex ecologies. For example, it has been pointed out that omnivorous baboons may scramble contest for leaves and grass while contest competition exists for flowers and fruits etc. (van Schaik, 1989; Cowlishaw, 1993). Indeed, pure scramble competition is probably rare in species that travel and forage together.

Feeding competition in primates has often been examined based solely on neighbour proximites and densities (e.g. Robinson, 1981). While a number of primate studies have examined the relationship between female rank and rates of supplantation from feeding sites (e.g. Post *et al.*, 1980; Whitten, 1983; Johnson, 1989; Amat & Obeso, 1991; Mitchell *et al.*, 1991) fewer have investigated the effect dominance rank has on *position* of individuals within a group (but see Collins, 1984; Janson, 1990; Barton, 1993). Indeed, social animals face a constant dilemma in maintaining optimal spacing within a group as spacing behaviour may be influenced by the somewhat contrary forces of predation risk and feeding competition. When individuals spread out it is assumed that feeding competition will be reduced (Altmann, 1974; Janson, 1992), while tighter aggregations are thought to reduce predation risk (Hamilton, 1971). A number of studies on bird flocks have demonstrated that individuals closer to the edge are more vigilant due to greater exposure to the risk of predation, and therefore have the lowest feeding rates (e.g. Powell, 1974; Inglis & Lazarus, 1981). It has also been noted that individuals at the front of progression orders are more exposed to the risk of predation (Rowell, 1969; Harding, 1977; Altmann, 1979; Collins, 1984; Rhine *et al.*, 1985; Cowlishaw, 1993). Barton (1993) found that dominance rank among female olive baboons was positively related to a measure of 'centrality' in the group while foraging and suggests that the importance of passive spatial mechanisms has been underestimated in patterns of primate feeding competition.

An examination of some of the above-mentioned phenomena with regards to gelada will be conducted in Chapter 6. Furthermore, if the matrilineal bonds observed within gelada units are maintained by some form of competition, larger or more dominant units might be expected to hold an advantage over smaller units in terms of foraging success, especially if gelada food resources are more clumped than previously thought. As the foraging herd moves, units at the leading edge might be expected to encounter a higher quantity or quality of food than units at the trailing edge of the herd (see Jarmen, 1974). Concurrently, units might compete in subtle ways for safer positions within the herd. Data will be analysed in Chapter 6 to test these various hypotheses.

As stated earlier, a trade-off may exist for primates between optimal foraging goals and the need to maintain acceptably low levels of predation risk (Houston *et al.*, 1993; Cowlishaw, 1993, 1997a,b,). For example, the large foraging herds created by gelada might involve costs in term of scramble competition for food resources, but are thought to be formed as a response to the risk of predation (Crook, 1966; Dunbar &

Dunbar, 1975; Kawai & Iwamoto, 1979). The assumption that larger primate groups are safer is backed up by the observation that larger groups both feed in more dangerous foraging habitats (van Schaik & van Noordwijk, 1988) and are commonly less vigilant (de Ruiter, 1985). The location of gelada sleeping sites exclusively on sheer and inaccessible cliffs serves presumably the same anti-predator function (Crook & Aldrich-Blake, 1968; Jolly, 1972; Dunbar & Dunbar, 1975), and indeed, there is substantial evidence that a number of natural predators prey on gelada throughout their home range. Gelada are considered at particular risk from predation since their general habitat is usually described as open and exposed grassland with no tree refuges. A number of studies have noted that baboons appear more nervous in open areas when they are far from suitable refuges (Byrne, 1981, Dunbar, 1989a).

Gelada group size, however, varies greatly between seasons and little is known about the suite of ecological parameters affecting it. Also, minimal attention has been paid to the fact that some gelada microhabitats support much denser and larger vegetation than the open grass areas and degree of bush level vegetative cover has been shown to be a positive correlate of predation risk for other baboon populations (e.g. Cowlishaw, 1997a,b; Hill, 1999). The purpose of Chapter 7 therefore, is to utilise the observable variation in gelada group size and habitat visibility as a framework in which to examine a novel source of data which attempts to measure predation risk, namely the gelada's level of flight in response to perceived threats.

1.5 Thesis outline

In this introductory chapter, I have attempted to touch on some aspects of primate behavioural ecology that I feel underpin the questions above (section 1.2) and set a framework for this current study on gelada foraging ecology. Chapter 2 will provide a natural history background of the Sankaber study site in the Ethiopian highlands and the gelada population inhabiting it, while Chapter 3 will detail the methods used for collecting observational and ecological data throughout the study. Chapters 4 to 7 represent the backbone of the study, in which data will be presented and analysed in relation to the general themes outlined above, beginning in Chapter 4 with descriptions of the ecological characteristics of the Sankaber gelada band's home range. In particular, the spatiotemporal distribution of food resources will be related to the patterns of movement and habitat preference of gelada throughout the home range recorded over one full annual cycle. The influence of water source distribution, sleeping refuges, topography, and climatic variables on ranging patterns will also be examined. Chapter 5 will adopt a more fine-grained analysis of the patterns of food acquisition by gelada food sources. More specifically, the seasonal patterns in which food availability varies will be examined in relation to seasonal activity budgets, dietary profile and levels of food and nutritional intake. Chapter 6 will step back from the details of feeding to look at the broader patterns of herd dynamics. Variation in group size, day journey length and the patterns of group fission and fusion will be related to certain environmental parameters that might be influencing them. Chapter 6 will conclude with a consideration of the spatial placement of individual family units within the herd and how this might apply to inter-unit differentials in foraging success and predation risk. Chapter 7 will move away from feeding ecology per se and continue with the theme of predation risk. The patterns of flight responses shown by the gelada will be assessed in relation to the cause of the alarm and an estimate of the relative risk of predation between habitat types. Each of the four main results chapters will begin with a more detailed introduction specific to the theme of the chapter, highlighting the main topics of investigation and listing a number of hypotheses or predictions to be tested in the chapter with the data presented, while ending with a brief discussion of the key findings and their importance. Chapter 8 will conclude the thesis with a synthesis of the key findings of the entire study and a discussion of their significance to gelada foraging ecology in general.

CHAPTER TWO

Methods

2.1 Ecological Sampling

The main body of this research was conducted between January 1st 1998 and January 1st 1999, and hereafter all months referred to were in 1998 unless otherwise stated. Ecological monitoring was conducted in all 12 months of 1998, although some simple procedures were recorded by a trained field assistant (as noted in the text) when I could not be present. Climate data were collected as described in Chapter 3, and will be further presented in Chapter 4.

2.1.1 Vegetation transects

Vegetation profiles were obtained using line transects across the 3 main habitat types (escarpment, plateau, and gorge) found in the study area. Three 500 metre transects were established on the plateau, two 500 metre transects in the gorge habitat and one 500m transect on the escarpment. Transects were carried out in October 1998, at the end of the wet season.

The escarpment transect was restricted to tracts of giant heather forest due to the inaccessible nature of the sheer cliffs on the escarpment (which constitute over 60% of the vertical area of the escarpment face). All transects were marked with pegs, using a

50m tape measure positioned along a compass bearing. The percentage cover of each plant species was recorded as a total distance occupancy (in cm) along the tape measure.

More generally, vegetation along the transects was also classified as:

1. Bare rock or dirt
2. Short grasses (< 10cm)
3. Long grasses, herbs (10 - 60cm)
4. Shrubs, bushes, small trees (60 - 300cm)
5. Tall trees (>300cm)

This classification was adopted where plants could not be identified to species level. Samples of unidentified vegetation were collected with the aim of taking them to the National Herbarium, Addis Ababa, for species identification. Unfortunately, almost all samples had to be abandoned at the fieldsite, although some post hoc identification was possible using descriptions and comparative samples.

2.1.2 Vegetation quadrat sampling

Food availability for each habitat type was examined using 40 (50 x 50cm) square quadrats. Quadrats were positioned in contiguous pairs so that each pair constituted, in effect, a rectangle of 100 x 50cm. Quadrat pairs were located at equidistant points along the established transects - 10 on the plateau (150m apart), five in the gorge (200m apart) and five on the escarpment (100m apart). The rectangular quadrats were initially marked with wire secured between four pegs but all wire and most pegs from the plateau and escarpment plots were stolen. However, it was possible to re-establish these quadrats by digging a corner mark and then replacing pegs temporarily on sampling days.

All quadrats were monitored for percent 'greenness'/desiccation and photographed with a digital camera at monthly intervals[1]. In April, at the height of the dry season, the percent cover and height of each plant species or type within one 50 x 50cm quadrat per pair were recorded before all above ground vegetation was clipped. As much care as possible was taken to collect and include loose seeds in the sample. The top 20 cm of soil was then dug up to extract all below ground roots, tubers and rhizomes. All vegetation samples were sorted and dried, and while identification was not possible for many species (especially grasses), most specimens could be sorted into 'food' or 'non-food' items with respect to gelada. This classification is not species-specific, in that some plant species were classified as 'food' when green during the wet season and 'non-food' when desiccated during the dry season. Although it proved unfeasible to repeat this procedure on a monthly basis as planned, the adjacent half of the quadrats were clipped in October at the end of the wet season, thus providing food availability samples from two extremes of the seasonal spectrum. All quadrat samples were completed within one week of both April and October. This method is not ideal as it assumes even distribution of food-plant species between neighbouring quadrats.

It was not possible to measure wet weight of clipped vegetation in the field, but dry weight of samples were measured at the University of Addis Ababa, thus providing an

---

[1] When I was not present at the fieldsite at the precise monthly interval, photos were taken by a trained field assistant. The digital camera provides the exact date and time assuring accuracy of the records.

estimate of dry weight of food-plant species per unit area for each habitat type (see Table 5.2, Chapter 5).

2.2 Behavioural Observations

Gelada are almost exclusively diurnal and a study by Kawai and Iwamoto (1979) using radio-telemetry transmitters, indicated that practically no activity besides resting occurs between 07:00 and 18:30 on the sleeping cliffs. Activity data were therefore recorded on randomly chosen male and female focal individuals within 11 one-hour time zones, beginning with 7:00-8:00 and ending with 17:00-18:00, during three dry season months (January, February and March) and three wet season months (June, September and October). Within each month all efforts were made to monitor focal animals within each time zone. As there is little annual variation in daylight at the fieldsite the designated time zones were used for the entire study (c.f. Hill, 1999).

While a number of individual gelada in the main Sankaber study band were easily identifiable, the majority were not. Similarly, Dunbar & Dunbar (1975) describe the extensive problems involved with identification of individuals and units (see also Kawai, 1979), and were unable to conduct the vast majority of their known focal behavioural records until their second field season (R. Dunbar, pers comm). Focal scans were of particular interest to the Dunbars as their study focused on fine-grained inter-individual social relationships. The purpose of the current study however, did not require individuals to be known in such detail, and 'focal' animals were therefore selected opportunistically because of constraints on identification due to the exceptionally large groups. However, a number of individual were known and thus observations could be guided by an attempt to follow as many *different* individuals in each age-sex class as possible (following Byrne *et al.*, 1993). Wrangham (1976) found that different age-sex classes of adult gelada varied very little in their feeding behaviour and activity budgets and therefore pooled all activity records into adult males and adult females. While some of the most readily identifiable individuals had physical defects or parasitic growths (most commonly large cestode larvae cysts), none of the focal animals had identifying features that were considered to affect them in any way.

2.2.1 Focal individual scan sampling

The activity of focal individuals was recorded at 30 one-minute, sequential scans within the hour time-zone. Due to low habitat visibility it was sometimes not possible to follow the focal animal for the full 30 scans. A sequence of 20 points within the scan was considered a minimum criteria, otherwise the focal observation was repeated within the same time zone on another day. Although activity of focal animals was recorded in detailed categories (see section 2.2.2), these fell unambiguously into one of four broad activity states: Feeding, Moving, Social or Resting. Over 95% of most primate's time is allocated to one of these four categories (Dunbar, 1992) and analyses will be restricted to these four activities, following the common methodology implemented in most previous studies on primate activity patterns (e.g. Nagel, 1973; Harding, 1976; Post, 1978; Rasmussen, 1978; Sharman, 1981; Barton, 1989; Dunbar & Dunbar, 1988; Dunbar, 1992). A number of studies focusing on baboon foraging combine feeding and moving as 'foraging' time (e.g. Barton, 1989; Byrne *et al.*, 1993), citing the fact that *Papio* baboons usually feed while moving continually. In contrast, gelada rarely move in the conventional sense while feeding. Instead, gelada will often employ a slow shuffle on the haunches while plucking at short grasses with both hands. This was often imperceptible when using the focal point sampling method, and because the gelada's hands remain free, it in no way interferes with normal feeding behaviour, and was therefore classified solely as 'feeding'.

Many of the other studies listed above refer to the activity category 'Grooming', since that is literally the primary behaviour it entails. However, I will hereafter refer to this category as 'Social', because in the following analyses it will include antagonistic interactions such as threatening behaviour and non-contact social behaviours. Time budgets were calculated using the following formula:

$$\frac{\sum(\text{records for activity x})}{\sum(\text{records for all activities})} \times 100$$

where activity x is one of the four primary time budget activities.

Although observation conditions were excellent throughout most of the home range, cliff areas of the escarpment were completely inaccessible and therefore proved problematic for recording the activity of gelada as they made their ascent from, or descent to, the sleeping ledges. However, on a few occasions it was possible to record the activity of gelada on cliff faces on the opposite side of a gorge to the observer. Although these observations were from some distance and recorded using binoculars, it is important to recognise that certain behaviours might occur more often at particular times of day (Clutton-Brock & Harvey, 1977).

Table 2.1 *Behavioural categories recorded during point scan sampling of focal individuals.*

General Behaviour	Specific Behaviour	Description
FEEDING	Grazing	Plucking or eating short grasses.
	Foraging	Plucking, manipulating (processing) or eating above ground food items other than grass.
	Excavating	Digging, manipulating or eating underground food items.
MOVING	Moving	Quadrapedal locomotion of 5 or more paces, with or without feeding (walking or running).
RESTING	Rest	Lying or sitting without other activity.
	Autogroom	self grooming.
	Standing	Immobile in quadrapedal stance.
SOCIAL	Allogroom	Individual grooming another individual, identities recorded where possible.
	Aggression	Fighting, chasing, threatening, screaming, displacing. Where possible, identity of aggressor and recipient was noted.
	Play	Non-aggressive, non-grooming playful contact (e.g. play fighting, wrestling).
	Mother-infant interaction	Where applicable, suckling or physical contact between mother and infant was noted.
	Other	Other interactions with individuals (e.g. presenting, copulation, embracing).

Although every attempt was made to record time budgets evenly throughout all hours of the day from 07:00 to 18:00, this was not always possible. Each hour sampling period was therefore weighted evenly within all months by calculating time correction factors using the following formula:

$$\frac{n_{ij}}{\text{mean } n_j}$$

where n_{ij} is the number of scan points within hourly time period i in month j, and mean n_j is the mean number of point scans for all hourly time periods in month j. Data from each scan were then weighted by their appropriate time correction factor to arrive at the final activity budget records presented in Chapter 5.

2.2.2 Group dynamics

Group size was recorded on a mechanical thumb-counter by counting the number of individual gelada at hourly intervals throughout the day on ten days per month and averaged to provide a mean daily group size. Infants being carried or breast fed by their mother were not included in the counts. Morning counts only began when it appeared that no further units remained on the sleeping cliffs below. This normally occurred when a majority of the group shifted from social behaviour to feeding behaviour, which almost always coincided with a group move, although often small, away from the cliff edge. Group size counts therefore, often did not begin until 9:00 or 10:00.

Whenever the main study band was observed to undergo internal fission, or fusion with another herd, the size of the merging or departing group was recorded along with the location and habitat type in which the event occurred. From these records it was possible to calculate the mean daily rate at which gelada herds underwent fission/fusion events in each month.

2.2.3 Spatial patterns of units

In October and November 2000 data were collected on the positional location of 17 known units within the herd. The unit's position was recorded both in relation to leading or trailing edge of the herd when the herd was 'travel-feeding' and whether the unit was located at the centre, middle or outer edge of the herd (see Figure 6.16). Crook (1966) pointed out the distinction between 'travel-feeding', whereby most animals are engaged in feeding activity while the herd slowly moves in one direction (individuals gradually move out to the perimeter along one edge of the herd), and a distinct group 'march' in which little feeding is done while all individuals of a herd walk determinedly in one direction. No unit-position data were collected during the latter group marches.

2.3 Resource utilisation

2.3.1 Home range use

A 1:25000 map of the Simen Mountains (Messerli & Aerni, 1978) was enlarged to extract a 1:6250 map of the Sankaber study area, which was divided into contiguous 200m x 200m grid squares (or 'quadrats'). The distance from each quadrat to the nearest permanent water source, sleeping site and refuge was calculated in metres. Habitat borders are reasonably distinct at Sankaber and could be marked accurately on the map by referring to well known, small-scale topographical features, therefore each quadrat could be categorised into one of seven microhabitats (see Figure 4.1, Chapter 4, for habitat distribution map). Every half hour during all day follows, the centre of mass of the herd was recorded and assigned to a quadrat (see Altmann & Altmann, 1970; Waser & Floody, 1974). Quadrat occupancy was recorded during five all day follows per month (two days in August were recorded by a trained field assistant) giving a total of 1320 quadrat occupancy points over the entire 12 months. The sum of all (40,000m^2) quadrats entered by the main band provided a measure of the home range area. Included in this calculation were quadrats totally enclosed by those occupied but not entered themselves, which constituted 12% of the home range area.

2.3.2 The problem of sleeping sites

Although quadrat occupancy data were recorded from 07:00 to 18:00 during all day follows, gelada were commonly observed to remain at a sleeping site until 08:00 and on two occasions until 11:00, and were often settled at a sleeping site before 17:00. Thus, if the gelada did not move from a sleeping site until 08:40, this quadrat would receive the first four 'occupancy' data points of the day (07:00, 07:30, 08:00 & 08:30). Therefore, quadrat usage data might be weighted towards quadrats in which sleeping sites are located. To lessen this effect quadrat occupancy data were only considered once the gelada had moved out of the first 'sleeping site quadrat' in the morning (i.e. beginning with the second quadrat entered each day), and ended with the penultimate quadrat of each day. This is not ideal, and will no doubt underestimate the use of cliff habitat being used for activities other than sleeping, but is similar to methods used by Whiten *et al.* (1987) for obtaining day ranging patterns of mountain baboons. It should be noted that this method does not exclude all records of cliff habitat use and in fact, cliff habitat was recorded as entered at least once during every half hour time interval throughout the study. Also, many cliff quadrats do not contain sleeping sites while sleeping sites are found in both cliff and gorge habitats. From all sleeping site quadrats it was possible for the gelada to enter more than one adjacent quadrat, the second quadrat entered during the day thereby representing, at least to some extent, a decision in ranging behaviour once the gelada left the sleeping site quadrat. Furthermore, all the following analyses were first carried out with first and last quadrats included. While the use of cliff habitat was substantially reduced, it was uniform across months (Kolmogorov-Smirnov 1 sample test: $z = 0.602$, $n = 12$, $p = 0.861$) and did not affect the nature or significance of the results presented. Therefore, although travelling to and from sleeping sites will have an effect on the analyses of quadrat occupancy, excluding the first and last quadrats of each day is considered the simplest way to mitigate this effect.

'Day journey length' was recorded by drawing the herd's movement onto the home range map and using a planimeter to calculate the day journey distance in metres. To account for the precipitous nature of the study area the distance travelled both horizontally (as drawn on the map) and vertically (estimated from the number of 50m contour lines crossed) were combined geometrically to calculate the actual ground area covered.

2.3.3 Feeding behaviour and dietary profiles

General dietary profiles were calculated for adult male and female gelada using records from focal animal sampling described in section 2.2. Continuous 10 minute observations were also conducted specifically on feeding activity of the focal animals.

Where possible, the plant species and part eaten were also recorded or, if unidentifiable, the food item was described more generally (e.g. short grasses, roots etc). For each food type the relative size and weight of mouthfuls and number of mouthfuls per minute were recorded, thus providing an estimate of rate of dry weight intake for different food items. For a number of food types, such as subterranean items and fruits, individual items were clearly distinct and ingested individually, making mean weight and intake rate a straightforward calculation. When feeding on food types such as green grass blades or thyme roots (*Thymus spp.*) gelada would often collect a number of items together in the hand before transferring it to the mouth. In such cases the number of items per mouthful was counted and an average mouthful was established for the food item and sex of the gelada. When a single food species ranged in size the average mouthful eaten by gelada was estimated visually (following Wrangham, 1976; Iwamoto, 1979; Barton, 1989). Due to the rapid rate at which gelada harvest short green grass blades in particular, feeding rates for grass intake were mainly recorded from digital video footage, enabling the number of plucks per mouthful to be recorded simultaneously with rate of mouthfuls and rate of grass blade ingestion.

Although the nature of some habitat types, notably the escarpment, meant detailed feeding observations were impossible when the gelada occupied these areas, it has been noted that very little feeding is done on the cliffs (see section 2.2, and Kawai & Iwamoto, 1979). It is therefore assumed that feeding data collected while the gelada moved throughout the other habitat types, away from the sleeping sites, offer an accurate representation of total daily food intake.

Samples were collected of as many different gelada food items as possible. Where applicable, food items were manipulated in a manner as close as possible to that performed by gelada. For some food samples, such as grasses, this entailed collecting a number of items (e.g. grass blades) equivalent to an average gelada mouthful (see above). Samples were partitioned into estimated gelada mouthfuls, dried in the field and stored in a cool, dark place.

2.4 Predation risk and alarm response

To examine a possible relationship between spatial foraging preferences, group size and predation risk, habitat visibility was recorded following the method described by Cowlishaw (1993). Directional visibility at gelada eye-level was estimated in eight compass directions from a central point within each map quadrat. The mean visibility distances at each point were then pooled to provide an estimate of the average visibility within each habitat, excluding the inaccessible E-cliff habitat type.

On 89 full days spread across 6 months (Feb-Jun 1998, Oct-Nov 1998, and Jan 1999), all flights in response to threats, or perceived threats, were recorded *ad libitum*. These observations included the cause of the alarm response (if known), the distance the gelada were dislocated, the distance to the nearest refuge, habitat type, and the number and percentage of the gelada herd responding. Although small trees exist in all three main habitat types, gelada were never observed to use them in response to a perceived threat and therefore only sheer rock faces are considered as refuges in the current study.

2.5 Statistical analysis

Prior to statistical analysis all data were assessed to determine whether they were normally distributed. If data were not normally distributed they were either log transformed or non-parametric statistical tests were used (Sokal & Rohlf, 1995). Where bivariate correlations are presented in figures, a dashed line of best fit is displayed for diagrammatic purposes only. All tests are two-tailed with a level of rejection set at $p = 0.05$, although if trends were apparent in the data, precise p values (or $p < 0.01$) may be listed. All statistical analysis were conducted using SPSS for Windows version 10.0.7.

CHAPTER THREE

Study Site and Population

3.1 Study site

3.1.1 Location

Gelada baboons are found in a number of areas throughout the northern Ethiopian highlands, and one isolated population exists south of the Rift valley in Arsi province (Mori & Belay, 1990). However, the Simen Mountains National Park (SMNP) represents, in theory, the only officially protected gelada habitat in the world and was therefore chosen as the site for the current study.

The Simen Mountains National Park is located in the Simen District, within the Gondar Province of northern Ethiopia (Figure 3.1). The Park covers an area of 169km^2, with roughly equal coverage of lowlands (1700-2800m) and highlands (2800-4070m), separated by a dramatic escarpment. Coincidently, the altitudinal range found within the Park corresponds closely to the altitudinal limits at which gelada can be found throughout their range in northern Ethiopia (1700-4200m). The National Park was established in 1969 with the primary aim of protecting the Walia ibex (*Capra ibex walie*), whose world population was limited to less than 130 individuals found only the Simen Mountains. The Park was listed as a World

Heritage Site in 1978, but due to the Ethiopian civil war, there has been little management or control of the area since.

Within the Park, research was carried out in the Sankaber area (13° 15′N, 38° 00′E), which consists of a rolling plateau approximately 3.5 km long and 0.5 km wide. The plateau is at approximately 3250 metres altitude and is well defined on the north by the main escarpment of the Simen Mountains - a sheer cliff approximately 800m high. The southern boundary, between the plateau and the 600m deep Khabau gorge, is less defined topographically but both northern and southern slopes include gelada sleeping sites which are inaccessible to humans. Three main habitat types will be referred to hereafter as plateau, escarpment and gorge.

The Simen Mountains, including the National Park, are heavily populated by humans, with widespread cultivation of barley up to an altitude of 3600m, and heavy grazing of livestock to 4000m. However, due to its small area and topographically isolated nature, the Sankaber plateau has experienced relatively little livestock grazing and no cultivation, and therefore represents one of the least disturbed gelada habitats in the region.

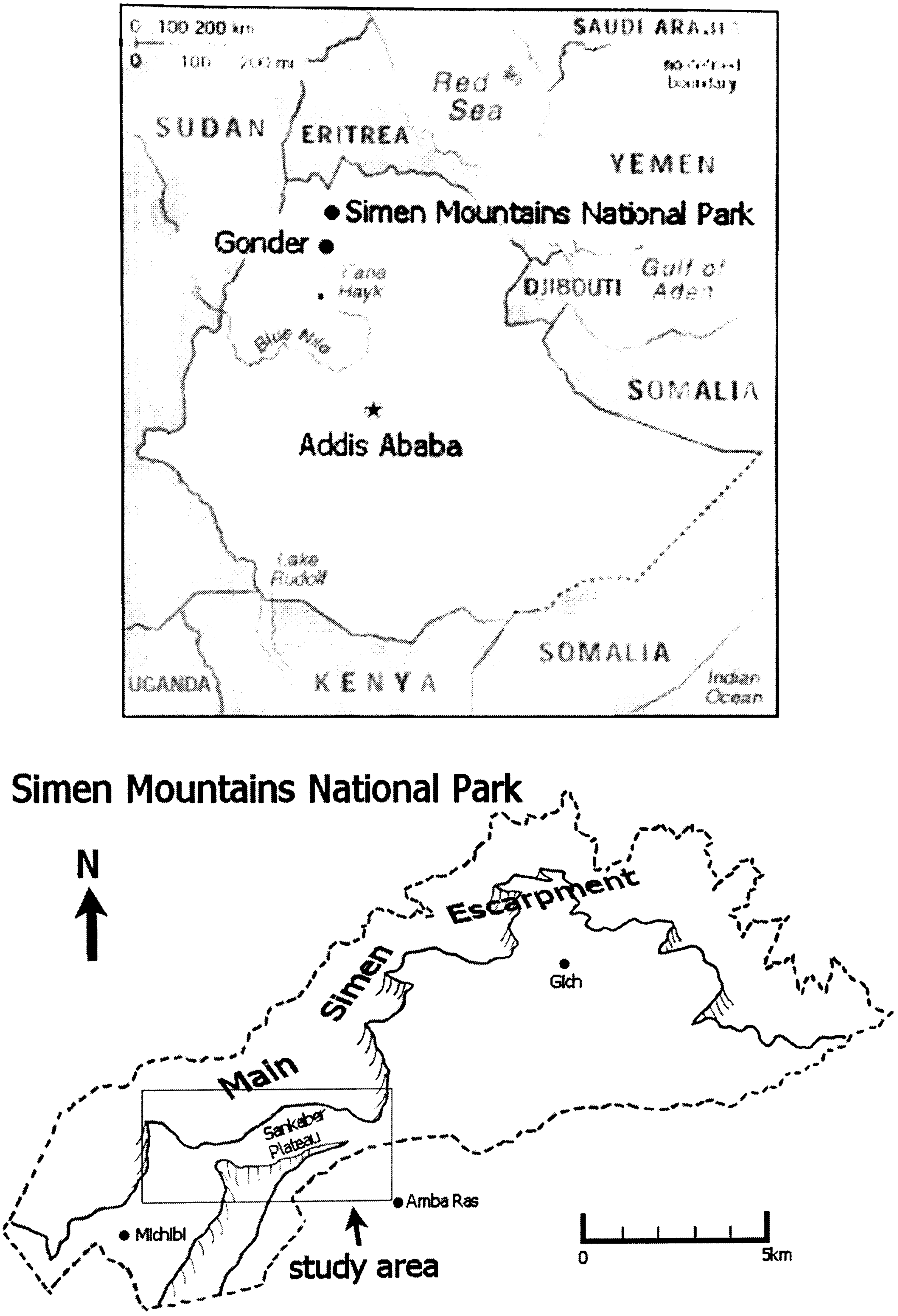


Figure 3.1 *Map of Ethiopia showing the location of Simen Mountains National Park (13 ° 15 'N, 38 ° 00 'E).*

3.1.2 Geology

The Simen Mountains represent the highest and northernmost edge of the central Ethiopian highlands, the largest assemblage of mountainous zones on the African continent. Many summits in the region are over 4000m, culminating in the highest peak in Ethiopia, Ras Dashen (4550m), just outside the Simen Mountain National Park. These highlands stretch from the Simen Mountains in the north (13'N) to the Guge Mountains and Bale Massif, 1100km to the south (6'N), and have been described as a 'cracked dome' (Kingdon, 1997), dissected by the Rift valley which runs from southern-central Ethiopia to the Danakil Depression and Djibouti in the north-east.

The Ethiopian highlands are the result of slow volcanic outpouring during the Oligocene period (40-25 mya) that produced a series of Trappean basalt layers up to 3000m thick (Hurni, 1982). Lava from the main Simen volcano covered an area of over 15,000 square kilometres and hardened with gentle slopes (approximately 5 degrees) radiating out from the main cone. The cooling of the basalt, combined with tectonic movement, lead to cracks developing. This opened the way for high rates of natural erosion during the Pleistocene ice ages when the Simen massif experienced glaciation and high precipitation. The cracks widened and deepened to produce the present landscape.

The gently sloping high plateaus (2800-4000m), dissected by large gorges, are more integral to the south and south-west while to the north the plateau gives way to the sheer Simen escarpment, up to 1500m high in places. North of the escarpment are fluvial lowlands (1500-2000m), a richly eroded landscape of peaks, valleys and terraces. These geological features are integral to the gelada's habitat as they produce the sheer cliffs on which the gelada sleep, and the altitude, combined with rich volcanic soil, supports the alpine grasslands on which the gelada graze.

3.1.3 Climate

The climate of the area has been described as temperate (Dunbar & Dunbar, 1975), although seasonality follows a characteristically tropical pattern of 'wet' and 'dry' seasons. There is little annual, but high diurnal, variation in temperature, especially in the dry season months of November to January, when daytime temperatures are commonly over 20°C and night time minima are commonly around 0-5°C (Figure 3.2).

Between 1973-1975 P. Stahli recorded a mean annual temperature of 9.8°C at the field site (Hurni, 1982). The mean annual temperature in the shade of the present study period was 11.1°C on the plateau. Weekly minimum and maximum temperature readings were also recorded on thermometers permanently located on the escarpment and gorge, as close as possible to gelada sleeping sites. While it was difficult to place these thermometers in suitable locations for accurate temperature recording, the mean annual temperatures of 13.0°C and 19.8°C, for the escarpment and gorge respectively, are considered qualitatively correct in the sense that these two habitats are generally warmer than the plateau top.

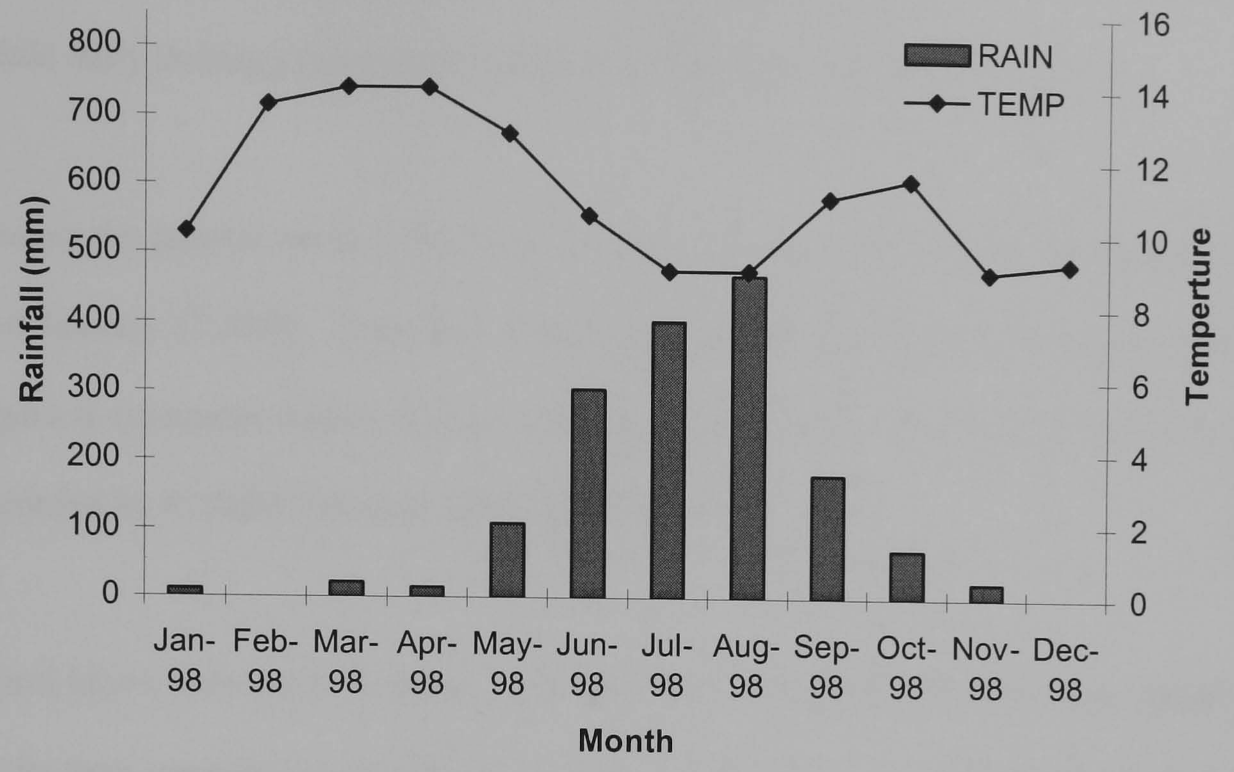


Figure 3.2 *Total monthly rainfall (mm) and mean monthly temperature (°C) at Sankaber camp during the study period.*

Throughout much of Ethiopia precipitation is convective, coming directly from the SW monsoon system. However, above 3000m (which includes the Sankaber field site) precipitation is advective, deriving from the northeast trade winds which extract moisture from the monsoon system below and release it with regular high altitude afternoon showers. This weather pattern creates two distinct rainfall peaks, at 1500m and 3400m, the latter directly influencing the gelada's habitat in the current study. Rain falls mostly during the wet season from June to September (Figure 3.2), when thunderstorms and heavy mist are common. During June, July and August 1998, rain fell on 79 of the possible 92 days (rain fell on all days in July) and the sun was visible for less than 20% of possible sunlight hours. Humidity records (which will be presented in Chapter 4) show a similar pattern to rainfall, with a maximum monthly average of 86% humidity in August and a minimum monthly average of 50% humidity in February. Although snow was never recorded during the study, heavy hail was common in the wet season, often staying on the ground for up to 48 hours, while daily morning frosts were common during November and December.

During the present study 1612.5 mm of rain was recorded between January 1st 1998 and January 1st 1999. Very little climate data are available from the region, but this figure is somewhat higher than an average annual rainfall of 1493mm (n=4, sd=129), recorded by P. Stahli between 1971 and 1974.

Wind blows constantly (average 17km/hr) from a northerly direction year round, but shifts from predominately NW to NE at the onset of the rains, and conditions can vary considerably between the three habitat areas in any given day. For example, the escarpment, which includes the majority of the study population's sleeping sites, faces north and therefore receives stronger and more constant wind and rain. In contrast, the more sheltered gorge is not only protected from the prevailing local weather patterns, meaning temperatures are generally higher and mist less common, but with a south facing aspect also receives more sunlight. Dunbar (1992b) has shown ambient temperature to be an important ecological parameter for gelada and these local variations raise important implications within the context of this study and gelada ecology in general (see also Iwamoto and Dunbar, 1983).

May and October are important inclusions when considering the 'wet' season discussed throughout this study, as the 109 mm that fell in late May was sufficient to bring through the first significant growth of fresh green grass in the year, and October's rainfall of 71.5 mm was enough to maintain the 'greenness' of the short grass areas.

3.1.4 Fauna

Native carnivores are considered rare at Sankaber but common jackals (*Canus aureus*) are seen frequently, often close to gelada herds. During the study, 15 gelada/jackal encounters were observed. Almost all encounters involved early detection of the jackal by the gelada, loud alarm calls from the entire herd and often a small contraction in group-spread. However, on 4 occasions, in bushy areas of the plateau, a pair of jackals was observed ambushing gelada from a short distance and chasing the herd over 30 metres. On both occasions, the jackals were repelled when adult male geladas turned on them abruptly at a distance of approximately 5 metres.

Spoor and faeces of the spotted hyena (*Crocuta crocuta*) are seen occasionally on the Sankaber plateau, but are considered more common in other areas of the park, such as the Gich plateau, 2km to the east (see map, Figure 3.1), where a hyena stool sample was found by the author containing a gelada fingernail. Leopard (*Panthera pardus*) were sighted twice during the study, once at about 150m below the top of the escarpment, and once at a similar altitude in the gorge. On the latter occasion the leopard was observed stalking a gelada herd, which elicited loud alarm calls from a distance of approximately 100m before the leopard disappeared 2 minutes later. During the study, a fresh Ethiopian genet (*Genetta abyssinica*) carcass was found at Sankaber while Caracal (*Felis caracal*), Servil (*Felis servil*) and African wildcat (*Felis lybica*) are considered present but rare (Nievergelt *et al.*, 1998). Gelada are also harassed by domestic dogs and humans, who pass through the study area regularly. While none of the abovementioned carnivores are considered common, the anecdotal evidence presented here suggest that leopard, hyena and jackal do prey on gelada at the fieldsite.

Gelada are the dominant native herbivore in the area (Dunbar, 1978), although klipspringer (*Oreotragus oreotragus*) and bushbuck (*Tragelaphus scriptus*) are common, while Rock Hyrax (*Procavia capensis*) and Hamadryas baboons (*Papio hamadryas*) are considered present. Walia ibex (*Capra ibex walie*) and duiker (*Sylvicapra grimmia*) were also common in the area before the civil war began in 1977 (R. Dunbar, pers comm) and although still present in certain parts of the Simen Mountains are no longer present in the Sankaber area. Domestic stock (cows, sheep and goats) are prevalent throughout the gelada's home range and represent the main competition for food resources. However, the Sankaber plateau receives far lighter grazing from domestic livestock than does the grassland at either end of the plateau, where the main gelada band's home range overlaps with farming areas.

Hamadryas baboons are sometimes sighted in the study area, although they more commonly occupy lowland habitats. While foraging, they move up the gorge slope and often form mixed herds with gelada, remaining mostly in bushy areas of the gorge habitat and returning to the lowlands before nightfall. However, in early April 1998 a group of 18 hamadryas baboons (including 5 adult males and 7 adult females) joined the main gelada study band on the Sankaber ridge and remained in close association with the gelada, including occupation of the same sleeping sites, until late July. According to locals, Park staff and the literature, it is highly unusual, firstly, for these two species to remain in such close association for so long, and secondly for hamadryas to occupy such high altitude habitats for extended periods. However, gelada and hamadryas have been known to hybridise in captivity and possible hybrids have been sighted in the wild (Dunbar & Dunbar, 1974).

3.1.5 Flora of the Simen Mountains

Natural vegetation varies greatly across the altitudinal range found within the Simen Mountains National Park (1700-4070m), and has been affected drastically by human activity at all altitudes (Nievergelt *et al.*, 1998). In the lowlands (1500-2700m), *Acacia* and *Euphorbia* trees remain common, if sparse, in locations with a thermophilic aspect and *Hargenia* is found in the steeper canyons. Forests of *Juniperus* (junipers), *Olea* (olives) and *Maesa*, which were once widespread, have been reduced dramatically by farming and human fuel-wood needs. Only a few pockets of such forests remain in the most inaccessible gorges and terraces. More specifically and more recently, this situation is now prevalent right up to the foot of the escarpment (2300-2700m). Here farming and wood chopping have mostly replaced the natural evergreen, broadleaved montane forest, which was often dominated by *Syzygium guineense* (Klotzli, 1986). Even in the remaining patches of natural vegetation Nievergelt *et al.* (1998) have reported dramatic decreases over the last 25 years in trees such as *Dombeya schimperiana* and *Shefflera abyssinica* (which is especially popular for manufacturing local furniture). Also, an increase in livestock grazing in the lowlands is likely to be related to the decline of the many smaller plant species such as the vine, *Clematis simensis*, the fern, *Adiantum thalictroides* and the herb, *Cyperus elegans*. Gelada are commonly sighted in the lowlands, although mostly foraging on recently harvested wheat and barley fields.

Above the escarpment (3000-3600m) the natural vegetation can be described as Afro-alpine. The plateau is dominated by a ground level vegetation cover of short Gramineae grasses and herbs, with scattered forests of giant heather (*Erica arborea)* and St. Johns wort (*Hypericum revolutum).* The *Erica/Hypericum* treeline varies according to aspect and soil condition but is considered to have risen 50-100m over the last 30 years (Nievergelt, *et al.* 1998) from a range of 3600-3800m to 3700-3900m. This naturally dissolved treeline corresponds almost exactly to the altitudinal limit for barley cultivation. Above this altitude, trees and cultivation give way to short and long grass steppe communities dotted with giant lobelias (*Lobelia rhynchopetala*) and heavily grazed by domestic livestock. Between 3600m and 4000m both the number of giant lobelias and intensity of domestic grazing have increased significantly over the last 30 years. This true afro-alpine grassland belt represents the upper limit at which gelada are common grazers. Gelada are rarely found above 4200m, where vegetation drops below 50% ground level cover, thus defining the Periglacial belt. Hurni (1982) estimates that between 20,000-12,000 years BP the local climate was 7°C cooler and altitudinal belts were 800m lower. This would have meant vastly greater areas of the Ethiopian highlands constituted afro-alpine grasslands and hence suitable gelada habitat.

3.1.6 Flora of Sankaber area

The Sankaber area represents one of the few remaining patches of natural vegetation within the *Erica/Hypericum* altitudinal belt of the Simien Mountains, whereas the majority has been cultivated for barley. The grassland of the Sankaber plateau is interspersed by dense thickets of *Rosa abyssinica* (the only wild rose native to Africa) and *Solanum sp.* bushes. In both the gorge and escarpment habitats bush and tree level cover are more predominant than grass. The escarpment is characterised by vertical rock faces, used by the gelada as sleeping sites, interspersed with steep patches of *Erica arborea* forest and long *Festuca spp.* grasses. The loose and crumbly soil of the gorge habitat supports less ground level vegetation, but a greater variety of plant species, than either the escarpment or plateau. Thickets of *Rosa abyssinica*, *Rumex nervosus* and *Clutia robusta* are common, although the bushes and small trees are concentrated in gullies. The succulent *Aloea sp.* features on the more exposed slopes of the gorge.

3.2 Study species

Gelada (*Theropithecus gelada*) represent the last extant species of a primate genus once found throughout eastern and southern Africa (Jolly, 1972). The genus *Theropithecus* was a very successful group of grass-eating primates and were the predominant non-human primate during the Pleistocene. Theropithecus once inhabited a treeless grass niche along the shores of shallow lakes and sandy rivers throughout most of Africa, and included species weighing up to 90kg.

There is no official or unanimous agreement on the *common* classification of the gelada. Crook (1966) first claimed the title gelada 'monkey' would be more apt than 'baboon', suggesting that similarities in morphology, ecology and behaviour were examples of convergent evolution. While accepting that it is often called a 'gelada baboon' in the literature, I will, for the sake of clarity, refer to the species within this thesis simply as 'gelada', and will reserve the title 'baboon' for species of the *Papio* genus.

A thorough description of the gelada social system is available in Kawai (1979), Dunbar and Dunbar (1975) and Dunbar (1984). In summary, the primary gelada social unit (as mentioned in Chapter 1) consists of one reproductive male and up to ten reproductive females and their young; hereafter one-male-, harem- or reproductive-units will be referred to simply as 'units'. Young males disperse from their natal units and either join reproductive units as 'followers' or form all male groups (AMGs). Neither followers nor males in AMGs have sexual access to reproductive females. Both reproductive units and AMGs congregate during the day into grazing herds which can number over 800 individuals. Units who share a common home range are considered 'bands', and bands may join temporarily to form mutli-band 'herds'. A more thorough description of higher levels of association and the terms used will be given in Chapter 6 (see also Kawai *et al.*, 1983, for a summary of gelada social system definitions).

3.2.1 Study population

During late 1997 an estimate was made of the number, size and home range of gelada bands using the Sankaber area. By January 1998 five herds could be identified, numbering approximately 33, 145, 150, 253, and 260 individuals respectively. From these, the 'Sankaber Main band' (253 individuals in January 1998) was chosen as the main study band due to its home range being most congruous with the Sankaber plateau and therefore incorporating the least disturbed habitats. Only the smallest 'E' band (33 individuals) shared its home range completely with the Sankaber Main band, while the other three bands that sometimes utilised the Sankaber plateau ranged mostly into areas beyond feasible monitoring. Sankaber main band consisted of approximately 20 to 25 reproductive units, within 17 of which the precise number of adult females was known (see Table 6.4, Chapter 6). The average size of reproductive units was 8.9 individuals (N = 17), with an average of 3.88 reproductive females per unit. A total of seven all male groups (mean size = 10.2 individuals) were regularly observed in the Sankaber area, three of which were considered to share the home range of the Sankaber main band.

Flight distances were roughly 20 metres at the beginning of the study in December 1997, and fell to approximately 10 metres for most of the duration of the study. 4.2 Home range Characteristics

3.3 Home range characteristics

A basic description of the three main habitat types found in the Sankaber area (Escarpment, Plateau, and Gorge) was given in section 3.1.5. While the fundamental difference between these three broad habitats types is one of aspect, they also differ in the dominant plant species and vegetational structure present, and variation exists within habitats to an extent that a further breakdown of habitat classification was possible (see below).

Based on continuous line transects the composition of the vegetative cover is presented in Table 3.1. Note that different vegetation types are based primarily on vertical height categories and are not mutually exclusive. For instance, presence of bush and small tree level vegetation along a portion of transect does not necessarily preclude the presence of ground level vegetation. Therefore, percentages of different vegetation types do not necessarily give a sum total of 100% within one habitat.

Table 3.1 *Vegetational cover in three main habitat types at Sankaber based on continuous line transects.*

	Plateau	Gorge	Escarpment
Transect length	1500m	1000m	500m
Percentage cover of:			
Rock, dirt	2.5	25.3	0.4
Short grass (0-15 cm)	81.5	7.5	17
Long grass, herbs (15-60 cm)	5.1	18.1	87.2
Shrubs, bushes, small trees (60-300 cm)	18.1	50.7	4.9
Trees (> 300 cm heigth)	4.1	10.7	71.3

A mixed short-grass community dominates the plateau, covering over 80% of ground area. However, thickets of *Rosa Abyssinica* and *Hypericum revolutum* are common and cover approximately 18% of the plateau. Trees, bushes and long grasses found on the plateau are almost exclusively associated with these thickets, thus creating a demarcation of two fairly distinct microhabitats on the plateau; open short grass paddocks interspersed with reasonably dense bushy areas. On a small scale these constitute very different habitat characteristics in terms of both visibility and gelada food availability, and will hereafter be referred to as Plateau-open (P-open) and

Plateau-bushy (P-bushy). The mixed short grass community of the plateau constitutes the gelada's main food source and feeding habitat and will therefore be examined in more detail in Chapter 5.

The gorge also consists of reasonably distinct open and bushy areas, with larger vegetation concentrated in gullies while more exposed areas are sparsely vegetated except for long grasses and *Aloe spp.* Therefore, similar to the plateau habitat, the area covered by shrubs and small trees in the gorge (around 50% of ground cover) is reasonably restricted to large and distinct clumps. Over a quarter of the ground area in the gorge is bare rock and dirt – plants being unable to take hold on the loose and crumbly soil. The gorge habitat was thus divided into the two habitat classifications of Gorge-open (G-open) and Gorge-bushy (G-bushy). Because of the extensive length of the main vegetation transects, both G-open and G-bushy habitat types are represented in appropriate measure to their respective proportions in the gorge and plateau habitat types.

Unfortunately, due to the precipitous nature of the escarpment the vegetation transect in this habitat type was restricted to the *Erica arborea* (giant heather) forests found on the shallower slopes, and does not cover the mostly bare rock faces and cliffs. This requires the further demarcation of the Escarpment habitat type into Escarpment-cliff (E-cliff) and Escarpment-heather (E-heather). The distribution of tree cover (71%) in the E-heather habitat is fairly uniform and is also characterised by an extensive ground cover of longer grasses, predominantly *Festuca spp* (over 87%).

One last type of habitat that is worth consideration is the cultivated barley 'fields' of nearby villages. Gelada were observed to enter these fields after the annual local harvest to pick residual grains from the ground and to pick over the threshing areas. As humans have spread extensively through the Ethiopian highlands most gelada populations now live adjacent to human settlements, and foraging on cultivated fields is likely to be a regular, if not extensive, part of the geladas foraging regime at certain times of year.

Thus, for all further reference to habitats and their characteristics, seven habitat types will be considered: 1) Escarpment – cliff (E-cliff); 2) Escarpment – heather (E-heather); 3) Plateau – open (P-open); 4) Plateau – bushy (P-bushy); 5) Gorge – open (G-open); 6) Gorge – bushy (G-bushy); 7) Fields.

3.3.1 Distribution of habitat types

A 1:6250 map of the study area was divided into quadrats of 200 m x 200 m. No single quadrat covered more than two habitat types and due to the reasonably strong habitat borders and fairly large, continuous tracts of each habitat type, each quadrat was easily assigned to one of seven categories based the predominant habitat type within that quadrat. Figure 2.3 shows a map of the study area and the distribution of the 7 habitat types.

A total of 232 (200m x 200m) quadrats covered all areas entered by the main gelada band during the study period, giving a home range area of 9.28 km^2. The numeric distribution of quadrats across habitat types is given in Table 3.2. The variation in use of these habitat types by gelada over time will be discussed in section 4.3.

Table 3.2 *Number of quadrats of each habitat type and relative percentage of total home range.*

	Habitat type							
	Escarpment		Plateau		Gorge		Fields	Total
	cliff	heather	Open	bushy	open	bushy		
No. quadrats	34	56	50	15	31	33	13	232
% of study range	14.7	24.1	21.6	6.5	13.4	14.2	5.6	100

3.3.2 Distribution of sleeping sites and refuges

The gelada's habitat is relatively treeless and the stands of giant heather (Erica arborea, the largest and most common tree species), are rarely more than a few metres tall and not considered to offer the gelada a form of refuge from predators. Sheer cliffs, however, are a ubiquitous feature of gelada habitat throughout Ethiopia and are used both as temporary refuge from danger or harassment and as nightly sleeping sites. In the current study a 'refuge' was defined as any part of the main escarpment rock face, whether used as a sleeping site or not, plus those locations in the gorge used as sleeping sites. In contrast, a section of cliff was only designated a 'sleeping site' if the gelada were actually observed sleeping there. The main Sankaber band used 19 discrete sleeping sites during the study; four in the gorge and 15 spread along 10.5 km of the main Simien escarpment.

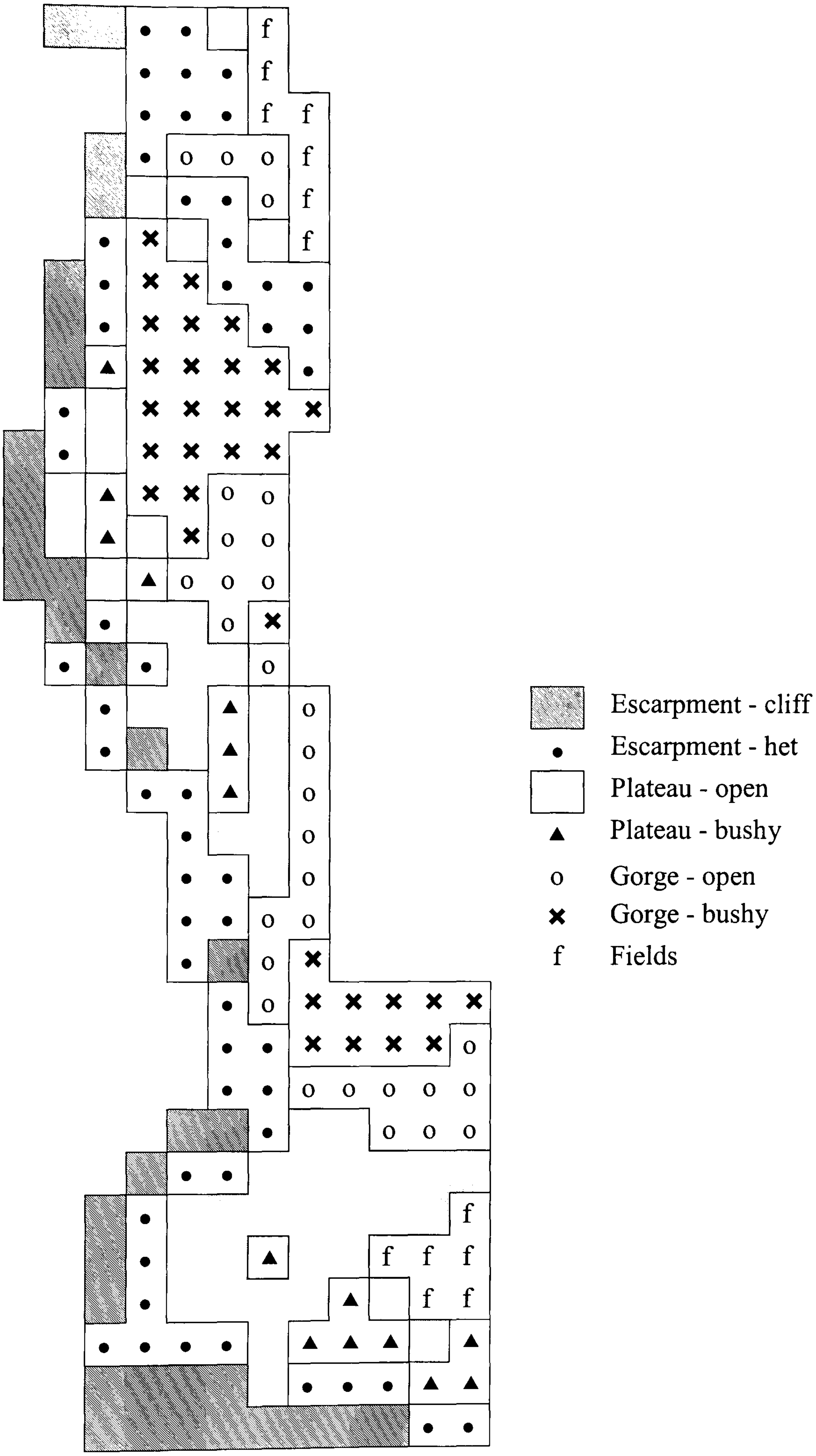


Figure 3.3 *Map of study are showing distribution of different habitat types*

3.3.3 Access to drinking water

A number of Papio spp. field studies have found that the distribution of surface water was a significant determinant of ranging patterns (Altmann & Altmann, 1970; Sigg & Stolba, 1981; Hamilton, 1986; Barton et al., 1992), although the strength of the constraints imposed by water needs are likely to be dependant on the local levels of precipitation.

Gelada drink from streams and ponds (both perennial and seasonal) found in all habitat types throughout their home range. Kawai & Iwamoto (1979) suggest, "water sites are one of the most important factors in deciding the daily nomadism" (p262) of the gelada population at Gich, 5km east of Sankaber. In their study focal individuals spent twice as long drinking per day in February (200 seconds) than in October (100 seconds). However, the annual rainfall of the Simien Mountains (1612.5 mm during the current study) is higher than for almost every Papio spp. field study for which data are available (mean = 765, sd = 512, n = 31; calculated from Table 7, Dunbar, 1992). Furthermore, during the months in which over 70 mm of rainfall was recorded (May to October) precipitation was so constant that drinking opportunities were freely available throughout the home range, and no quadrat in the current study was more than 700 m from a permanent water source (mean distance = 191.0m, sd = 160.0, n=232). Distribution of water sources is therefore not considered a limiting factor in gelada ranging patterns although it will be examined in relation to quadrat use in section 4.4.1.

CHAPTER FOUR

Factors Affecting Home Range Use and Habitat Selectivity

4.1 Introduction

The patterns in which an animal uses the space around it have long been one of the central paths of investigation in behavioural ecology (Charnov, 1976), as it is assumed that these patterns will represent an attempt by a species to maximise resource utilisation (primarily nutrient intake), balanced against time and energy costs (Krebs, 1989). Most medium to long-term field studies of primates have included an examination of the patterns in which the species in question utilise their home range, both temporally and spatially. Detailed descriptions of variation in home range use are available for almost all the large terrestrial and semi-terrestrial primates (see Barton *et al.*, 1992; Dunbar, 1988, for reviews), including a rich pool of a data for *Papio spp.* across different environments (Amboseli: Altmann & Altmann, 1970; Post, 1978; Cape Point: Davidge, 1978b; Drakensburg: Henzi *et al.*, 1992; Gilgil: Harding, 1976; Kuiseb: Hamilton *et al.*, 1976; Chololo: Barton *et al.*, 1992; Mikumi: Rasmussen, 1978, 1983; Mkuzi: Gaynor, 1994; Mt. Assirik: Sharman, 1981; Okavango: Hamilton *et al.*, 1976; Suikerbosrand: Anderson, 1981a; Tsaobis: Cowlishaw, 1993, 1997a). Many of these studies have demonstrated significant variation in the degree to which different areas or habitats are utilised within the primate group's home range (e.g. Post, 1978; Sigg & Stolba, 1981; Rasmussen, 1983; Whiten *et al.*, 1987; Barton *et al.*, 1992; Henzi *et al.*, 1992; Gaynor, 1994; Bronikowski & Altmann, 1996; Cowlishaw, 1997a, 1997b;).

It is generally agreed that the most important factor influencing primate ranging patterns and habitat use is the spatial and temporal distribution of food (Davidge, 1978; Anderson, 1981a; Dunbar, 1988). Unlike the patchily distributed food sources of many large primate species, previous gelada studies have noted that the short grasses on which the gelada graze are predominant throughout their environment (Crook, 1966; Crook & Aldrich-Blake, 1968; Dunbar, 1977; Iwamoto, 1979), and therefore assumed to be evenly distributed. However, as described in Chapter 2, gelada at Sankaber occupy a complex environment of different habitat types incorporating large inter-habitat variation in vegetative cover, altitude, topography and microclimate. Furthermore, given the general observation that gelada must spend a relatively large proportion of time obtaining a relatively low nutrient diet (Iwamoto, 1993a,b), food availability might be expected to be a stronger limiting factor than previously acknowledged. In the present study, data were collected in order to examine the extent to which food availability is the primary determinant of habitat selection.

The gelada's reliance on short green grasses in an environment of strong seasonal precipitation, presents the problem that most of the grasses are perennial and therefore desiccated during the dry season. In order to circumvent this dilemma gelada have two main options. Firstly, as the green grasses dry out they can shift their foraging profile to digging for more subterranean food sources which are available year round.

Depending on the distribution of underground food resources, this may or may not necessitate a shift in habitat selectivity. Alternatively, they can shift their home range use to habitats types which harbour green grasses longer due to shade protection from higher level foliage. A third option is that they could turn to cannibalising each other, of which there is little mention in the literature but would provide a rich source of protein.

While it is acknowledged that factors such as distribution of food resources and predation risk (to be examined in Chapter 7) are likely to be important in shaping the ranging patterns of primates, at least three different primate field studies found no significant seasonal variation in the day range length of *Papio* baboons (see Sharman, 1981; Altmann & Altmann, 1970; Post, 1978), even though it was assumed in these studies that the dry season represented a period of decreased food availability. Although no measures were available, it is unlikely that food availability remained at a constant level throughout these studies. Since group size was not found to vary accordingly, it highlights the importance of examining the influence of factors other than food levels on ranging behaviour. Indeed, little is known about how the gelada's ranging behaviour and habitat selection may be influenced by variation in ecological parameters such as habitat structure, microclimate and the distribution of potentially key resources such as sleeping sites, water sources and refuges.

Distribution of drinking water has been shown to affect patterns of movement within the home range of baboons in general (Altmann & Altmann, 1970; Barton *et al.*, 1992) and *Papio cynocephalus* (Post, 1978) and *Papio cynocephalus ursinus* (Gaynor, 1994; Hamilton, 1986; Brain, 1990) in particular. A number of studies have also described how the location of sleeping sites play an important role in day journey length (Barton *et al.*, 1992) and day journey routing (e.g. hamadryas baboons: Sigg & Stolba, 1981; spider monkeys: Chapman *et al.*, 1989). Gaynor (1994) and Whiten *et al.* (1987) also point out the simple but important relationship between frequency of occupation of an area and proximity to the centre of the groups home range.

The influence of variation in microclimate and thermoregulation on ranging patterns has also received scarce attention (but see Stelzner & Hausfater 1986; Stelzner, 1988; Hill, 1999), while those studies in which it has been considered have tended to focus on the upper limits of thermal constraints (baboons: Stolz & Saymann, 1970; Altmann & Altmann, 1970; Hill, 1999; pigtail macaques: Bernstein, 1972; sooty mangabeys: Bernstein, 1976). Hill (1999) found that high day time temperatures placed a thermal constraint on non-foraging activities and habitat choice of chacma baboons, while the unusually large variation in day length experienced at the fieldsite also imposed seasonal constraints on the animals' time budgets. Furthermore, Hill (1999) suggested that safe habitats were being selected for non-foraging activities when thermal constraints forced the baboons into more sedentary activities. But Stelzner (1988) found no evidence for baboons utilising more shaded habitats as environmental temperatures increased. Instead, he concluded that the baboons at Amboseli only exploited shade opportunistically as they encountered it. In contrast, gelada habitat is characterised by high altitude and cold temperatures, often involving harsh alpine weather. Given the complex nature of the gelada's environmental topography, these weather conditions may vary between habitat types and the gelada might be expected to shift ranging patterns in order to avoid the most severe microclimatic conditions.

An aim within the current chapter is to recognise the potential influence of a suite of environmental factors on the gelada's ranging patterns, including those characterised by habitat structure and geography, mentioned above. However, given the physical and temporal investment gelada make to feeding, the analyses will be guided by the following predictions:

1) It is predicted that gelada will primarily use their home range in a way that is determined by the spatial and temporal distribution of food resources, such that habitat selectivity will reflect food availability.

2) Food availability is predicted to be a stronger limiting factor in the dry season and should therefore exert a stronger influence on ranging patterns during dry season months than wet season months.

3) More specifically, given the dry-season shift to a more subterranean diet, it might be predicted that habitat selectivity should be driven by above-ground food availability when green grass is available but by below-ground food availability during the driest months.

4) Environmental factors other than food availability are expected to affect the ranging patterns of gelada to a lesser, but varied, extent. For instance, while water availability is predicted to play practically no role in determining ranging patterns (see

section 2.3.3), adverse seasonal climatic conditions are predicted to drive gelada into more sheltered habitat types.

The analyses in the current chapter will begin with a description of the patterns of food available to the gelada across habitat types and seasons (section 4.2). The distribution of food resources will presumably underpin much of the gelada's ranging decisions. Therefore, patterns of home range and habitat usage will be detailed on a monthly and seasonal basis (section 4.3), before an examination of how food availability affects these ranging patterns. Once this relationship has been established, the distribution of sleeping sites, refuges and water sources in the Sankaber home range will be analysed in relation to their possible influence on gelada ranging (section 4.4). Variation in habitat use will also be examined in relation to shifts in microclimate experienced by gelada between habitats (section 4.4.3). Actual measurements of feeding and nutrient intake will be examined in Chapter 5, while the possible trade-off between foraging and predation risk will be covered in Chapter 7.

4.2 Patterns of food availability

A detailed description of the methods used to calculate food availability was given in Chapter 3 (section 3.1.2). Because quadrats were located along established transects (which themselves ran across different habitats), not all habitat types were represented by the same number of quadrats. Quadrats were photographed at monthly intervals and monitored visually in all months for percentage cover of food and non-food plants and degree of desiccation.

4.2.1 Monthly variation in green cover

Although gelada eat a variety of food types, they rely so heavily on the abundance of short green grasses throughout their environment that any analysis on the levels of food available to them must focus primarily on the amount of appropriate fresh grass forage. Short grasses typically respond rapidly to fluctuations in local precipitation (Boutton *et al.*, 1988) and the Sankaber area experiences dramatic seasonal variation in rainfall (see Figure 2.2). Therefore, the percentage of green grass cover can be expected to show concurrent seasonal shifts. Since the gelada eat strictly green and not desiccated grasses, many of which are annual species, variation in levels of green grass cover represents an important resource variable.

The mean estimated percentages of green (as opposed to desiccated) plant parts for quadrats in different habitat types are given in Figure 4.1. A striking feature of the results in Figure 4.1 is the variation in maintenance of green vegetation between habitat types as the dry season progresses. From November onwards the percentage of green vegetation in P-open and G-open habitat types declines dramatically in comparison to quadrats in the more shaded P-bushy, G-bushy and E-heather habitat types. Conversely, the P-open and G-open habitat types show a more rapid increase in percentage of green cover as the short grasses that characterise these habitat types sprout fresh growth in response to the onset of the rains. The lowest seasonal variation in green cover is to be found in the E-heather habitat type, where shaded protection from the sun enables some degree of green vegetation to persist year round.

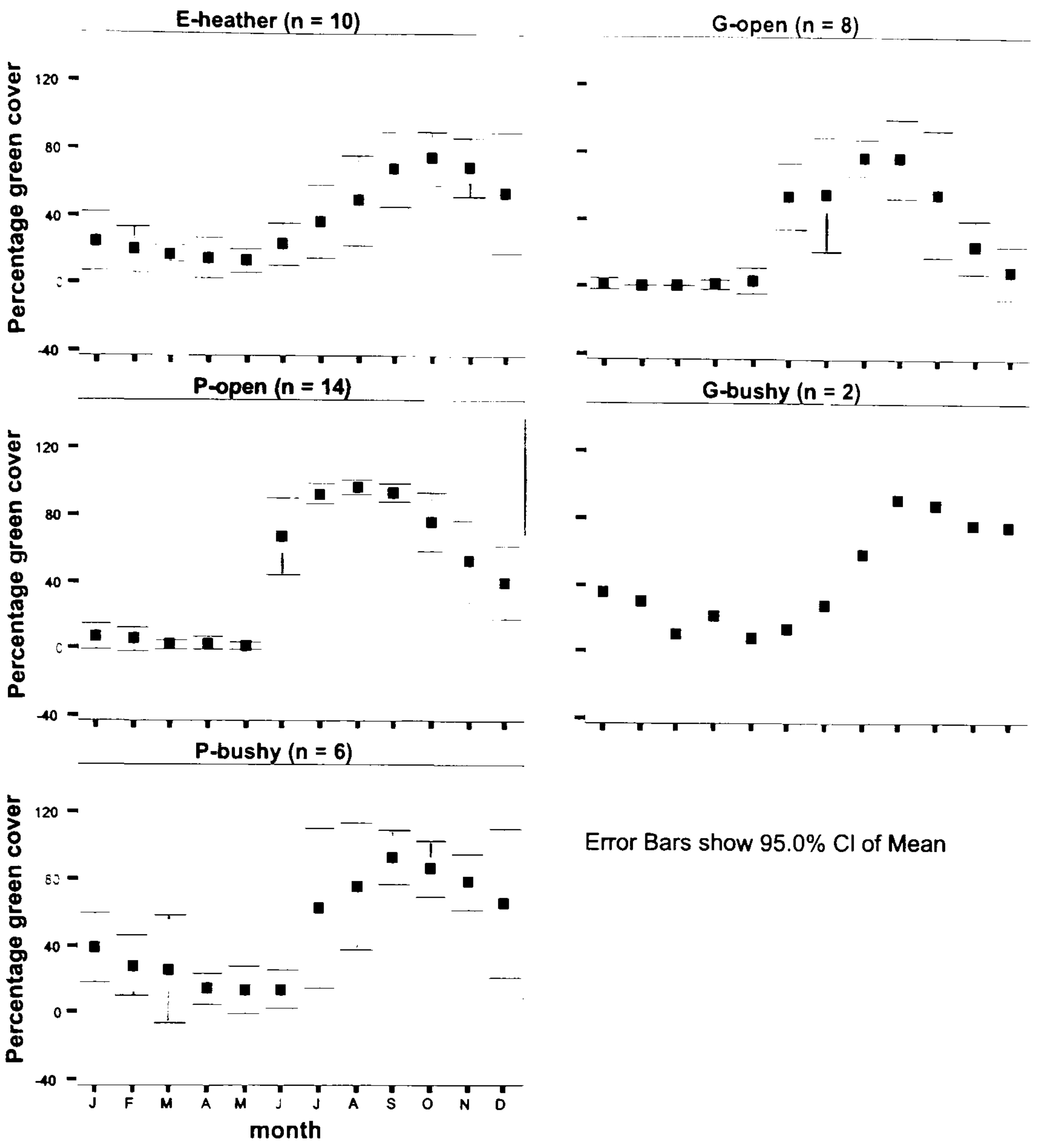


Figure 4.1 *Mean monthly percentage of green cover for quadrats in different habitat types, estimated visually in the field and from digital colour pictures taken at exact monthly interval (N quadrats displayed above each habitat box)*

Although tree cover in the heather forest is not as dense as in the P-bushy or G-bushy habitat types, the ground level vegetation consists of long grasses which cover over 87% of ground area (see Table 2.1). This is a very high level of low vegetation cover, even when compared with open areas of the plateau which support a mean cover of 82% short grasses. The predominant *Festuca spp.* grasses in the heather forest grow in dense clumps thereby sheltering a certain amount of green blades closer to the ground.

Although no whole habitat type experienced 0% green plant cover or 100% green plant cover in any month, individual quadrats did show such extremes and there was large variation between individual quadrats within habitat types and months. In two habitat types, P-open and P-bushy, this variation is especially pronounced at the beginning and end of the wet season, suggesting that food resources, in the form of green grass forage, might be more patchily distributed during these periods. Given that previous studies have usually assumed a very even distribution of the gelada's food resources (see Crook & Aldrich-Blake, 1968; Dunbar, 1977; Iwamoto, 1978), this is an important consideration and will be examined in more detail in Chapter 6.

4.2.2 The influence of rainfall on green cover

Variation in annual rainfall between habitats has been shown to be a reliable index of the primary production of those habitats (Rosenzweig, 1968; Coe *et al*, 1976; Barret *et al.*, 1992). However, although 'the influence of rainfall on green cover' may initially seem obvious, it is important to consider the temporal scale of the relationship. In some studies, monthly rainfall has been shown to correlate strongly with monthly primary productivity (e.g. Deshmukh, 1984). In a number of primate field studies, however, a lag effect has been observed and stronger correlations were observed between food availability and levels of rainfall in the preceding month or months. For example, Barton *et al.* (1992) describe a correlation delay of two months between accumulated rainfall and production of baboon foods at Laikipia, Kenya, while Gaynor (1994) found availability of baboon food at Mkuzi, South Africa, lagged three months behind monthly rainfall. Different forms of vegetation respond very differently to seasonal fluctuations in climate and in any comparative discussion about food availability it is important to take into consideration variations in the diet of different species. For instance, Gaynor (1994) describes the high percentage of fruits in the diet of the baboons at Mkuzi, which are slower to develop than many other forms of vegetation, and might account for the three month lag between rainfall and food biomass observed at the fieldsite. In contrast Hill (1999) found a somewhat counterintuitive, negative correlation between food availability and rainfall in a number of habitats at De Hoop, South Africa, and concluded that in areas of such high latitude, variation in day length may be a more important predictor of food availability than rainfall. These results bring into question the common assumption that a wet and dry season dichotomy--typical of African primate field sites--accurately reflects seasonal difference in food availability (see Altmann & Altmann, 1970; Anderson, 1981a; Sharman, 1981). This consideration is particularly pertinent with regards to the gelada given the extreme seasonal variation they experience in precipitation. The four months of June to September constituted 84.2% of the total annual rainfall for 1998, while the six months of May to October accounted for 95.4% of total rainfall. As noted in Chapter 2, May and October are important inclusions when considering the 'wet' and 'dry' seasons discussed in this study, as the 109 mm that fell in late May is enough to bring through the first significant growth of fresh green grass in the year, and October's rainfall of 71.5 mm is enough to maintain the 'greenness' of the short grass areas.

Monthly rainfall figures were presented in Figure 3.2, while monthly rainfall and accumulated rainfall, are correlated with mean levels of green cover in Table 4.1.

Table 4.1 shows that the percentage of green cover in all habitat types correlates with some measure of rainfall in the preceding month or months.

Table 4.1 *Pearson correlations between mean percentage green cover of quadrats in different habitat types and cumulative rainfall totals. * indicates significance at the <0.05 level, ** indicates significance at the <0.01 level, r values in* ***bold*** *represent the strongest correlation per habitat type.*

Habitat	**Total rainfall (mm)** current month	 previous month	 current plus previous month	 current plus previous 2 months	**N**
	r	**r**	**r**	**r**	
P-open	0.751**	**0.885****	0.870**	0.732**	14
P-bushy	0.223	0.684*	0.829**	**0.886****	6
G-open	0.786**	**0.925****	0.905**	0.707*	8
G-bushy	-0.051	0.492	0.705*	**0.865****	2
E-heather	0.095	0.549	0.756**	**0.917****	10
Mean of all quadrats	0.575	0.859**	**0.922****	0.864**	20

The mean percentage of green cover across all quadrats correlates most strongly with the total rainfall of the previous two months. However, when habitats are examined individually, no one habitat type replicates this relationship. Instead, the levels of green vegetation cover in three habitat types, P-bushy, G-bushy and E-heather, correlate most strongly with rainfall totals in the three preceding months combined. In contrast, variation in the level of green cover in the P-open and G-open habitat types shows the strongest correlation with rainfall in the preceding month alone. This is understandable given the open nature of these habitat types and the fact that open grassland typically responds rapidly to rainfall (Boutton *et al.*, 1988). After the onset of the rains in May the open areas of the plateau and gorge are very soon flush with fresh new green grass growth. Indeed, the percentage of green cover observed in P-open and G-open quadrats also correlates strongly with rainfall in the immediate month suggesting a very rapid vegetative response to precipitation. Conversely, in the habitat types with denser levels of tree and bush cover, vegetation takes longer to respond to rainfall and the mean percentage of green cover in the G-bushy and E-heather habitats does not correlate to rainfall in the corresponding month or previous month. It thus appears the relationship between rainfall and green vegetative cover varies considerably between different habitat types, and this raises the implication that patterns observed across entire gelada home ranges might mask habitat-specific resource availability on a finer scale.

4.2.3 Seasonal variation in food availability

Dry-weight of both above and below-ground vegetation was measured directly using the clipping method at the height of the dry season (April) and towards the end of the wet season (October). Identification of food plants to species level was usually impossible, especially in the case of short grasses, which bore no flowers or seeds for most of the months in which they were eaten by the gelada. However, it was possible to sort vegetation on the basis of 'food' or 'non-food' items. As mentioned in section 3.1.2, this classification is not species-specific, in that some plant species were classified as 'food' when green and observed eaten during the wet season and 'non-food' when desiccated during the dry season.

At the same time as above-ground clipping, the top 20cm of quadrat ground was excavated and all below-ground food sifted from the soil. The classification of 'food and 'non food' proved more problematic for underground food items since certain roots and rhizomes are present all year round but were only observed to be eaten during the dry season. This detail may seem of little importance considering the gelada's clear preference for fresh green grass, when available, over underground items. However, gelada were observed to dig for underground food items in all months, and some subterranean food items (such as the highly sort after rhizome nodules of *Meredera abyssinica*) were only found in the soil, and exhumed by the gelada, during the wet season. Therefore, for the purpose of the present analyses, it was assumed that if the underground part of a plant species, that was eaten at any time of the year, was present in the sample, then it constituted a *possible* 'food' and was classified as such. Samples were preserved as described in Chapter 3 and count and weight measurements were divided by the mean quadrat area per habitat to provide an estimate of the amount of food per unit area in different habitat types and seasons. These data are presented in Table 4.2.

The overall mean density of above-ground food across all habitat types is far higher in the wet season (mean = 66.2 mg/m^2, sd = 39.8, n = 20) than in the dry season (mean = 10.7 mg/m^2, sd = 8.8, n = 20), and the difference was found to be significant ($t = 8.348$, df = 38, $p < 0.001$). On a smaller scale, this pattern is expressed within all but the G-bushy habitat type, where the reverse trend is observed and can be attributed to the fact that *Rosa abyssinica* bushes bear fruit (a major seasonal food for the gelada) towards the end of the dry season. Although it is impossible to draw any conclusions from this result as there was only one quadrat pair located in the G-bushy habitat type, the fruit of *Rosa abyssinica* are common in the P-bushy and G-bushy habitat types and constitute the single most important food item in the gelada's diet at a height above ground level vegetation (see section 5.3.1).

Table 4.2 *Mean dry-weight (and standard deviation) of above and below-ground food for quadrats in different habitat types and seasons, expressed as g/m².*

Habitat type	**Wet season** Above-ground food (g/m²)	Below-ground food (g/m²)	**Dry season** Above-ground food (g/m²)	Below-ground food (g/m²)	**N (per season)**
P-open	101.6 (± 43.4)	93.2 (±29.2)	7.3 (±2.4)	85.6 (±54.8)	7
P-bushy	43.3 (±10.4)	21.0 (±5.9)	9.5 (±3.2)	8.2 (±2.0)	3
G-open	39.4 (±19.9)	5.1 (±2.3)	1.3 (±0.5)	0 (±0)	4
G-bushy	15.8	13.8	20.2	11.5	1
E-heather	63.1 (±12.0)	4.6 (±1.7)	21.9 (±6.1)	1.4 (±2.1)	5
MEAN	66.2 (±39.8)	38.7 (±45.8)	10.7 (±8.8)	32.2(±50.7)	20 (total)

The P-open habitat clearly supports the highest food biomass in both wet and dry seasons. However, there is less variation between the habitat types in terms of above-ground food density in the wet season when green vegetation grows prolifically throughout the home range. Furthermore, in the dry season the profitability of the P-open habitat type over others is restricted solely to the amount of below-ground food. In other words, three other habitat types (P-bushy, G-bushy and E-heather) contain more above-ground food per unit area than P-open in the dry season. As noted above, this is due to the higher densities of bush and tree cover present in these habitat types, which provides shade for ground level vegetation and protection from the desiccating effects of the solar radiation.

Following the high density of short grass forage found in the P-open habitat during the wet season (which averaged above 100 g/m^2), it is important to note that the second highest mean food density level is to be found in the subterranean items also in the P-open habitat type, also during the wet season. Most of these underground food items are still available to the gelada in the dry season, and the overall mean density of underground food items is not significantly lower in the dry season (mean = 32.2 g/m^2, sd = 50.7, n = 20) than in the wet season (mean = 38.7 g/m^2, sd = 45.8, n = 20) (t = 0.503, df = 38, p = 0.618).

Another conspicuous feature of the results presented in Table 4.2 is the large standard deviations associated with the mean dry-weight of food per quadrat. The amount of above-ground food in P-open quadrats during the wet season varied from a minimum of 33.1 g/m^2 to a maximum of 153.5 g/m^2. This variation is in line with the range in percentage of green cover described in section 4.2.1, and suggests that although food may be readily available to the gelada in the wet season, it might not be as evenly distributed as previously thought. Furthermore, when quadrats were sampled in April, an even greater variation was observed in the amount of underground food per quadrat. Quadrats in the open areas of the plateau varied from a minimum 5.6 g/m^2 dry-weight of underground food, to a maximum of 165.7 g/m^2. However, it is important to acknowledge the small sample size (seven P-open quadrats) from which these results are drawn, and it cannot, therefore, be concluded that such variation is indicative of the complete spatial distribution of gelada food resources. Nonetheless, even small amounts of variation in the distribution of food resources can be important in shaping the nature of an animal's foraging decisions and in turn the overall behavioural ecology of the species.

4.3 Patterns of home range use

The previous section presented a detailed description of the levels of food (both above- and below-ground) available to gelada across six different habitat types in the wet and dry seasons. Before assessing the degree to which food availability drives the ranging behaviour of gelada (section 4.4), the current section will examine the patterns in which gelada utilise the different habitat types in their home range.

In the present study, habitat usage was recorded by systematically marking on a map the (200m x 200m) quadrats in which the centre of mass of the gelada herd was located at half hourly intervals from 07:00 until 18:00. Quadrat occupancy was recorded during a minimum of five all day follows per month as described in Chapter 3. To test the evenness of range use the distribution of quadrat use was compared to the theoretical distribution of quadrat usage if all quadrats were used equally. The difference between the two distributions was highly significant (Kolmogorov-Smirnov 2-sample test: $z = 10.005$; $n = 232$; $p < 0.01$), indicating that that gelada are not using their home range in a uniform fashion. Indeed, the 52 most used quadrats (22% of all quadrats) accounted for 75% of all occupancy time. Clearly the gelada are showing strong selectivity down to a very fine spatial scale.

4.3.1 Habitat selectivity

Although the main gelada band entered all seven habitat types during the study, there was significant variation in the degree to which quadrats of different habitats types were utilised (**ANOVA**: $F_{(6,225)} = 14.014$; $p = < 0.001$). Figure 4.2 shows the mean number of times the gelada were recorded in quadrats of specific habitat types.

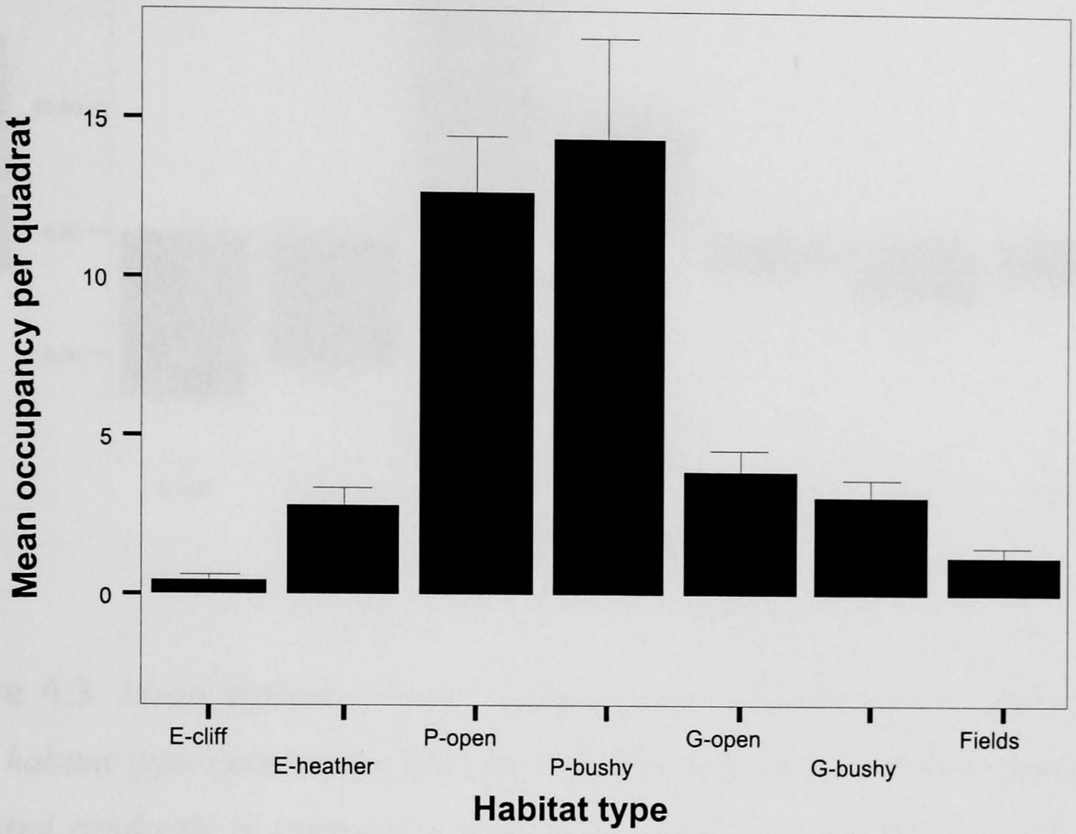


Figure 4.2 *Mean (and standard error) counts of occupancy for quadrats of different habitat types, taken from number of half-hour time-point intervals that gelada occupied each quadrat over the entire study (N = 1162 records across 232 quadrats).*

Post hoc analyses indicate that all significant variation exists between the Plateau-open and Plateau-bushy quadrats on the one hand, and quadrats of all other habitat types on the other (Tukey: $p<0.05$, in all cases). However, as the seven habitat types vary in their respective proportions of the total home range, variation in usage may simply reflect their availability. In order to examine this relationship the mean monthly difference between the intensity of habitat use and their respective availabilities is displayed in Figure 4.3.

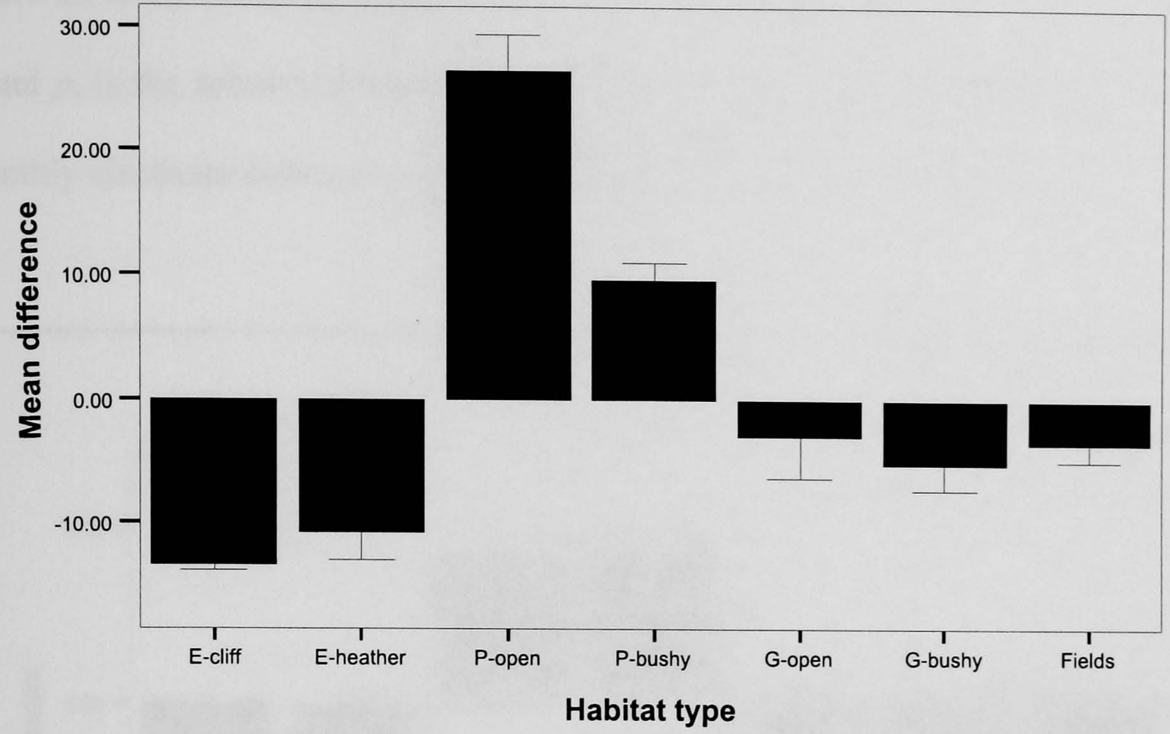


Figure 4.3 *Mean difference (and standard error) in proportion of time observed in each habitat type each month and the expected time in each habitat type if habitats are used randomly in proportion to their availability in the home range (N = 1162 occupancy records).*

There is clear preference for, and avoidance of, certain habitat types in relation to their overall availability. However, the deviations between predicted and expected values displayed in Fig 4.3 cannot themselves be taken as the basis for statistical analysis. Instead, the deviations must be considered in *proportion* to the predicted values. In order to do this, Kreb's (1989) Electivity Index was calculated to determine the relative preference for each habitat type. The Electivity Index varies between +1 (strongly selected) and –1 (strongly avoided), and was calculated on the basis of the following formula:

$$\mathrm{EI} = \frac{(h_i - p_i)}{(h_i + p_i)}$$

where EI is the electivity index, h_i is the observed proportion of time spent in habitat i, and p_i is the relative availability of habitat i in the entire home range. The mean monthly electivity indices for each habitat type are displayed in Fig 4.4.

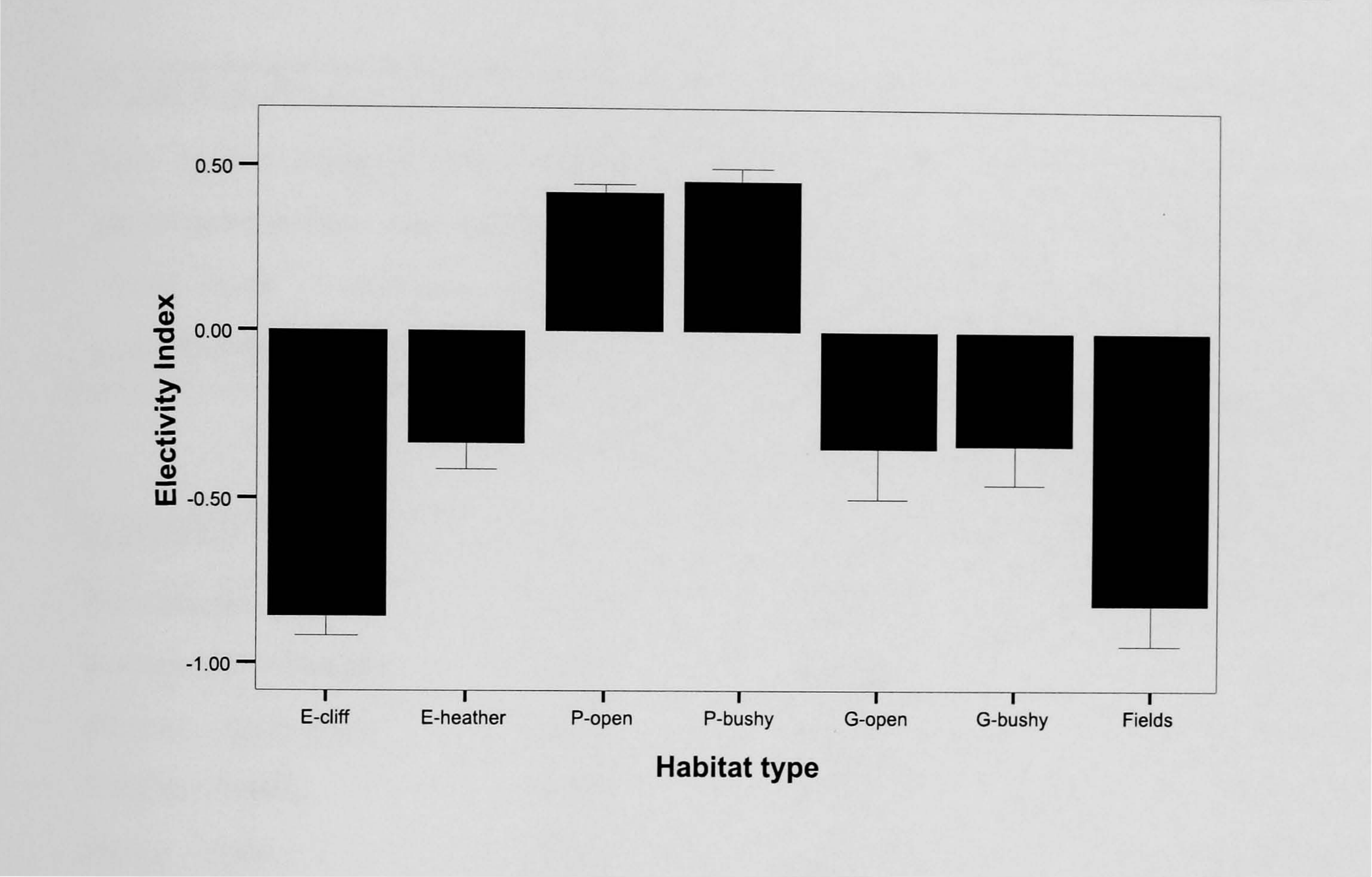


Figure 4.4 *Mean monthly habitat electivity indices for each habitat type based upon the proportion of each habitat within the home range.*

The Electivity Indices presented in Figure 4.4 display analogous preferences and avoidances for habitat types as those shown in Figure 4.2. However, the relative degree of preference (in proportion to the predicted values) is lower for P-open, whilst the proportional avoidance of E-cliff, G-open, G-bushy and Field habitats has increased. Another important feature of the results presented in Fig 4.4 is the large error bars associated with the means for most habitat types. This suggests there is large variation in the Electivity indices for each habitat between months. It is clear that the geladas use of all habitat types, apart from gorge-open, was significantly different to that predicted by the proportional distribution of habitat types. This relationship is also displayed in Table 4.3, along with the important caveat that, despite significance over the entire year, most habitat selection patterns do not hold across all months.

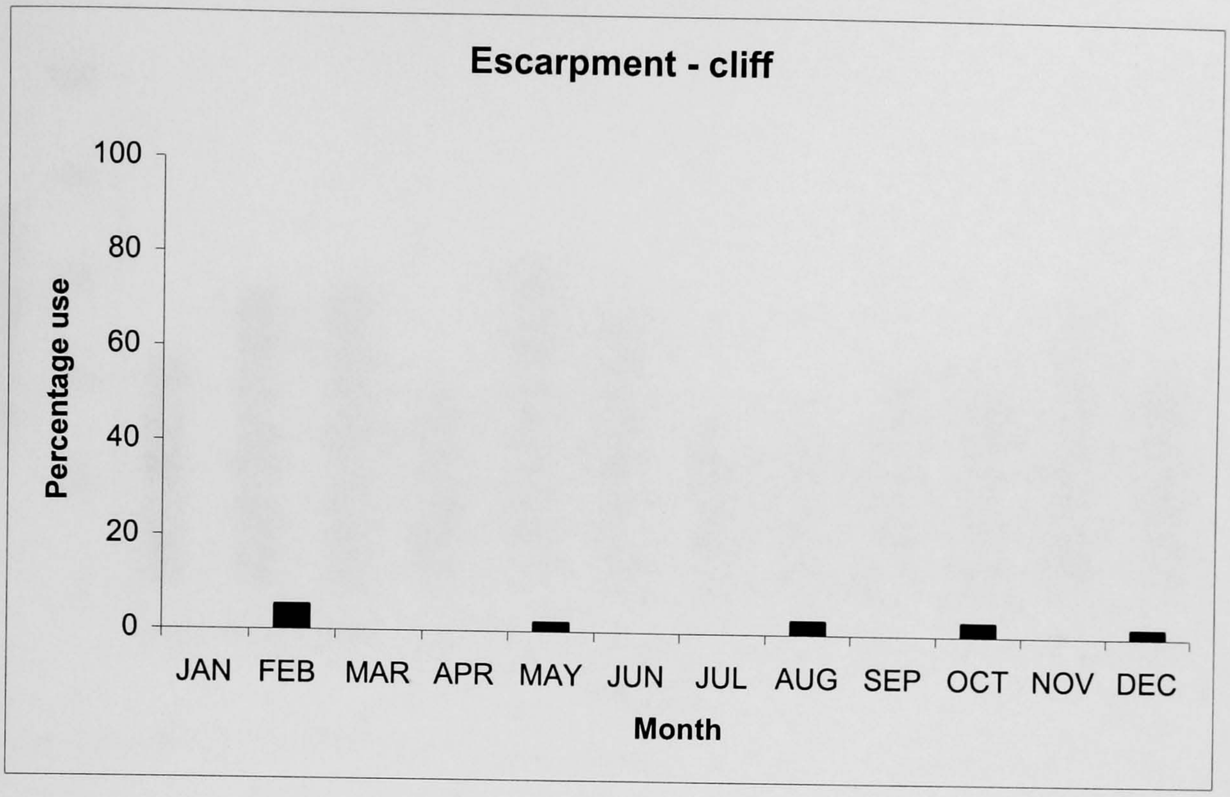
Table 4.3 *Wilcoxon signed ranks tests on proportion of time observed in each habitat type against expected time in each habitat type if habitats are used randomly in proportion to their availability in the home range. (** indicates significance at the <0.01 level, * indicates significance at the <0.05) and the number of months contributing to the rank variations.*

	Wilcoxon pairs tests		number of months in rank directions	
HABITAT	z	p	+ve	-ve
Escarpment – cliff	-3.130	**0.002****	0	12
Escarpment – heather	-2.903	**0.004****	1	11
Plateau – open grass	-3.059	**0.002****	12	0
Plateau – bushy	-3.062	**0.002****	12	0
Gorge – open	-0.943	0.346	3	9
Gorge – bushy	-2.040	**0.041***	3	9
Fields	-3.106	**0.002****	1	11

The E-cliff habitat is occupied less than expected in all 12 months (although it should be noted that first and last quadrats of each day, during which the gelada were often in E-cliff quadrats, remain excluded from these analyses; see section 3.3.2). Conversely, the strong preference for P-open and P-bushy habitat types is also found in all months. However, it is important to note that while three habitat types (E-heather, G-bushy and Fields) were used significantly less than expected from their proportional availability, this relationship does not hold through all months. While these habitat types are being avoided on average, clearly there are some periods in which they are favoured more (or avoided less) than others. Hence, variations in habitat use over time will be examined in the following section.

4.3.2 Monthly variation in habitat use

In the previous section variation in habitat use (that differed from the expected) was not found to be consistent across all months (Table 4.3). Further analysis shows there was significant variation in use of different habitat types between different months ($\chi^2 = 410.0$; df = 11; $p < 0.01$). Although the P-open habitat was the most used habitat type in all months, no other habitat type maintained a single rank position, with respect to proportional monthly occupancy, throughout the year. All other habitat types varied in rank (if '1' is the most used and '7' the least used) across the year: E-cliff (rank range: 4-7), E-heather (2-5), P-open (1), P-bushy (2-4), G-open (2-6), G-bushy (2-6), Fields (4-7). Monthly variation in habitat use can be examined better in Figure 4.5 (a-g), in which the percentage use per month is shown individually for each habitat type. While differential preference between habitat types was shown vividly in the previous section, the primary feature of Figure 4.5 (a-g) is the variation in use of a *single* habitat across time. Key examples are the heavier use of both G-open and G-bushy habitat types during the wet season months, and the significantly higher use of the E-heather habitat type during dry over wet season months (**Mann Whitney** U: $z = -2.201$, $n = 2$, $p < 0.05$). The 'Fields' habitat type represents the only unnatural habitat as it constitutes cultivated barely fields at the outer limits of the geladas ranging area. Access to this food source, however, is highly seasonal and is restricted to a short period immediately after the harvest. The fields were only occupied by gelada in three months (January, March and November) and the percentage use of fields showed the greatest variation from a uniform distribution across months of any habitat type (Kolmogorov-Smirnov 2 sample test: $z = 2.598$, $n = 12$, $p < 0.001$). although the field habitat type represents a relatively small and peripheral component of the gelada's ranging patterns, it is nonetheless considered important in an examination of seasonal patterns of ranging behaviour.



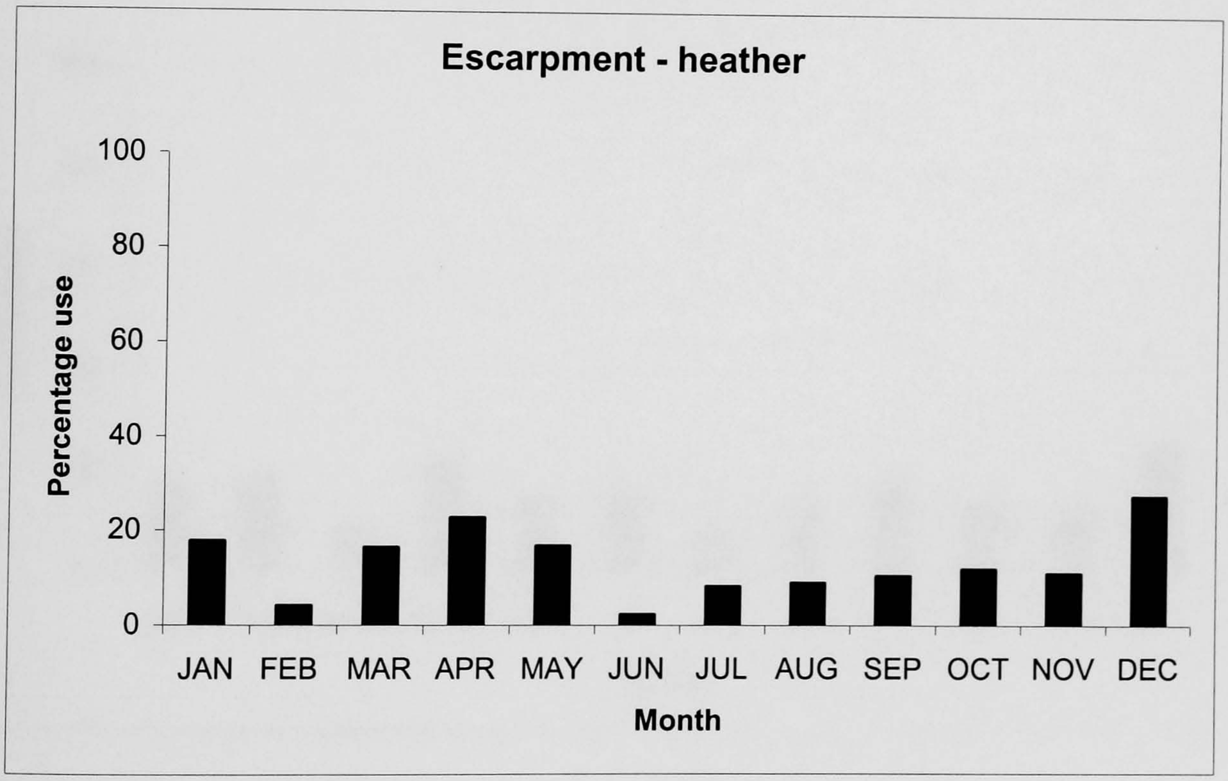


Figure 4.5 (a,b) *Percent of time spent in Escarpment-cliff quadrats (a) and Escarpment-heather quadrats (b) in each month.*

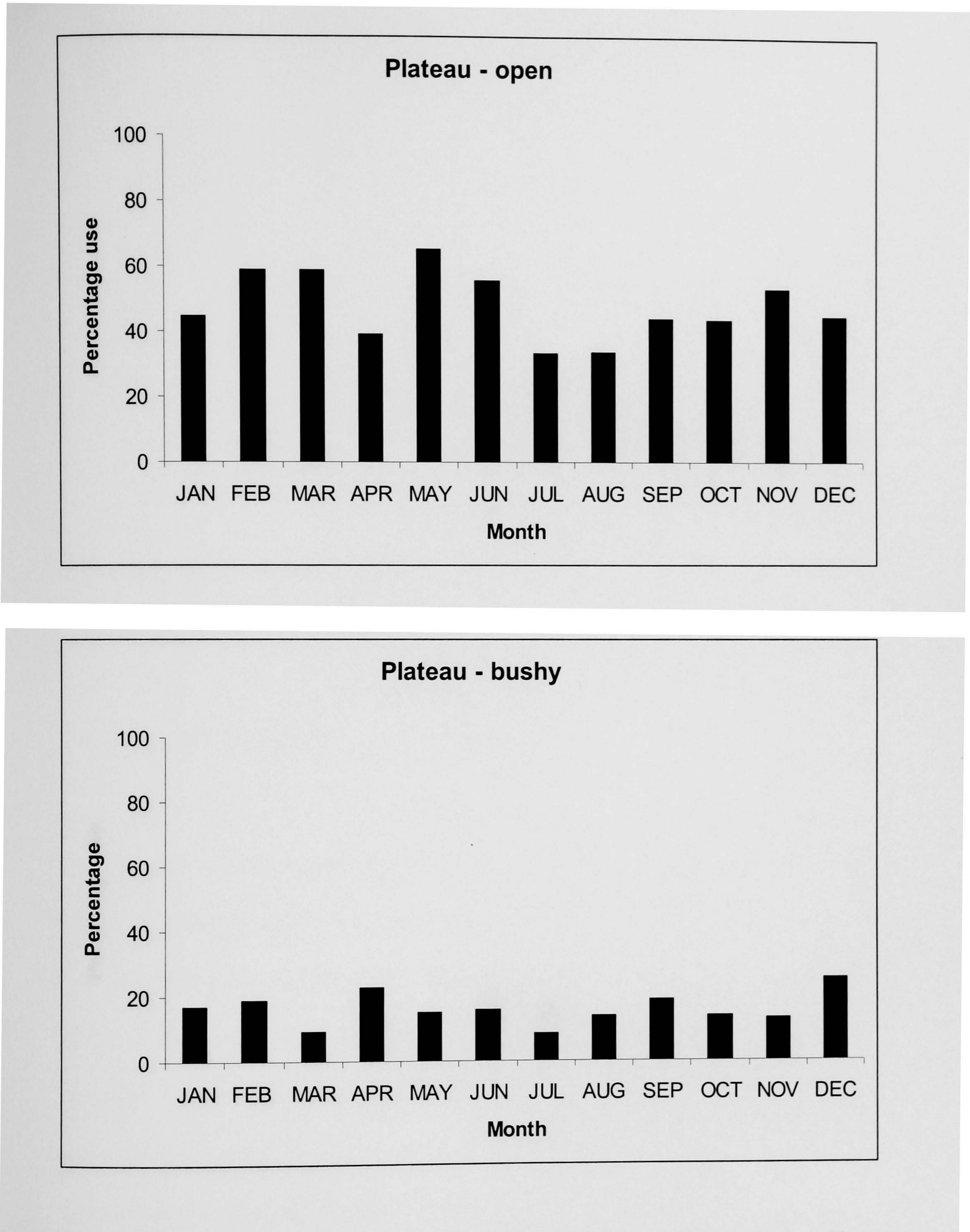


Figure 4.5 (c,d) *Percent of time spent in Plateau-open quadrats (c) and Plateau-bushy quadrats(d) in each month.*

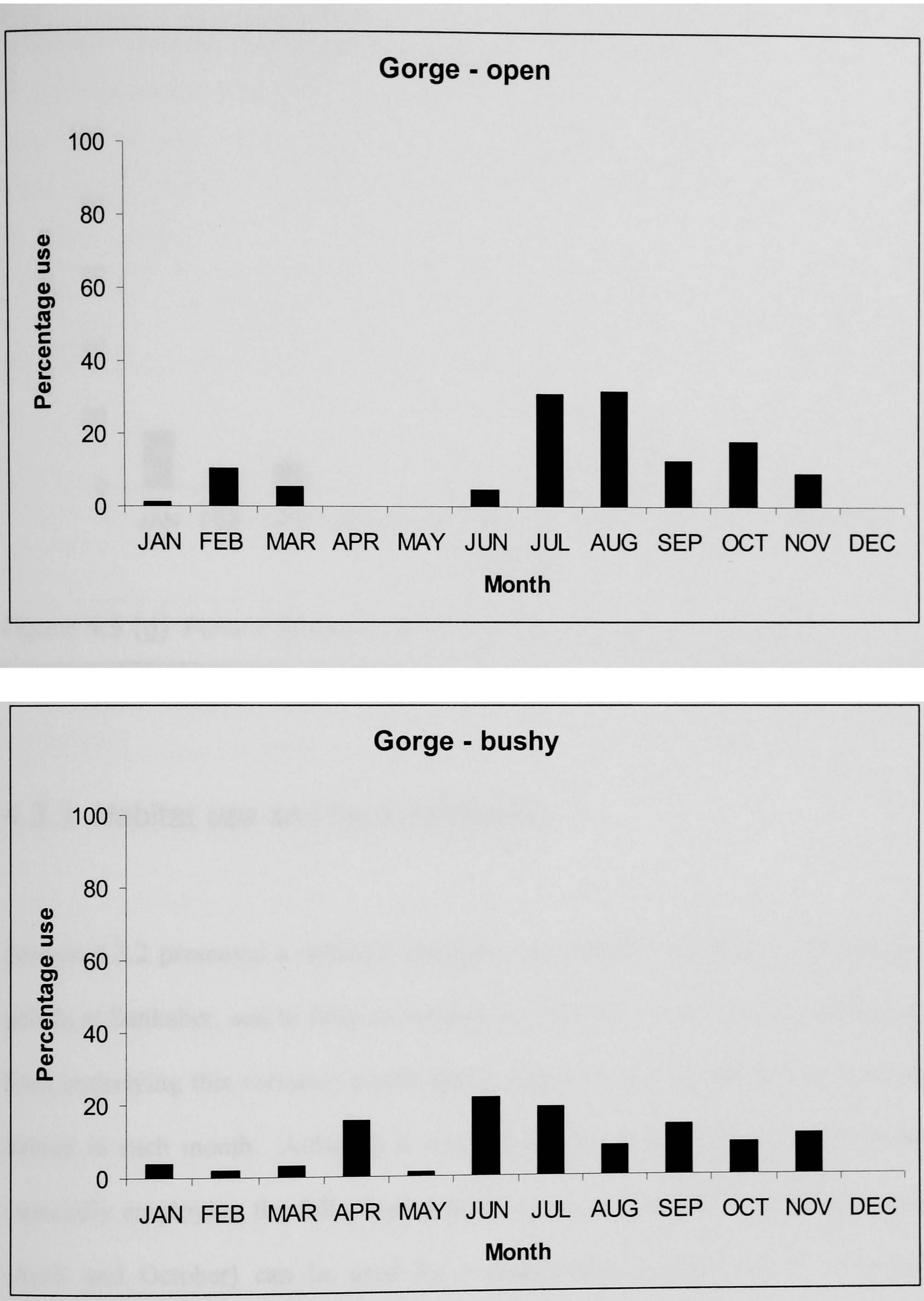


Figure 4.5 (e,f) *Percent of time spent in Gorge-open quadrats (e) and Gorge-bushy quadrats (f) in each month.*

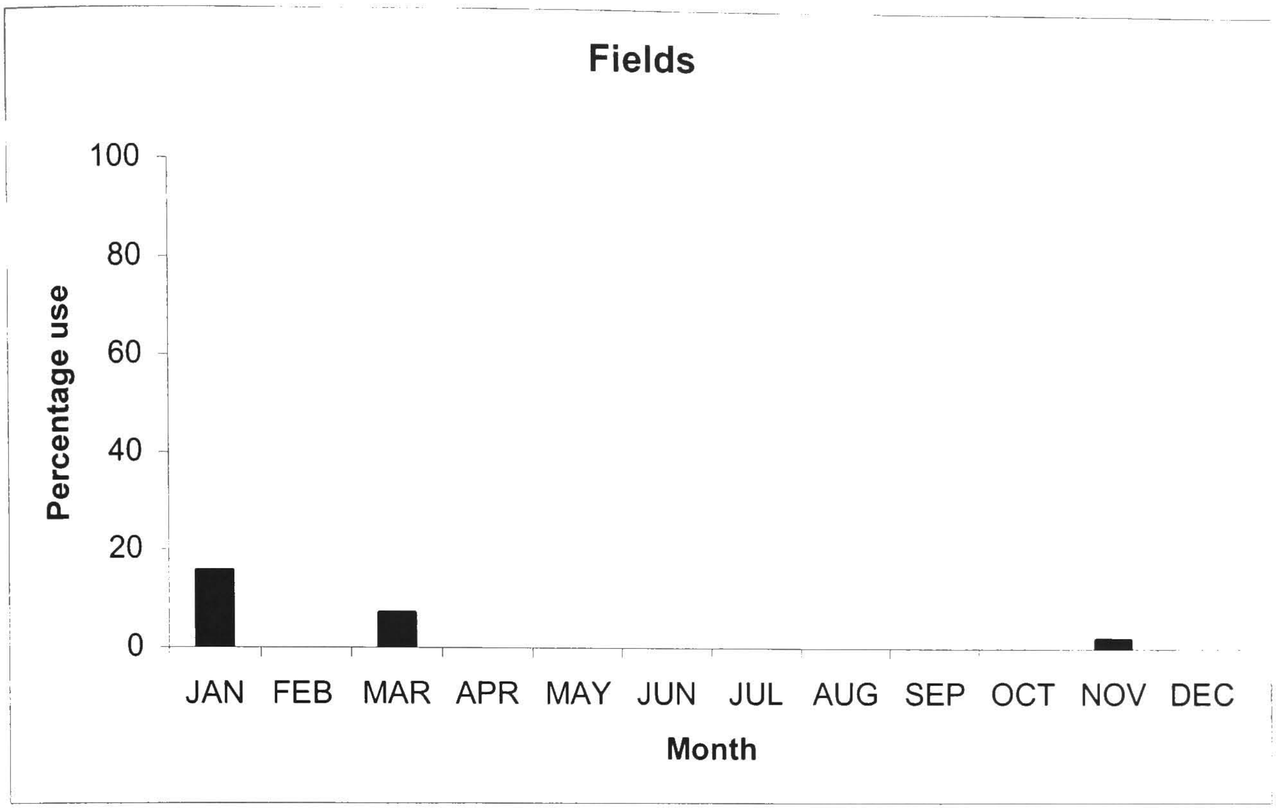


Figure 4.5 (g) *Percent of time spent in Field quadrats (g) in each month.*

4.3.3 Habitat use and food availability

Section 4.3.2 presented a detailed description of monthly variation in habitat use by gelada at Sankaber, and to fully investigate the influence of the spatial distribution of food underlying this variation would ideally require food availability data from each habitat in each month. Although it was not possible to collect these data monthly, especially employing the full clipping method, the two 'seasonal' sampling periods (April and October) can be used for a rudimentary analysis of the relationship between food availability and habitat use. In order to test the prediction that habitat selectivity will reflect food availability, the mean occupancy counts of individual quadrats per habitat type in the wet and dry seasons (and April and October specifically) was correlated with habitat-specific food availability. The Pearson's correlation coefficients are presented in Table 4.4.

Table 4.4 *Pearson's correlations between above and below-ground food availability in different habitat types and mean quadrat occupancy of those habitat types in April and October, and wet and dry season months combined. P values in bold indicate significance. * indicates significance at the <0.05 level, ** indicates significance at the <0.01 level.*

Period of habitat occupancy	***Wet season***				***Dry season***			
	Above-ground food (g/m^2)		*Below-ground food (g/m^2)*		*Above-ground food (g/m^2)*		*Below-ground food (g/m^2)*	
	r	p	**r**	p	**r**	p	**r**	p
April occupancy					0.034	0.657	0.069	0.362
Mean dry season occupancy					-0.129	0.087	0.334	**<0.01****
October occupancy	0.151	**<0.05***	0.206	**<0.01****				
Mean wet season occupancy	0.226	**<0.01****	0.343	**<0.01****				

In support of the first prediction of this chapter, there are a number of significant positive relationships between the occupancy of quadrats and the mean food availability within the habitat types of those quadrats. For instance, the habitat type supporting the highest food biomass in both wet and dry seasons, P-open, is also most preferred habitat type. The mean occupancy of quadrats in all wet season months combined was significantly positively correlated to the mean amount of both above and below-ground food available in those quadrats. Likewise, when October records are considered alone a significant correlation exists between quadrat occupancy and both above and below-ground food availability. In the dry season however, only one significant relationship was found, that between mean occupancy records of all dry season months combined and the amount of food available underground. This might be expected given the relative importance of underground food items to gelada in the dry season, but it is interesting to note the apparent lack of a relationship between above-ground food availability and the gelada's movements in April alone, and all dry season months combined. This result supports the second prediction listed in the introduction of the chapter:- that in the dry season, the distribution of below-ground food sources will be a stronger predictor of ranging patterns than the distribution of above-ground food. Indeed, the distribution of below-ground food appears to be the *only* measure of food availability influencing the gelada's habitat usage in the dry season.

In reference to prediction 3, if the dry season represented a period of relative food scarcity, as has been assumed in previous studies (Crook, 1966; Dunbar & Dunbar, 1974), it was proposed that food availability would be a more limiting factor on ranging patterns than in the wet season. Although this does not appear to hold true in April alone, or for above-ground food availability at all, below-ground food availability in the dry season appears to be a slightly stronger predictor of quadrat occupancy than above-ground food availability in the wet season. While it impossible to draw strong inference from these statistics, the result is in the predicted direction, suggesting that gelada might be forced to marry their ranging behaviour to the distribution of food resources to a greater extent in the drier months.

4.4 Other ecological factors and habitat use

4.4.1 Quadrat use and surface water

It was predicted at the beginning of this chapter that proximity to drinking water is not expected to influence patterns of home range use and indeed there was no significant correlation between the distance to nearest surface water and total quadrat use (r_s = -0.095, n = 232, p = 0.148). However, given the high seasonal variation in rainfall, a relationship between quadrat use and distance to water might be expected during dry season months when examined alone. The analyses were repeated on a seasonal basis, and a significant relationship was found in the wet season (r = -0.189, n = 232, $p < 0.05$) but not the dry season (r = -0.011, n =232, p = 0.864). This result is opposite to what might be expected and caution is warranted before drawing conclusions from it. Firstly, during wet season months rainfall is exceptionally high (mean = 256.9 mm per month, sd = 162.2 , n = 6) and water so abundant throughout the home range as to render the location of 'permanent' water sources redundant. Secondly, as there is no effect in the dry season, when it might be expected, it is highly unlikely that the gelada would alter their ranging behaviour in order to get access to drinking water in the wet season. Thirdly, a number of other ecological factors need to be considered. For instance, the vegetational outlines presented in Chapter 2 (section 2.3) describe how the habitat type G-bushy is characterised by its presence in gullies, which in turn is a likely location for a permanent water source. The gelada's use of quadrats nearer water sources might therefore simply be an artefact of increased use of certain habitat types, such as G-bushy, by the gelada in the wet season (see section 4.3, above).

4.4.2 Quadrat use and distribution of refuges

The difference between 'refuges' and 'sleeping sites' was outlined in Chapter 2 (section 2.3.2), although for the following analyses it is recognised that they are related. Because sleeping sites constitute, by definition, a refuge (but not vice versa), no quadrat could be further from a sleeping site than from a refuge. Table 4.5 shows the mean distance of quadrats from both sleeping sites and refuges throughout the home range, and their correlation coefficient with quadrat use. The mean distance of quadrats from the nearest refuge and/or sleeping site is relatively small indicating that refuges and sleeping sites are readily accessible throughout the home range. No quadrat in the home range is over 1310m from a refuge or 1600m from a sleeping site. These distances are a direct indicator of how far the gelada would range from the cliffs and are slightly higher than those reported by other studies. Crook and Aldrich-Blake (1968) reported gelada ranging no more than 1 km from cliffs at Amba Ras, while Kawai and Iwamoto (1979) found single bands at Gich strayed only 600m from the escarpment, although mixed-band herds would move up to 1 km 'inland'.

Table 4.5 *Distance from all quadrats to nearest sleeping site and refuge, and correlation between distance and total quadrat occupancy.*

	distance from quadrat				quadrat use correlation	
distance to:	min	max	mean	sd	r_s	p
sleeping site	0	1573	425.4	(333.7)	0.164	< 0.05*
refuge	0	1310	351.3	(327.8)	0.079	0.231

It should be noted that the Sankaber fieldsite, due to its location on a narrow ridge, might represent an unusually high concentration of refuge and sleeping site opportunities for gelada. Just over 95% of quadrats are within 1000m of a refuge and 50% of quadrats are within 250m of a refuge.

The distance from a quadrat to the nearest sleeping site is positively correlated with the use of that quadrat (Table 4.5). This is surprising as it appears to suggest that gelada are favouring quadrats which are further from their sleeping sites. This result lends support to Hamilton and Watt's (1970) 'refuging model' in which they suggest that animals might avoid a 'biodeterioration zone' proximal to their sleeping sites while ranging further afield to 'zones of resource acquisition'. However, the relationship between quadrat use and distance to sleeping sites is problematic in that it is difficult to disentangle preference for quadrats that just happen to be near sleeping sites, from 'by product' occupancy of those quadrats as the animals make their way to and from sleeping sites. Also, a more detailed analysis reveals that the overall pattern is confounded by differential use of habitat types. Table 4.6 shows the Spearmans correlation between quadrat use and distance to nearest sleeping site for each habitat type.

Table 4.6 *Correlation between total use of a quadrat and its distance to the nearest sleeping site, divided into quadrats of different habitat types (** indicates significance at the <0.01 level, * indicates significance at the <0.05, † indicates correlation approaching significance).*

Habitat type	Spearmans correlation	
	r_s	p
E-cliff	0.176	0.343
E-heather	0.193	0.281
P-open	-0.465	**< 0.001****
P-bushy	-0.536	0.059†
G-open	0.054	0.767
G-bushy	0.120	0.498
Fields	-0.454	**< 0.05***

The positive relationship is strongest (although not significant) in the E-cliff and E-heather habitat types. Both theses habitat types are located on the escarpment, and therefore more likely to be proximal to sleeping sites (see map; Figure 2.3), but are avoided for foraging and must often be passed through in order for the gelada to get to more favoured habitat types. However, a *negative* relationship (approaching significance) is found between the use of P-bushy quadrats and their distance to the nearest sleeping site, while significant negative relationship is found in the P-open quadrats (the most used habitat; see section 4.3.1) and the Fields, indicating that once the gelada arrive at these habitat types they are more likely to use quadrats closer to their sleeping sites.

4.4.3 Habitat use and microclimate

All gelada habitats are located at low latitude and therefore experience very little variation in day length, and due to the altitude of their habitat it is unlikely that they face any thermal constraints derived from high-temperatures. Although solar radiation is strong at the high altitudes inhabited by gelada, mean monthly maximum temperatures rarely rise above 20°C in the shade (Figure 4.6), and averaged at or below 17°C for nine of the 12 months during the current study. Much more likely to impose pressure on gelada thermoregulation are the severe low temperatures experienced, especially at night. The mean monthly minimum reached its lowest levels during November (2°C) and December (1.5°C), when night time temperatures were commonly below zero and fell to minus -4°C on two nights (Dec 10th and 12th). Mean day time temperatures were lowest during the wet season months, averaging only 10°C in August.

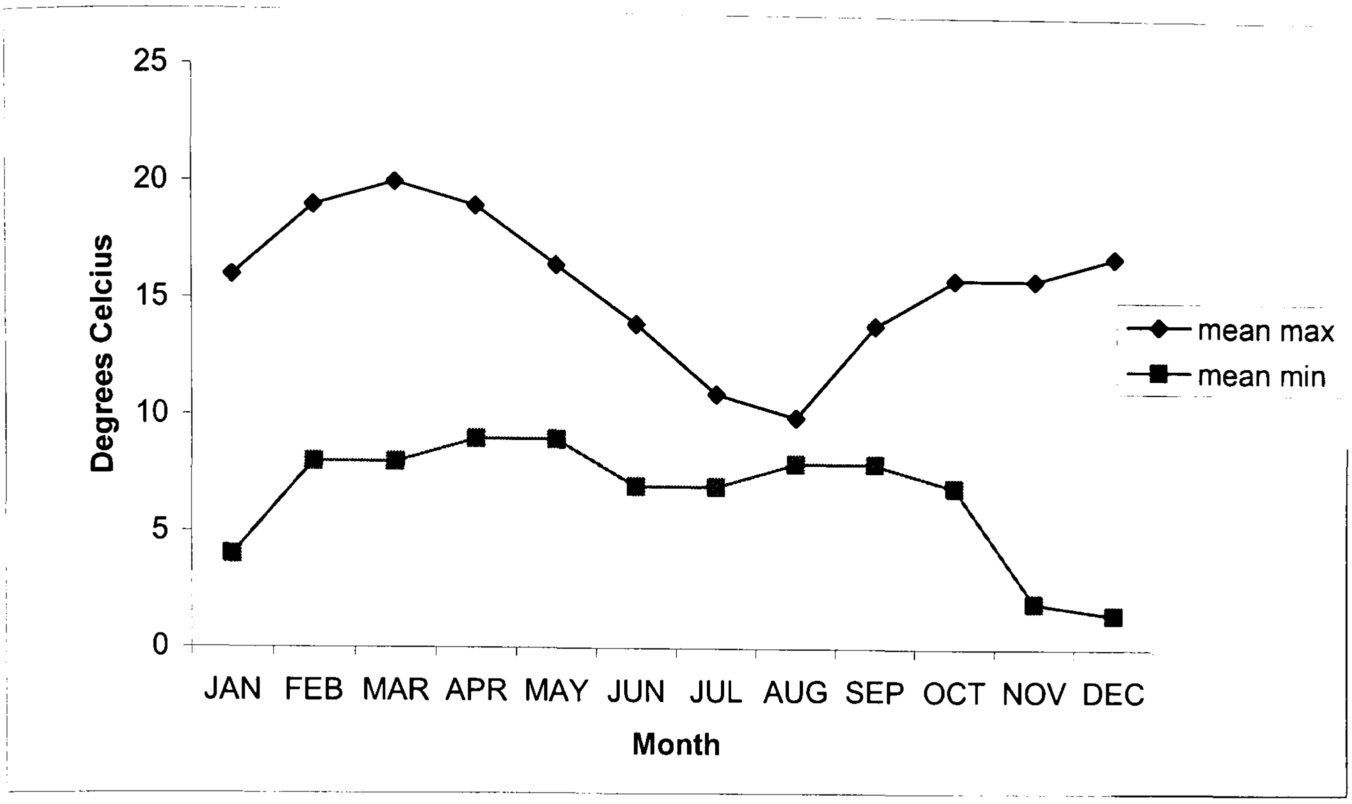


Figure 4.6 *Mean monthly minimum and maximum temperatures at Sankaber camp taken from daily records. Recorded by the National Park Scouts at Sankaber when the author was not present at the field site.*

The pressure that these low temperatures impose on gelada thermoregulation has received little attention, and could be of even greater importance to gelada when coupled with wind-chill factor and the high levels of humidity, experienced especially during the wet season (Figure 4.7). For example, during August, when maximum day time temperatures where at their lowest, the mean percent humidity was 86%. Another characteristic of the wet season is low lying cloud which blankets the high Simien plateau in thick mist for extended periods from June to September.

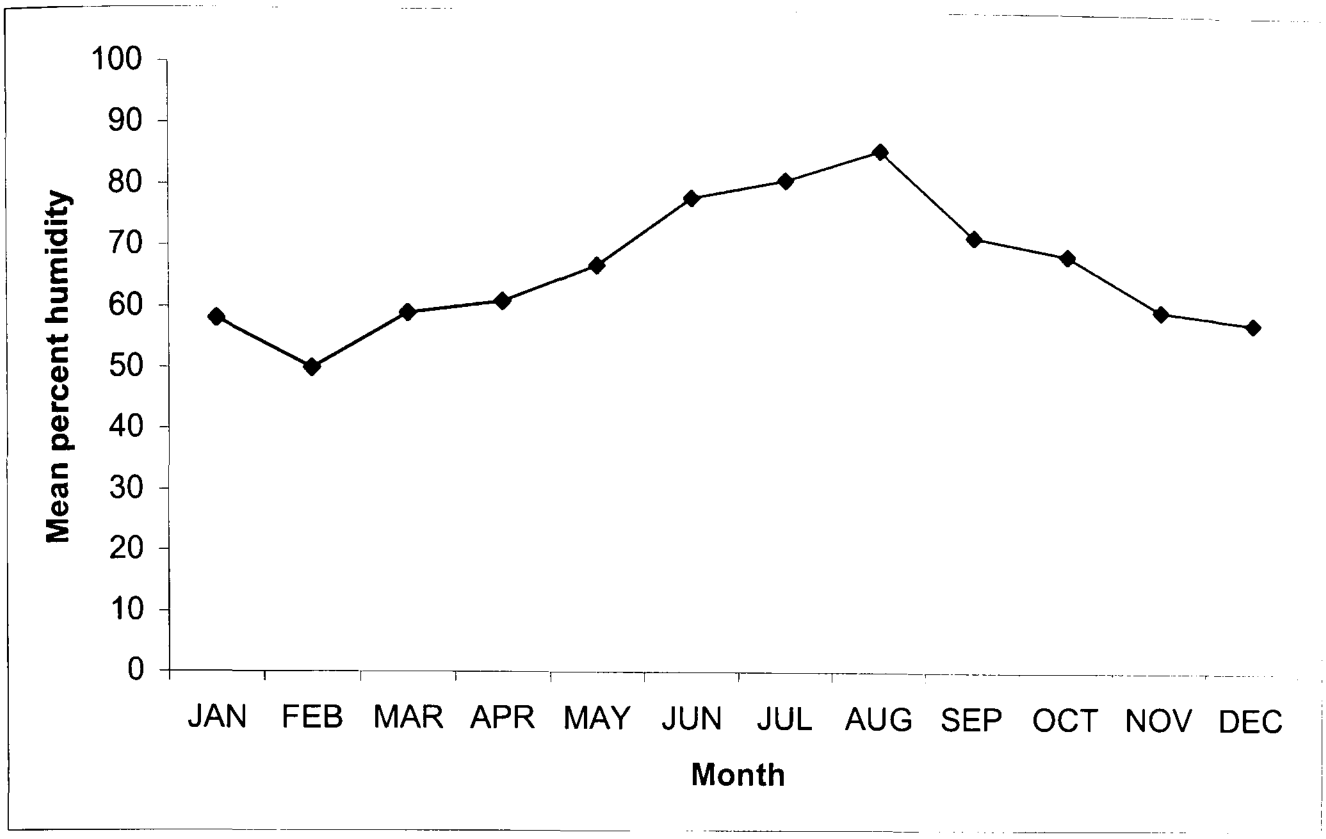


Figure 4.7 *Mean monthly percent humidity at the Sankaber field site; measured at midday and recorded during all day follows (n = minimum five days per month).*

Thick mist usually preceded, and was accompanied by, heavy rain and the proportional number of misty days per month correlated strongly with monthly rainfall ($r = 0.995$, $n = 12$, $p < 0.01$). Cloud formations usually approach the Sankaber ridge from the north or northeast (see section 3.1.3) hitting the escarpment face first, rolling across the plateau and commonly dissipating over the gorge.

During periods of heavy mist visibility is usually reduced to less than 20 m and commonly as low as 10m. Gelada behaviour was often severely disrupted during periods of heavy mist and rain, and the band commonly moved into the more sheltered gorge habitat, where visibility was relatively greater, when thick mist enveloped the plateau. The proportion of heavy mist days per month (defined as days in which the gelada were in mist for more than 4 day-light hours) is significantly correlated with the monthly proportion of time spent in gorge quadrats ($r = 0.839$, $n = 12$, $p < 0.01$). The relationship is plotted in Figure 4.8.

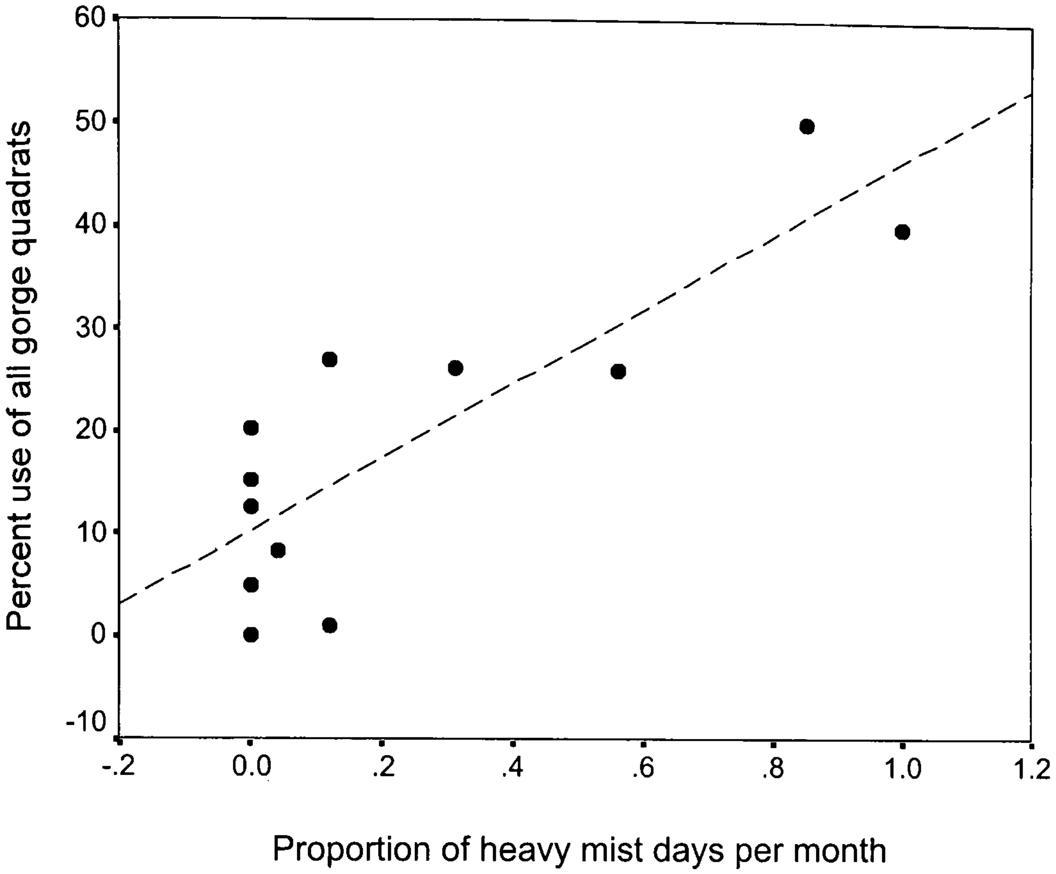
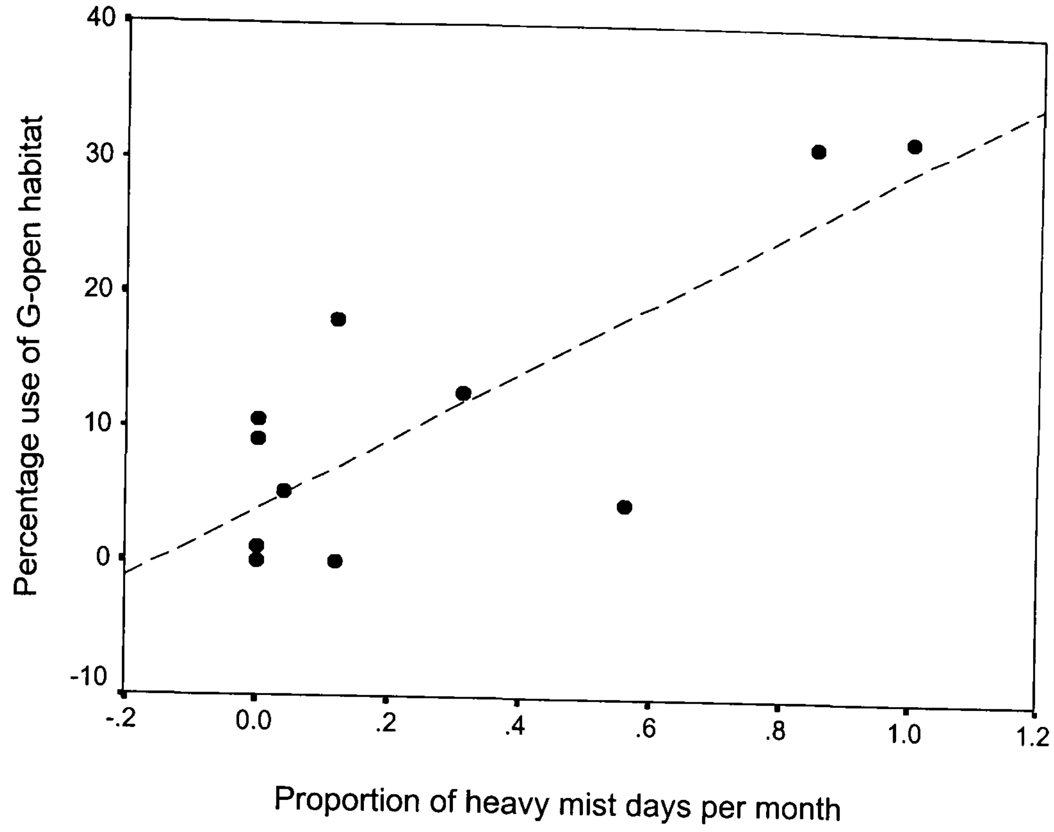


Figure 4.8 *The proportion of heavy mist days per month plotted against the percentage use of all gorge quadrats in the corresponding month*

If the gelada are entering the gorge habitats during periods of heavy mist in order to experience higher levels of visibility, we might predict that they would occupy gorge habitats differentially on the basis of the relative improvement in visibility. The percentage of time spent in G-open and G-bushy habitat types is plotted independently against the proportion of heavy mist days in the corresponding months in Figure 4.9 a) and b). Only the use of the G-open habitat type is found to be significantly correlated to the proportion of misty days (G-open: $r = 0.805$, $n = 12$, $p <$



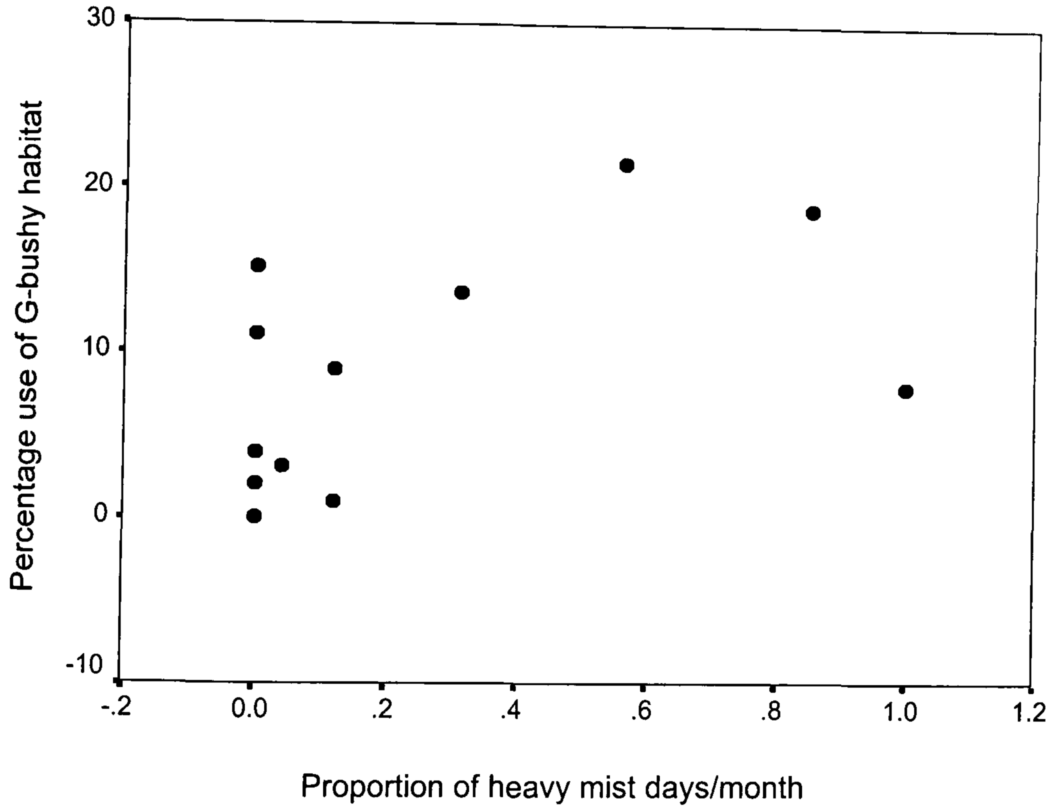


Figure 4.9 a,b) *The percentage use of G-open (a) and G-bushy (b) habitats per month plotted against the monthly proportion of heavy mist days. Based on a minimum of five days per month.*

0.01; G-bushy: $r = 0.336$, $n = 12$, $p = 0.285$). This result is emphasised by a partial correlation test showing that use of G-open quadrats correlated with levels of mist cover even when controlling for use of the neighbouring G-bushy quadrats ($r_{\text{partial}} = 0.783$, $n = 12$, $p < 0.05$). These results suggest that it is preference for the G-open quadrats in particular that is driving the overall preference for gorge areas. Although the relationship between the use of G-bushy quadrats and monthly proportion of misty days is also in the expected positive direction (G-bushy: $r = 0.518$, $n = 12$, $p = 0.084$), indicating that it is contributing to the gelada's overall use of gorge areas in misty conditions, as shown in Figure 4.8.

It would appear that the gorge habitats are being favoured more in the wet season than dry season, presumably due to the gorge representing the most sheltered area of the gelada's home range in conditions of severe weather, especially in the wet season. A further piece of evidence to suggest that the gorge constitutes a more benign microclimate comes from monthly maximum temperatures that were collected on a thermometer permanently located in the gorge (until it went missing in May 1998). Maximum monthly day time temperatures are shown in Table 4.7. Maximum monthly day time temperatures were on average 2°C warmer (sd = 0.25, n = 4) in the gorge than the plateau for the first four months of the year.

Table 4.7 *Maximum temperature during the first four months of 1998, recorded by thermometers located in the Plateau and Gorge habitats.*

Thermometer location	Month				Mean
	January	February	March	April	
Plateau	20	21	25	25	22.75
Gorge	21	23	27	28	24.75

4.5 Discussion

The gelada inhabit a variable environment quite unlike that of any other primate species (Crook, 1966), yet previous research has largely described the gelada's habitat in terms of topography, while the main foraging areas are portrayed as treeless and dominated by short grasses (Crook & Aldrich-Blake, 1968; Kawai, 1979; Dunbar, 1984). In the current study a more detailed investigation revealed a complex mosaic of seven distinct habitat types at the Sankaber field site, all of which are utilised by gelada, and include striking variation not only in topographical aspect, vegetation structure, and food availability, but in microclimatic conditions. The aim of this chapter was to examine some of the basic patterns in which one band of gelada, located at the Sankaber fieldsite, utilise their home range both temporally and spatially, and elucidate some of the environmental parameters underpinning these ranging patterns.

Gelada are specialist graminivores whose diet focuses heavily on fresh green grass blades and whose habitat experiences large seasonal variation in rainfall. Since the growth of monocotyledon grasses correlates strongly with levels of rainfall, the availability of appropriate green forage for gelada varies extensively between months and seasons. In section 4.2, large variation was also found in levels of green forage between different habitat types within each month, suggesting that it might be problematic to examine the effect of rainfall on food availability across entire home ranges. Significant variation in food availability was also found between quadrats within habitat types, highlighting the importance of considering food availability on as small a scale as possible, and indicating that gelada food resources might not be as evenly distributed as previously assumed. The distribution of food available to gelada was also analysed by employing the clipping method, making it possible to gain accurate measures of the dry weight of above- and below-ground food per unit area within each habitat type at the peak of both wet and dry seasons.

It was shown in section 4.3 that significant variation exists in the length of the time gelada occupied quadrats firstly between months, but primarily between different habitat types. Furthermore, habitat selectivity was strongly correlated to overall patterns of food availability between habitats, thus supporting the first prediction presented in the introduction. For instance, the gelada spend a disproportionate amount of time in the P-open and P-bushy habitat types on the plateau where the highest overall level of food resources are to be found. However, a key finding in section 4.3 demonstrates that the relative preference for different habitats was found to vary significantly in strength between months. Most notably, the gorge habitats are significantly more important in the wet season ranging patterns, while the seasonal harvest of cultivated barley fields seems to represent an important, albeit brief, influence on ranging patterns in the dry season. The presumably sparser food resources in the dry season were predicted to place stronger limits on the gelada's ranging behaviour than in the wet season. Although the evidence to support prediction 2 was equivocal, these results highlight the importance of the temporal scale on which the relationship between food availability and ranging behaviour is examined.

During the dry season, short grasses exposed to direct sunlight become highly desiccated and levels of green forage in the most commonly occupied habitat type, P-open, approached zero and were well below those of other habitats types (Table 4.1). Accordingly, shifts in habitat selection allowed the gelada more access to those areas supporting the highest percentages of green forage in the dry season, most notably the E-heather habitat type. Despite the dry-season paucity of green grass, the P-open habitat also supported the highest amounts of subterranean food (roots, bulbs, tubers, corms), the levels of which did not vary significantly between seasons. Underground food items were also found to be the most highly clumped food resource especially during the dry season when they were exploited the most. The importance of underground food sources to gelada in the dry season is also reflected in the results obtained in section 4.3.3. While habitat occupancy was found to correlate with all measure of food availability in the wet season, only the levels of *below*-ground food availability were significantly correlated to occupancy in the dry season, thus providing strong evidence for prediction 3. i.e. that habitat selectivity is driven by above-ground food availability when green grass is available but by below-ground food availability during the driest months. In other words, despite being a very strong predictor in the wet season, patterns of above-ground food availability cease entirely to be a predictor of habitat use in the dry season.

Although striking desiccation of the gelada's foraging vegetation was observed in the dry season months, sources of drinking water were prevalent throughout the gelada's home range, especially in the wet season, and their distribution was not expected to influence gelada ranging patterns. It was perhaps surprising that the use of quadrats was *positively* correlated to their distance from the nearest water source during the wet season only (section 4.4.1). This finding is contrary to almost every previous primate field study which has examined the influence of water distribution on ranging patterns (e.g. Altmann & Altmann, 1970; Post, 1978; Hamilton, 1986; Brain, 1990; Barton *et al.*, 1992; Gaynor, 1994). However, an important feature of the results in section 4.4.3 was the extreme weather conditions experienced by the gelada in the wet season, notably a combination of very high rainfall, high humidity and low mean temperature. Dunbar (1980) found some evidence that adverse wet season conditions led to higher adult mortality and that infant mortality correlated to number of wet season months the neonate had to experience in it's natal coat. Furthermore, since the gelada mainly forage in a sitting posture, the counter-intuitive result found in section 4.4.1 might be explained by the fact that gelada are actually avoiding the wettest quadrats in low lying areas.

Section 4.4.2 also revealed a surprising positive correlation between the use of quadrats and their distance from sleeping sites. However, when examined on a habitat by habitat basis, it did not appear that the gelada were avoiding a zone of 'biodeterioration' proximal to their sleeping sites, as suggested by Hamilton and Watt (1970). Instead, the gelada were merely passing through the escarpment areas where sleeping sites were located and once in the preferred foraging areas (P-open and P-bushy) were in fact favouring quadrats closer to the sleeping sites.

Climatic variables such as mean maximum and minimum temperatures, rainfall, humidity and fog levels were also found to vary dramatically between months and seasons. The gorge habitats were found to experience a more benign microclimate than the plateau or escarpment, especially during the wet season (section 4.2.4). This difference in microclimate fits with the gelada's greater relative preference for the gorge both for foraging and sleeping sites during the wet season. In contrast, Kawai and Iwamoto (1979) describe gelada at Gich, where no gorge habitat exists, taking refuge from hail and heavy rain under Lobelia plants or rock overhangs, and spending over 50% of daylight hours during the wet season on the escarpment. The occupancy of gorge quadrats was significantly correlated to the number of heavy mist days in each month, and the relationship was strongest for G-open (as opposed to G-bushy) quadrats, suggesting that ranging in the wet season might be more influenced by low visibility levels associated with thick mist than protection from rainfall. However, at this stage it is impossible to disentangle the microclimatic advantages of using the gorge habitats during wet season months from the possible influence of seasonal food availability driving the gelada into these areas. In order to ascertain the degree to which each of these parameters are operating on the ranging behaviour of gelada would require monthly habitat-specific food availability records and multivariate analyses. Nonetheless, the fact that within the gorge the gelada are favouring the G-open over G-bushy habitats during heavy mist periods, when a number of other habitat types would be more profitable for foraging, is in line with the hypothesis that gelada are ranging into the G-open quadrats in order to avoid adverse weather and increase their surrounding visibility.

CHAPTER FIVE

Food Availability and Feeding Behaviour

5.1 Introduction

Maintaining adequate energy and nutrient intake is not only paramount to the survival of an animal, but directly affects an individual's physical and behavioural capabilities, and therefore lifetime reproductive output (Schoener, 1971, 1987; Altmann, 1991). As examples from primate field studies, birth rates in Japanese macaques (*Macaca fuscata*) are significantly positively correlated to nutritional intake (Ross, 1992), and Altmann (1998) has demonstrated convincingly that the diet of young baboons strongly predicts their survival and later reproductive success. Animals are thus expected to maximise their nutritional intake wherever possible, although factors such as predation risk and constraints on time and energy budgets will be expected to impinge on a species foraging goals.

Results from the previous chapter confirmed the strong influence of food availability on the ranging behaviour of gelada at Sankaber. However, there were indications that the spatial and temporal scale of the investigation was important in describing the relationship. For example, while overall habitat selectivity correlated strongly with overall food availability, only levels of below-ground food predicted ranging patterns in the dry season. Also, current understanding suggests that patterns of home range use are affected by the species diet, feeding behaviour, nutritional quality of food and distribution of food (Dunbar, 1988). While patterns of food availability were a key feature of the previous chapter, the next step is to examine the specific modes in which the gelada at Sankaber obtain these food resources. The focus of the current chapter is to therefore ascertain how patterns of food availability lead to actual nutritional intake for the gelada.

As discussed in Chapter 1, gelada are the world's only graminivorous primate and show a higher level of *dietetic* specialisation than all other terrestrial primate species. It is perhaps this perception of such a simplistic diet that has led to little research on the details of the gelada's feeding ecology, with most studies simply citing the predominance of grasses in the gelada's diet (Crook, 1966; Dunbar, 1977; Wrangham, 1976; but see Iwamoto, 1979). Monocotyledon grasses are undoubtedly the key feature of the gelada's diet and this is reflected in the predominance of short grassland throughout the gelada's environmental niche. In concordance, Whiten *et al.* (1992) have shown that primate food selection is generally related to broad patterns of food availability, although they also conclude that on a finer scale dietary selection might be based on the need to balance intake levels of protein, lipid, fibre, phenolics, alkaloids and micronutrients. It is perhaps not surprising therefore, that the annual feeding regime of gelada includes a range of dietary categories similar in breadth to other *Papio* baboons, incorporating stems, roots, herbs, leaves, fruits, flowers, seeds, invertebrates and underground storage organs, although little research has been done on the relative importance of these non-grass food sources to gelada.

Iwamoto (1978) has shown that the percentage of time gelada spend eating various food items is strongly correlated to the ingested dry-weight of those food items. However, his study was conducted at Gich where he recognised that subterranean items make a far smaller contribution to the overall diet than at Sankaber (Iwamoto & Dunbar, 1983), and Whiten *et al.* (1990) have shown that harvesting time becomes crucially important when considering subterranean food items. Furthermore, very little is known about the relationship between dry weight intake and the actual rate of calorific intake experienced by the gelada.

It has been noted that the gelada's reliance on grasses poses a number of important constraints on their behavioural ecology. It is generally assumed that a diet based on grass requires a bulk feeding strategy, which in turn will impinge on the animal's time budget as extra time is required for feeding. This may also be confounded by seasonal fluctuations in the food yield of the gelada's habitat and it has usually been presumed that the long dry season imposes conditions of nutritional stress (Crook, 1966; Crook and Aldrich-Blake, 1968, Dunbar, 1977; Wrangham, 1976; Iwamoto, 1979). Janis (1976) suggested that when herbivores were faced with lowered food quality, such as in a dry season, they should increase their bulk food intake. Gelada at Sankaber are indeed faced with a 'dry' season, as described in Chapter 2, and therefore the primary aim of the current chapter will be based around the following hypotheses:

1) Due to seasonally lower rainfall, and the subsequent desiccation of the gelada forage, the dry season represents a period of lower levels of food availability and thus a 'nutritional bottleneck'.

If food resources are found to be constrained seasonally, this will lead logically to an investigation into how the gelada respond to such conditions. If the dry season presents gelada with lower quality or quantity of food, it is predicted that:

2) The gelada will respond to the seasonal shortfall by varying their habitat selectivity or increasing either the time invested in feeding and/or the volume of their food intake during the dry season.

Gelada display a number of behavioural adaptations enabling them to utilise such a specialised diet and also a presumably sparser dry season diet. For instance, previous studies have noted the shift to underground foods in the dry season. The prevalent distribution of underground food items was shown in the previous chapter, so if this dietary shift from above-ground to below-ground food sources does in fact drive the nutritional shortfall then it is predicted that:

3) Subterranean food items will be either lower in nutritional quality, or take significantly longer to process. Further, if the dry season handicap is merely an artefact of the longer processing time associated with subterranean foods then the daily rate of actual nutrient intake is expected to be slower during the dry season, regardless of time invested in feeding.

In order to gauge the temporal investment gelada make to feeding, a preliminary analysis of seasonal variation in gelada time budgets will be presented (section 5.2). This will precede a more specialised investigation into how the gelada spend their feeding time in both wet and dry seasons and what this effort translates to in terms of dry-weight intake of food (section 5.3). Once patterns of physical food intake rates have been established, nutritional analyses will be incorporated (section 5.4) to hone in on the true nature of the gelada's seasonal feeding regime.

5.2 Seasonal variation in activity budgets

As the primary purpose of this chapter is to examine patterns in feeding behaviour and dietary intake, the following analyses of gelada time budgets *per se* will not be extensive. Instead, I merely aim to paint a broad picture of overall activity patterns to provide a context in which the importance of variation in feeding time can be assessed in the subsequent sections. To examine possible seasonal variation, the activity budgets of gelada in the current study were partitioned into dry season records (collected in January, February and March) and wet season records (collected in June, September and October). Activity budget data were collected as described in Chapter 3 (section 3.2). The mean percentage times spent in feeding, social, moving and resting by adult gelada in the wet and dry season are presented in Figures 5.1 and 5.2 respectively. It is interesting that males and females spend almost exactly the same proportion of their time feeding, especially in the wet season, given that males are almost twice the size of females (26 kg ♂, 14 kg ♀; Ohsawa, 1979) and would therefore be expected to have greater energy requirements. During the dry season however (Figure 5.2), the distribution of activities by both sexes differs markedly from those observed in the wet season.

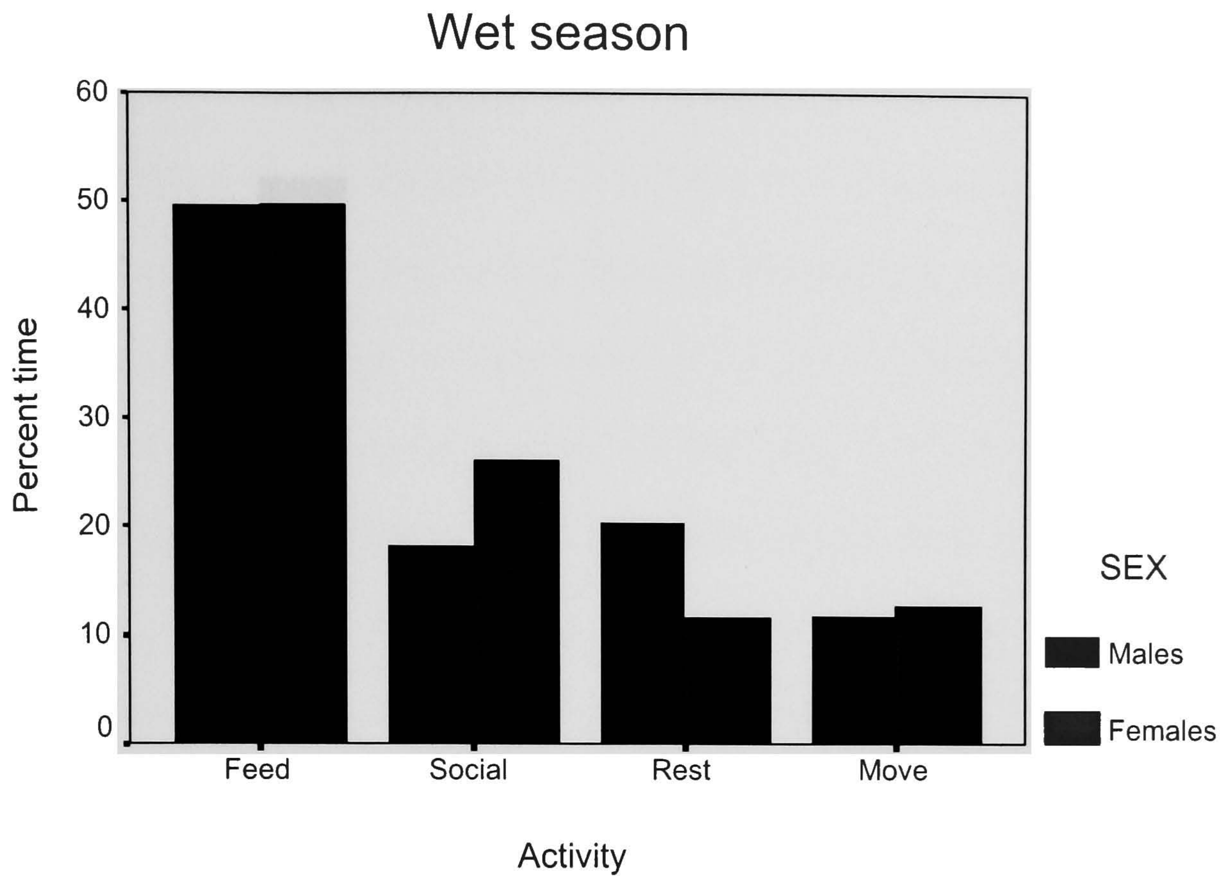


Figure 5.1 *Percentage of total time budget spent by adult males and females in each of the four main categories of activity during the wet season.*

The most striking feature of Figures 5.1 and 5.2 is the relatively large amount of time (over 50%) that both male and female gelada dedicate to feeding over other activities. This is presumed to be a direct consequence of the bulk feeding adaptation arising from a highly specialised graminivorous diet. Combined with the proportion of time spent moving, which is predominantly a function of getting from one feeding site to the next, the gelada devote more time to meeting their nutrient requirements than almost all other frugivorous baboons. For example, across 21 separate field studies, *Papio* baboons were found to spend a mean of 37.5% (sd = 12.1%) of their time feeding (calculated from Table 2, Dunbar, 1992a).

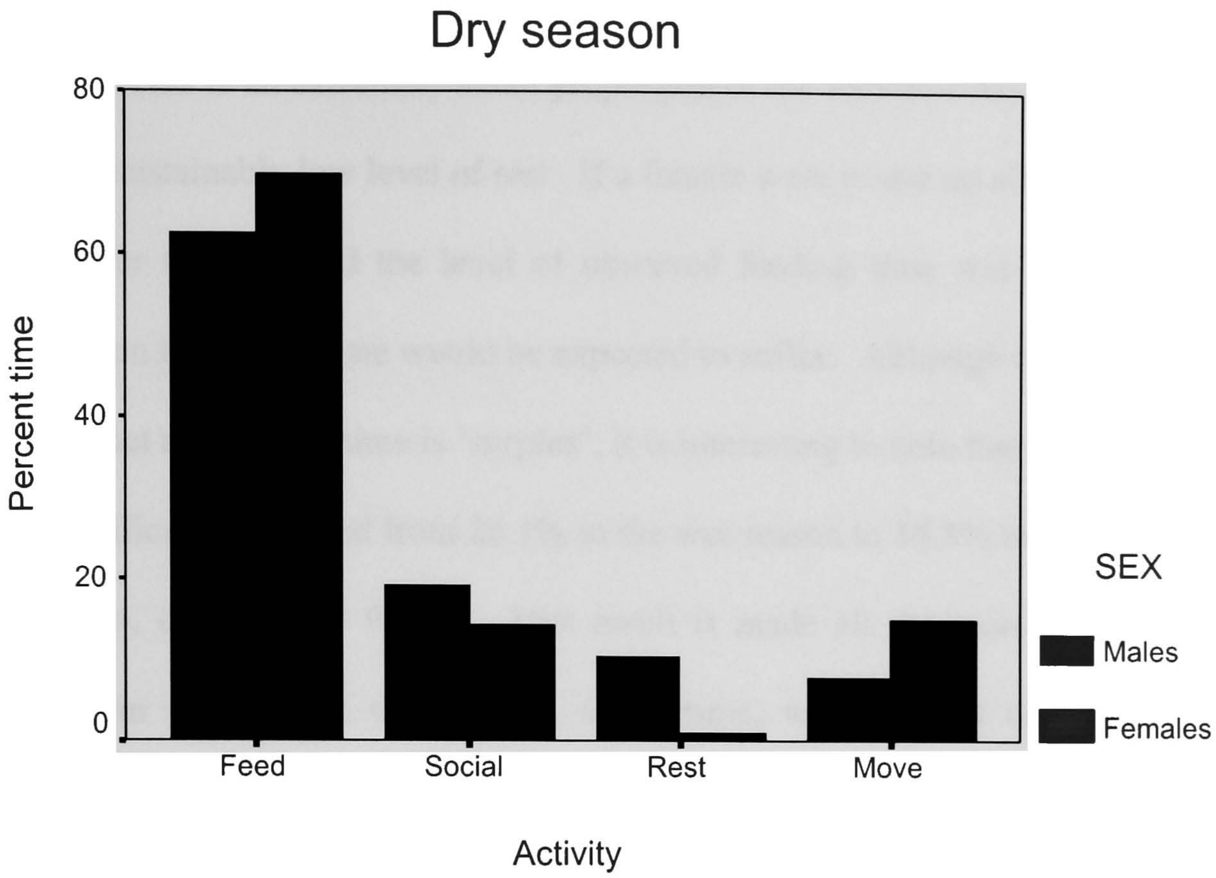


Figure 5.2 *Percentage of total time budget spent by adult males and females in each of the four main categories of activity during the dry season.*

Both males and females spent significantly more time feeding in the dry season (**Mann Whitney U**; males: z = -4.47, p = < 0.001; females: z = -8.97, p < 0.001) although this difference is more pronounced for females who spend 20% more time feeding in the dry season (69.8%) than in the wet season (49.7%). Interestingly, females spend even more time feeding than males in the dry season, which again is surprising considering the females smaller body size.

Much of the extra time that both sexes devote to feeding in the dry season clearly comes from resting. Males rest approximately half as much in the dry season (10.4%) as they do in the wet season (20.3%), which represents a significant difference (**Mann Whitney U**: z = -4.47, p = < 0.001). Moreover, females resting time was reduced dramatically from 11.6% of their time in the wet season to only 1.0% in the dry season, a difference which is also highly significant (**Mann Whitney U**: $z = -7.97$, $p = < 0.001$). This is an extremely small proportion of the female's day time, and most likely an unsustainably low level of rest. If a female were to use up all surplus resting time in order to feed, and the level of observed feeding time was assumed to be essential, then her social time would be expected to suffer. Although it is problematic to assume that any resting time is 'surplus', it is interesting to note that female's social time is significantly reduced from 26.1% in the wet season to 14.3% in the dry season ($\chi^2 = 37.564$, df = 1, $p < 0.001$). This result is made all the more striking when considered in conjunction with male's social time, which is not only maintained between seasons but is slightly higher in the dry season (19.3%) than in the wet season (18.2%). Although the details of social requirements are not within the focus of the current study, this result is an important piece of information given the disparate characteristics of male and female social roles within the broader gelada social system and the seasonal variation in group dynamics which will be discussed in Chapter 6.

Time spent 'moving' varies less than the other main activities between seasons, although it is worth noting that males and females showed seasonal variation in opposite directions. Females showed a slight increase in time spent moving, from 12.6% in the dry season to 15.0% in the wet season, although the difference is not significant (**Mann Whitney U**: $z = -1.48$, $p = 0.138$). Males however, were observed to move less in the dry season (7.8%) than in the wet season (11.8%), a difference that is significant (**Mann Whitney U**: $z = -2.22$, $p < 0.05$). This is possibly due to the shift in diet to more subterranean food items, which often require a great deal of strength to extract. Males, being almost twice the size of females, might be in a better position to exploit more or larger underground items within a certain patch, while females might be forced to search, and therefore move, more regularly to find obtainable items.

5.3 Feeding Behaviour

As discussed in Chapter 1, gelada posses a number of behavioural and morphological adaptations which enable them to exploit their specialised ecological niche. Previous studies have often cited 'bulk feeding' as an important strategy adopted by gelada to gain the required levels of nutrition from a relatively poor diet (Dunbar & Bose, 1991; Iwamoto, 1993). Few studies, however, acknowledge that an increase in time spent feeding *per se* does not automatically lead to an increase in the dry-weight intake and thus does not automatically constitute 'bulk' feeding in terms of volume (see Whiten *et al.*, 1990). Little can be concluded from the temporal investment an animal makes in feeding behaviour without a more detailed investigation into the nature and payoffs of that investment. Therefore, in this section, the time spent by gelada feeding will be further analysed to examine variation in dietetic diversity and the rates at which gelada ingest the food available to them.

5.3.1 Seasonal variation in diet

Grass leaves comprise the largest single food component of the gelada's diet and Iwamoto (1979) suggests that gelada appear to eat almost all the gramineae species available to them. However, the gelada diet does include a range of food items similar to those eaten by *Papio* baboons. Apart from grass blades, the stems, flowers, leaves and seeds of grasses and herbs are eaten, while fruit from bushes and insects are also eaten above ground, and roots, tubers and corms provide a significant contribution to the diet from underground. A number of previous studies have mentioned large shifts in gelada diet as the preferred green grass blades desiccate in the dry season (Crook, 1966; Dunbar, 1977; Iwamoto, 1979), although little data are available on the details of seasonal variation in diet. The separate feeding profiles for males and females in both wet and dry seasons are displayed in Table 5.1.

Table 5.1 *Percentage of time spent eating different food items by male and female gelada in both wet and dry seasons. * denotes underground items.*

Food item	Dry season			Wet season		
	males (%)	females (%)	all adults (%)	males (%)	females (%)	all adults (%)
grass blades	21.9	26.8	24.8	87.6	84.1	85.6
herbs	9.1	9.0	9.0	1.2	3.1	2.1
herb roots*	46.5	36.3	40.4	1.5	0	0.7
grass roots*	13.2	15.5	14.6	0.1	0.8	0.5
bulbs/corms*	0.9	2.1	1.6	6.1	9.0	7.1
fruit	4.1	6.5	5.5	0.6	1.6	1.2
seeds	3.9	3.2	3.5	0.1	0	0
flowers	0.2	0	0.1	1.0	1.5	1.2
invertebrates	0	0	0	0.2	0	0.1
other	0.2	0.6	0.4	2.2	1.3	1.8
N (records)	1234	1680	2914	1355	2022	3378

Table 5.1 shows the marked shift in dietary profile made by the gelada between wet and dry seasons. Although green grass blades are clearly preferred when available in the wet season, accounting for 85.6% of feeding records, it is worth noting that

roughly 14% of the wet season diet is made up of other food items including almost 9% subterranean items.

The shift to more subterranean food in the dry season is striking, with over 56% of gelada's feeding time accounted for by underground food items. Males spend slightly more time (60.6%) than females (53.9%) extracting and eating underground food items in the dry season. Byrne *et al.* (1993) found that male mountain baboons (*Papio ursinus*) also relied more heavily on underground storage organs than females. The higher quota of underground food items in the diet of gelada males is mostly due to the high proportion of time (46.5%) males spend in the process of eating herb roots, primarily *Thymus spp.* Thyme roots, which usually range in length between 10-20 cm, are typically the largest individual food item eaten by gelada, either above or below ground, and require the most strength to extract. It is perhaps not surprising that males with their larger body size are more likely to exploit this food source than females. Some evidence in support of this is the fact that males are able to extract and ingest herb roots at a faster rate (mean = 7.8/minute, sd = 5.8, n = 53) than females (mean = 5.9/minute, sd = 2.1, n = 27), although the difference is not significant (**t** = 1.446, df = 78, p = 0.156). Females spent a relatively higher proportion of their time on underground food sources eating smaller grass roots and bulbs.

Green grass blades account for approximately 25% of feeding time even in the dry season. This is a very high proportion of the dry season feeding records given the apparent paucity of green grass cover during the dry season months. Figure 4.1 revealed that open areas of the plateau and gorge fell to almost zero percent green cover in the dry season, while above-ground dry season food availability in the corresponding habitat types averaged only 5 mg/m^2 (P-open and G-open quadrats combined, n = 11; Table 4.1). The gelada overcome this deficiency, to some extent, by varying their habitat use seasonally. The G-open habitat offered the lowest food availability, both above and below ground, of all habitat types in the dry season (Table 4.1), and accordingly was only occupied a mean 4.3% of dry season ranging time, compared with 16.4% of wet season ranging time (Figure 4.5). Conversely, the long *Festuca* grasses in the E-heather habitat are protected from desiccation by the canopy cover of heather trees and the dense clumps of *Festuca* itself, thereby retaining a certain amount of green blades year round. This is reflected in the results presented in Figure 4.1, where the E-heather quadrats maintained a mean percentage green cover of 32.9% through the dry season months. This was significantly higher than the P-open and G-open quadrats combined (**t** = -2.193, df = 16, $p < 0.05$), which supported a mean green percentage cover of only 11.8% across dry season months. Therefore, in order to maintain the intake of roughly 25% green grass blades in the dry season, the gelada vary their ranging pattern accordingly. E-heather is the only habitat type occupied significantly more in the dry season than the wet season (**Mann Whitney U**: z = -2.201, n = 2, $p < 0.05$). The relatively high proportion of green grass blades in the gelada's dry season diet, especially given their evident sparseness during these months, is also facilitated by the unique proficiency with which gelada are able to collect individual blades from among less desirable forage.

5.3.2 Rate of graminivorous intake

While focal point sampling methods were adequate to establish activity budgets and feeding profiles, data on feeding rates were mainly recorded from digital video footage. This method enabled the number of plucks per mouthful to be recorded simultaneously with rate of mouthfuls and rate of grass blade ingestion, and was almost essential given that gelada collected short grass at rates up to 126 individual plucks per minute. The amount of grass ingested per mouthful varied greatly and usually depended on the length of the sward. The mean number of grass blades per mouthful was 16.6 (sd = 9.1) for males and 15.5 (sd = 7.7) for females. Although mouthfuls sometimes consisted of no more than one grass blade, on other occasions up to 60 individual blades might be plucked and stored in one hand before being moved to the mouth.

Since the percentage of green cover varies so markedly between seasons the rate at which gelada are able to collect grass blades might be compromised in areas or times of lower green grass density. When measures of short grass intake were examined across time no significant variation was found in the mean number of grass blades per mouthful between months (**ANOVA**: $F_{(2,156)} = 0.226$, $p = 0.802$). However, there was significant variation in the mean number of grass blades ingested per minute in different months (**ANOVA**: $F_{(4,192)} = 9.491$, $p < 0.05$). The monthly mean rates of grass blade ingestion are presented in Figure 5.3.

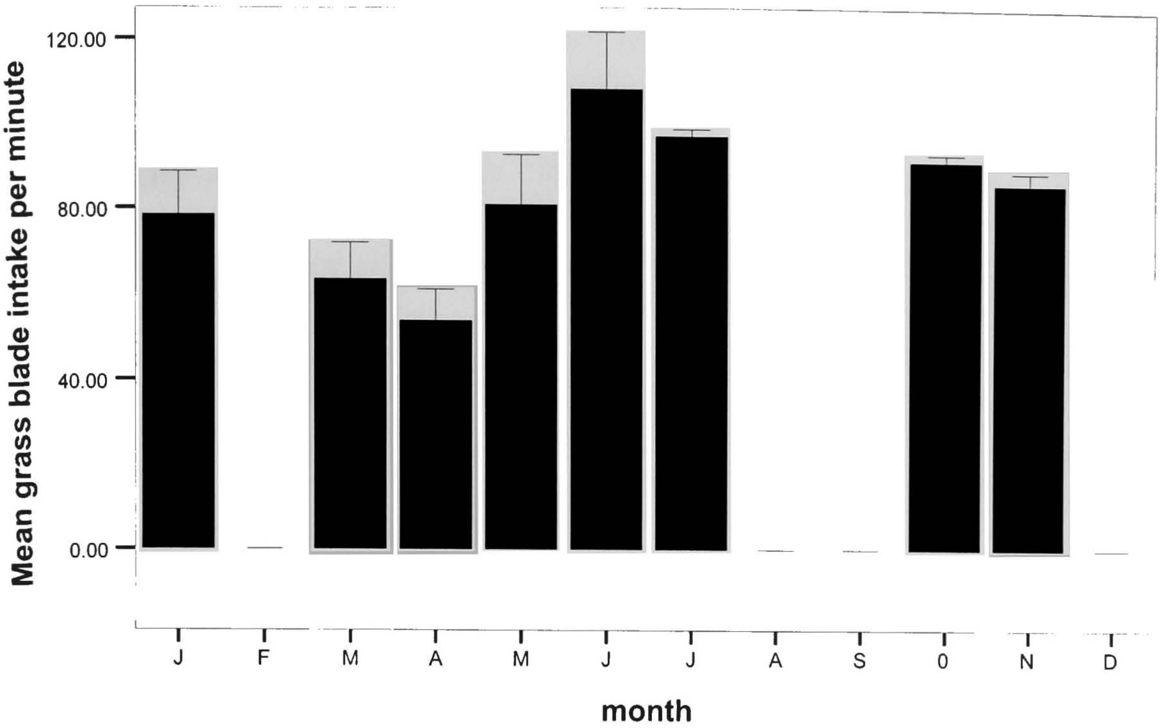


Figure 5.3 *Monthly mean (and standard error) number of grass blades ingested per minute when gelada were feeding on short green grasses. No data are available for February, August, September and December. (N = 278 minutes, minimum 20 minutes per month)*

Post hoc analyses of the results presented in Figure 5.3 revealed that the crucial variation existed between the intake rate in June (mean = 108.1 blades/minute, sd = 23.5) and the intake rates in both March (mean = 61.3 blades/minute, sd = 15.2) and April (mean = 55.8 blades/minute, sd = 12.4). This can be attributed to the disparate levels of availability, and hence density, of green grass between these months. On the one hand, March and April exhibit some of the lowest levels of green cover throughout the year (Figure 4.1), which means the gelada much cover more ground, and therefore take more time, to obtain a similar amount of grass blades. This detail is reflected in the lower representation of green grass in the diet in the dry season months. On the other hand, a dense flush of fresh grass growth in June follows the start of the rains in May and the gelada dramatically shift their feeding attention to these new shoots which they are able to collect at a substantially faster rate. In Chapter 4, Figure 4.5 revealed that the gelada's occupancy of the P-open habitat, which supports the majority of the short open grassland, increases dramatically in a period of only one month, from below 40% in April to over 65% in May. Interestingly, the number of grass blades per mouthful did not vary significantly in line with the rate of intake, indicating that the gelada employ a similar grass collecting method year round but, due to the denser grass biomass in the wet season, are able to collect blades at almost twice the speed.

5.4 Food intake and nutrition

Section 5.3 focused on the proportion of feeding time gelada devoted to different food items in both wet and dry season. This provides the foundation for assessing the importance of different food sources in different seasons and how the gelada might vary their feeding regimes in relation to the availability of such food sources. However, food items will vary in their nutritional value and the rate at which an animal can process and ingest them (Post, 1982; Norton *et al.*, 1987), and the current section will therefore investigate these considerations as experienced by the gelada.

Hladik (1977) reported that for the largely folivorous Purple faced leaf monkey (*Presbytis senex*) there was practically no difference between the percentage of time spent eating particular food items and their corresponding percentage contribution to the overall diet in terms of dry-weight. Although gelada are largely folivorous, a closer examination of the nature of their food sources is required, particularly given the large dry-season shift to more subterranean food items which require extra time and energy to obtain. In this respect, feeding records were assigned to different food types not only if the gelada were actually eating the item, but if they were in any way engaged in the process of acquiring the food source. This might include behaviour such prolonged digging to extract subterranean items, pushing aside thorny branches of rose bushes or careful manipulation of thistle leaves before a thistle flower could be obtained. In this section a more detailed analysis of the gelada's foraging profile will take into account the processing and intake rates of the different food components of their diet. Once intake rates of different categories of food items are established, the rate of dry-weight intake will be combined with nutritional analyses to obtain a more precise overview of the gelada's feeding ecology.

5.4.1 Rates of dry-weight food intake

Section 5.3.2 highlighted the efficient method in which the gelada collect many blades of grass per mouthful, enabling ingestion at a mean rate of approximately 1.4 blades per second. However, the collection of underground food items, which combined form the second largest component of the gelada's diet after grass blades, is likely to impose much greater costs in terms of the energy and time required to extract each item. Although it is important to note that the effect may be ameliorated to some extent if food items that are costly to handle are concurrently of higher nutritional value (see for example, Oftadel, 1992; Byrne *et al.*, 1993). The mean rates at which gelada collect and ingest dry-weight of key food items were calculated as described in Chapter 3, section 3.4.3. Although it was not possible to record wet weight of samples in the field, water is far from a limited resource in the Sankaber area (see section 4.4.1), and the amount of water gained from food plants is likely to be of little relevance.

Samples of easily demarcated food items such as individual fruits, roots and flowers, were collected from sites as soon as the gelada had finished feeding there, and weighed to give a mean weight per piece of food. Grass blade counts were taken from the data described in section 5.3.2, and mouthfuls of less defined food sources, such as mixed whole herbs, were handled in as similar a fashion as possible to the process used by gelada. The mean daily amount of time spent feeding on different food items is based on the calculation:

$$T_{is} = F_{is} \times F_s \times 660$$

Where T_{is} is the mean total number of minutes spent eating food source i per day in season s, F_{is} is the percent of all feeding records devoted to eating food item i in season s (from Table 5.1), F_s is the mean percent of the total time budget devoted to feeding in season s, (from Figures 5.1 and 5.2), multiplied by 660 minutes observation time per day (07:00 – 18:00). The mean intake rates of the gelada's main food sources are presented in Table 5.2.

The results reveal that the mean weight of different food items varies considerably (column a), from short dry-season grass blades with a mean weight of 14 mg (0.014 g) up to a mean weight of 300 mg (0.3 g) for the fruit of *Rosa abyssinica.* The mean weight of individual food items in the wet dry season (0.140g, sd = 0.110, n = 242) is slightly greater than the mean weight of individual food items in the wet season

(0.128g, sd = 0.138, n = 295), although the difference is not significant (**t** = -0.128, df = 6, p = 0.903). Large variation is also found in the number of food items ingested per minute (column b), with wet-season grass blades ingested at the rapid rate of 94.4 per minute, compared with herb roots which the gelada process and ingest at the rate of only 5.7 per minute.

Table 5.2 *Mean rate of intake for key gelada food sources, in terms of dry-weight. Rate of food item intake is based on a minimum (n ≥ 20) focal feeding observations for each food type. See text for details.*

Food item (n = number items weighed)	**Food intake** (a) mean weight of food item (g)	(b) rate of food item intake (no./minute)	(c) rate of dry-weight intake (g/min) (a x b)	(d) No. feeding minutes per day	(e) intake weight per day (g) (c x d)
Wet season					
grass blades (n = 200)	0.021	94.4	1.98	280.2	555.5
bulbs/corms (n = 50)	0.005	52.7	0.26	23.2	6.1
herbs (n = 25)	0.201	15.4	3.01	6.9	20.7
flowers (n = 20)	0.286	8.7	2.49	3.9	9.78
Total					592.1 g/day
Dry season					
grass blades (n = 100)	0.014	70.4	0.99	109.5	108.4
herb roots (n = 50)	0.277	6.7	1.86	178.4	332.1
grass roots (n = 50)	0.104	16.5	1.72	64.5	110.9
herbs (n = 20)	0.163	10.4	1.69	39.7	67.3
fruit (n = 22)	0.300	13.1	3.93	24.2	95.4
Total					714.1 g/day

The mean daily total intake rates calculated in Table 5.2, do not however, represent all feeding records. The four wet season food sources listed represent 96.0% of the total wet season diet, while the five dry season food sources represent 94.3% of the total dry season diet (see Table 5.1).

Therefore, if the mean dry-weight intake rate across the main food items listed in Table 5.2 is assumed for those food sources not listed (items for which inadequate samples were available for dry-weight measure), a corrected mean daily estimate can be calculated as:

$$W_{cs} = \frac{W_s}{P_{fs}}$$

Where W_{cs} is the corrected estimate of mean dry-weight of food ingested per day in season *s*, W_s is the dry-weight of food intake (estimated in Table 5.2), and P_{fs} is the percent of *total* feeding records devoted to the food sources for which measurements were available (i.e. those listed in Table 5.1) in season *s* (P_{fs} is thus 0.96 and 0.943 for the wet and dry seasons respectively). The above calculation produced a 'corrected' dry-weight intake of 616.8 g/day for the wet season and 757.3 g/day for the dry season.

Clearly adult gelada are not only spending more time feeding in the dry season than wet, as was shown in section 5.2, but this also results in a higher dry-weight of food intake in the dry season. Although the ratio of wet-season/dry-season food intake (616.8 / 757.3 (g/day) = 0.817) is similar to the ratio of wet-season/dry-season activity budget spent feeding (49.6% / 66.9% = 0.741), the former ratio is slightly higher than the latter. This difference suggests that although the gelada are spending longer feeding in the dry season the comparatively poorer or more dispersed forage means they are unable to increase their gross intake to the same extent.

5.4.2 Calorific intake

In the preceding sections of this chapter, both the volume of food intake and time invested in feeding by gelada were observed to increase in the dry season in support of the second prediction in the introduction. However, the makeup of the gelada's diet was also found to vary between seasons and variation in digestibility and nutritional content between different food sources needs to be taken into account before assuming that a seasonal increase in intake represents a genuine gain to the gelada. Table 5.3 displays the mean calorific content of different gelada food types as found by Iwamoto (1979, page 305, Table 12.14) and the corresponding individual intake of calories based on the dry-weight of each food type ingested (Table 5.2, above). Iwamoto (1979) found no significant variation between the calorific content of the same part of different plant species (e.g. blades of all grasses), therefore concluding that nutritional analysis could be based on the mean calorific content of food-type categories.

Obviously the calorific intake of various food items displayed in column (e), Table 5.3, has only been calculated where calorific values are available. However, the listed wet season food sources for which calorific content is available (grass blades, bulbs/corms, herbs and flowers) constitute 96.0% of wet season feeding records.

Table 5.3 *Rates of individual calorific intake per food item and unit time based on dry-weight intake rates presented in Table 5.2 and food-specific calorific values reported by Iwamoto (1979).*

	Intake rates				
Food item	(a) calorific content (kcal/g), from Iwamoto, 1979	(b) weight of intake (g/min), from Table 5.8	(c) rate of calorific intake (kcal/min) (a x b)	(d) intake weight (g/day), from Table 5.8	(e) calorific intake per (kcal/day) (a x d)
Wet season					
grass blades	4.059	1.98	8.04	555.5	2254.8
bulbs/corms	4.311	0.26	1.12	6.1	26.3
herbs	4.192	3.01	12.62	20.7	86.8
flowers	3.939	2.49	9.81	9.78	38.6
Total				592.1 g/day	2406.5 kcal/day
corrected estimates, extrapolated from 0.96 of all wet season feeding records (see text for details).				616.8 g/day	2406.5 kcal/day
Dry season					
grass blades	3.805	0.99	3.77	108.4	412.5
herb roots	4.009	1.86	7.46	332.1	1331.4
grass roots	4.068	1.72	7.00	110.9	451.1
herbs	4.192	1.69	7.08	67.3	282.1
fruit	-	3.93	-	95.4	-
Total				714.1 g/day	2477.1 kcal/day
corrected estimates, extrapolated from 0.888 of all dry season feeding records (see text for details).				757.3 g/day	2789.5 kcal/day

Likewise, the dry season food sources for which calorific values are available (grass blades, grass roots, herbs and herb roots, but not fruit) represent 88.8% of dry season feeding records. If the daily wet season calorific intake value (2406.5 g/day) is adjusted as was the daily dry-weight intake records (i.e. dividing by 0.96, see section

5.5.1), we arrive at a corrected estimate of 2506.8 kcal/day in the wet season. The corresponding dry season adjustment (dividing by 0.888) gives a daily calorific intake estimate of 2789.5 kcal/day. Thus it appears that the increased time spent feeding and increased volume of food ingested in the dry season, does lead to correspondingly higher nutrient intakes.

Another important piece of information presented in Table 5.3 is that the mean calorific value of the dry season foods does not differ significantly from that of wet season foods (**t** = 0.935, df = 6, p = 0.386). Although nutritional analyses are only available for four food-source categories in each season, these food sources, as mentioned above, constitute 96.0% and 88.8% of all feeding records in the wet and dry seasons respectively. It is therefore unlikely that the nutritional value of food items not listed would effect a significant seasonal difference in the calorific content of food items. In fact, fruits (5.5%) and seeds (3.5%) make up the bulk of the remaining 11.2% dry season feeding records and these items are typically among the more nutritious food sources for herbivorous primates (Barton, 1989; Whiten *et al.*, 1990). For instance, fruits are usually high in simple sugars (Byrne *et al.*, 1993) and seeds typically provide a very high protein to fibre ratio (Altmann *et al.*, 1987; Barton *et al.*, 1993). It therefore appears highly unlikely that the 'quality' of food eaten by gelada (at least in terms of calorific content) decreases in the dry season. While this result casts doubt on the oft held assumption that the dry season represents a period of nutritional stress to the gelada (see Crook, 1966; Crook and Aldrich-Blake, 1968, Dunbar, 1977; Iwamoto, 1979), it also raises the question of why gelada spend significantly more of their time budget engaged in feeding activity in the dry season (66.9%) than in the wet season (49.6%).

One possible explanation was suggested in the third prediction of this chapter's introduction, namely that the shift to more subterranean foods in the dry season incurs extra costs in terms processing time (see Hladik, 1977; Whiten *et al.*, 1992). Although this is true simply in terms of the number of items extracted per unit time, Table 5.2 revealed that individual underground items, especially those eaten in the dry season, are typically much heavier. In fact, when converting to the common currency of dry-weight intake per unit time, above ground food sources are ingested at a slightly faster rate (mean = 1.73 g/min, sd = 0.46, n = 440) than underground food sources (mean = 1.69 g/min, sd = 0.45, n = 266), although the difference is not significant (**t** = 1.188, df = 704, p = 0.235). Furthermore, the mean calorific value of underground items (4.13 kcal/g, sd = 0.16, n = 3) is slightly higher than that of above ground items (4.04 kcal/g, sd = 0.16, n = 5) although this is largely due to the relatively low calorific value of the dry season grasses (3.805 kcal/g) and the difference is not significant (**t** = -0.763, df = 6, p = 0.474). Nonetheless, the first part of prediction three, that subterranean food items would either be lower in nutritional quality or take significantly longer to process, was not upheld by the data presented here.

Accordingly, given that above and below ground food sources do not differ significantly in calorific value nor dry-weight of intake, there is no significant difference in the mean rate at which gelada ingest calories from above and below ground food items (**t** = 1.215, df = 704, p = 0.214). It therefore appears highly unlikely that the prevalence of subterranean food items in the dry season diet underlies the need for significantly greater time to be devoted to feeding in that season. It should also be remembered that gelada feed on both above and below ground food items in both wet and dry seasons.

Although there is no apparent dichotomy between the intake of above and below ground food sources, there remains however, large variation among the mean dry-weight intake rates of different food sources, as demonstrated in Table 5.2. This variation is similarly apparent in the rates of calorific intake obtained from different food sources (column c, Table 5.3). For example, gelada ingest calories from bulbs and corms at a mean rate of only 1.12 kcal/minute, whereas herbs provide the gelada with calories that are ingested at a mean rate of 12.62 kcal/min. Is it possible that the mean intake rate of *all* dry season food sources is substantially lower than that of wet season foods? The mean rate of dry-weight intake in the wet season (1.94 g/min, sd = 1.19, n = 4) is indeed higher than in the dry season (1.57 g/min, sd = 0.39, n = 4) but the difference is far from significant (**t** = 0.589, df = 6, p = 0.577). Likewise, when converting to the common currency of calorific intake per unit time, gelada ingest calories from the wet season food sources at a faster rate (7.90 kcal/min, sd = 4.90, n = 4) than calories from dry season food sources (6.33 kcal/min, sd = 1.72, n = 4), although again the difference is not significant (**t** = 0.605, df = 6, p = 6.567). However, it is important to note that different food type categories do not contribute evenly to the overall mean daily intake of either dry-weight or calories. For instance, the mean daily intake of calories from all wet season food sources needs to account for the fact that 89% percent of those calories come from grass alone (at a mean rate of 8.04 kcal/min) whereas only 1% came from bulbs and corms (at a mean rate of 1.12 kcal/min). The mean seasonal rates of intake must therefore be calculated using the proportional contribution of each food source. Hence, the intake of dry-weight per minute (column b, Table 5.3) and the calorific intake per minute (column c, Table 5.3) for each food source, were 'weighted' by the mean number of minutes per day that the gelada spent feeding on those food items (column d, Table 5.2). This resulted in a mean wet season dry-weight intake rate of 1.88 g/min (sd = 0.49, n = 314 minutes) which was significantly faster than mean dry season dry-weight intake rate of 1.58 g/min (sd = 0.37, n = 392 minutes)(**t** = 9.461, df = 704, p <0.01).

Furthermore, when the calorific intake rate of each food source is weighted by its relative contribution (in terms of minutes) to the seasonal feeding profile, the mean calorific intake rate during the wet season (7.65 kcal/min, sd = 1.97, n = 314 minutes) is significantly higher than the mean calorific intake rate in the dry season (6.32 kcal/min, sd = 1.60, n = 392 minutes)(**t** = 9.946, df =704, p < 0.001).

5.5 Discussion

In Chapter 4, the distribution of gelada food resources was shown to fluctuate significantly between habitat types and between seasons. Given these seasonal shifts in resource distribution, the primary aim of this chapter was to test the common hypothesis that the dry season represents a period of nutritional shortfall to the gelada (Crook, 1966). Monitoring levels of food availability, however, provides only part of the picture. In order to address the main hypothesis, we then needed to examine the investment made by gelada in acquiring these resources and how this translates into actual levels of intake.

As shown in section 5.2 the gelada's dietary specialisation requires a very large proportion of their time to be dedicated to feeding over other activities, and, as predicted, both adult males and females spend significantly more time feeding in the dry season than in the wet season. The difference is especially pronounced among adult females, whose 'resting' and 'social' time are both significantly reduced in the dry season. Shifts in activity budgets represent an adaptation to the fact that gelada rely very heavily on fresh green grass and despite overall levels of green cover dropping to less than 10% in the dry season green grass blades still constituted 25% of dry season feeding records (Table 5.1). As described in section 5.3.2, the gelada's precise and rapid harvesting technique enable them to pluck single green grass blades from amongst large amounts of dead vegetation. This not only affords them a foraging advantage relative to ungulate herbivores who are unable to graze as selectively, but their technique for collecting grass blades allows more rapid grass intake than that of sympatric primates. For example, Hamadryas baboons sometimes joined gelada foraging herds and fed sympatrically on the short open grassland. However, due to the hamadryas' method of moving each plucked grass blade to the mouth individually, they collected grass at a mean rate of only 45.9 blades/min (sd = 19.3, n = 53 minutes). This was significantly slower than the mean rate of 85.8 blades/min (sd = 16.9), at which gelada collected grass blades (**t** test = -5.058, df = 80, $p < 0.05$).

Despite the gelada's proficient foraging techniques, it was also noted in section 5.3.2 that gelada ingested grass blades at a significantly slower rate in the dry season due to the lower density of green forage. As green grass becomes less available gelada diversify their diet and increase their intake of herbs, fruits, seeds and especially underground food items increased. The importance of below-ground foods to gelada is highlighted by the fact that gelada dig for underground food items at all times of year (i.e. even when fresh green grass was plentiful). Moreover, while habitat occupancy was found to correlate with all measures of food availability in the wet season, only the levels of below-ground food availability were significantly correlated to occupancy in the dry season, despite constituting only 56% of all dry season feeding records.

It was predicted in the introduction to this chapter that the increase in feeding time in the dry season is due to this shift to a more subterranean diet of lower quality food and/or the increased processing time this incurs (see Crook, 1966; Dunbar, 1977; Iwamoto, 1979). This prediction was not upheld, as it was shown in section 5.4.2 that underground sources food were not only nutritionally comparable (at least in calorific value) to above-ground food sources, but that the rate at which they ingested dry-weight and calories did not differ significantly between above and below-ground food sources. Similarly, the prediction that if the dry season handicap was merely an artefact of the longer processing time associated with subterranean foods then the daily rate of actual nutrient intake is expected to be slower during the dry season, regardless of time invested in feeding, was not upheld. This is an important finding as it has long been assumed that underground food items require a much longer processing time per unit calorific value than do blades (e.g. Barret *et al.*, 1992), although little is known about the presumed extra physical energy required to extract underground items. Nonetheless, when *all* dry-season food types were pooled, the mean intake rate of dry-weight and calories was found to be significantly less than the mean rate at which wet season foods were ingested. This is almost exclusively an consequence of the low nutritional value of grass in the dry season.

Nevertheless, a slower rate of nutrient intake in the dry season does not automatically translate to a lower overall nutrient intake. In section 5.4 the greater time devoted to feeding activity in the dry season was found to result in a higher mean volume of dry-weight intake, supporting the second prediction in the introduction. However, this shift in temporal feeding investment by gelada in turn corresponded to a slightly higher calorific intake in the dry season. This is a striking result and throws doubt on the key hypothesis (prediction 1) that the dry season represents a 'nutritional bottleneck' for gelada (Crook and Aldrich-Blake, 1968).

Another consideration regarding the seasonal disparity in gelada feeding ecology, is the thermoregulatory burden associated with the near freezing night-time temperatures experienced in the dry season. Iwamoto and Dunbar (1983) suggested that gelada invest more time in feeding as altitude increases, due to the increased metabolic energy requirements resulting from lower ambient temperatures, combined with an altitudinal decrease in resource quality. While mean daily temperatures at Sankaber vary little between months, diurnal temperatures showed far greater variation in dry season months when gelada typically experienced clear nights at or near 0°C.

CHAPTER SIX

Group Dynamics and Spatial Patterns

6.1 Introduction

A number of studies have pointed out the foraging costs associated with group living in primates (van Schaik, 1983; Stacey, 1986; Henzi *et al.*, 1997a). As resource levels decline, increased scramble competition is thought to result in decreased group size. In line with this, Crook (1966) suggested that the smaller gelada herds he observed in the dry season were a result of a decline in forage quality and quantity. However, the results presented in Chapter 5 indicated that neither the quality of gelada food nor the rate of food intake appear to decline in the dry season, and Ohsawa (1979) reported that the largest multi-band gelada herds (up to 620 animals) at Gich occurred most often in January and February, in the middle of the dry season. It appears therefore, that the rules governing variation in gelada group size might not be as straight forward as Crook's (1996) original hypothesis.

Given that gelada herd size varies so greatly, the species offers a unique opportunity for investigating the ecological causes and consequences of fluctuations in group size, and this constitutes a primary objective of the current chapter. For example, the fact that larger groups are more likely to go further 'inland', away from the safety of the escarpment, might be due to either a decrease in individual risk of predation or the need for larger herds to cover more ground for each individual's food needs, or both. Dramatic variation in group size also provides a unique opportunity to test the often cited positive relationship between primate group size and day journey length (e.g. Anderson, 1981b; Altmann & Maruthi, 1988; Henzi *et al.*, 1992), which is commonly thought to be a function of food availability (Davidge, 1978; Dunbar, 1988). Indeed, the distance that a group of animals needs to travel in a day will be influenced by factors such as the size of the group and amount of food encountered on the journey (Altmann, 1979). Terrestrial primates vary greatly in the distance they travel in a day with field studies on savannah baboons reporting day journeys ranging between 2.0 km to 19.2 km (see Devore & Hall, 1965; Stoltz & Sayman, 1970; Altmann & Altmann, 1970; Melnick & Pearl, 1987). Dunbar (1992) listed 21 Papio baboon field studies in which the mean day journey length was 4.94 km (sd = 2.44, min = 1.10 km, max. = 9.00 km; calculated from Table 2). Highlighting the variation in day journey length possible within a species, Kummer (1968) found a population of hamadryas baboons at Erer Gota, Ethiopia, moved an average 13.9 km per day, while Nagel (1973) reported mean day journeys for a similar hamadryas population at nearby Awash of 6.5 km. Henzi *et al* (1992) noted that day journey lengths were longer for a group of mountain baboons during periods of food scarcity and Anderson (1981b) also found that baboons at Suikerbosrand increased their home range and day journey length in the dry season. Barton *et al.* (1992) were able to show that annual rainfall, which is commonly used as an estimate of food availability (see Gaynor, 1994; Barrett *et al.*, 1992), was a significant negative correlate of day journey length for *P.anubis* baboons. Although Gaynor (1994) found no correlation between day journey length and monthly rainfall, day journeys were positively correlated with cumulative rainfall for the previous three months. Given the common lag effect between rainfall and food availability it is not surprising that a number of studies have found no variation in day journey lengths between seasons demarcated purely on the basis of rainfall (e.g. Altmann & Altmann, 1970; Post, 1978; Sharman, 1981).

It was predicted in Chapter 4 that food availability would exert stronger pressure on ranging patterns of gelada during the dry season than wet season. Although the results based on food availability and habitat usage proved equivocal (see section 4.3.3), data presented here on group size and day journey length offer another opportunity to test this hypothesis.

Kawai *et al.* (1983) pointed out that gelada bands do not constitute a consistent social grouping in the same sense as *Papio* 'troops' or *P. Hamadryas* bands. Although many units may form a cohesive assembly for much of the time, bands often join other bands or split into smaller groups. Furthermore, although some associations of units were never observed apart, units may join and leave herds individually, and sometimes travel alone. Ohsawa (1979) found that some units spread their time evenly between different bands and were therefore hard to ascribe to one band in particular. Also, some units were significantly more likely than others to split from their bands when in certain areas of the Gich plateau, leading Ohsawa (1979) to describe 'western edge units' or 'eastern edge units'. Various studies have speculated on the ecological benefits of the gelada social system being able to pare down or amalgamate (Crook, 1966; Wrangham, 1976; Ohsawa, 1979). This phenomenon is typically considered a response to fluctuations in the resource base, although these studies have focused more on group size shifts on a large temporal scale (mainly seasonal), and relatively little on the actual dynamics of the group's fission and fusion. Another aim of the current analyses therefore, is to ascertain which ecological parameters have the greatest influence on the fission-fusion system at a finer temporal scale.

It has been suggested that in a moving group of foraging animals, individuals at the leading edge will have access to less exploited resources than those at the trailing edge (Jarmen, 1974; Norton, 1986). A number of studies describe definite progression orders among individual baboons (Devore and Hall, 1965; Harding, 1977; Rhine & Westlund, 1981; but see, Altmanm, 1979), while Kummer (1968) noted that Hamadryas herd movement and direction was determined by old post-reproductive males. Barton (1993) found that dominant olive baboons (*P. anubis*) were more likely to be found in a central position when the baboon troop was feeding, citing the ability of higher ranked individuals to monopolise clumped food resources and allowing the more dominant females to harvest food at a greater rate than lower ranking females (see also Rutberg, 1986; Harcourt, 1987). Although lower ranking females were forced to the edges they were then less likely to encounter supplantation from higher ranked individuals. Barton (1993) thus suggests that the role of feeding competition in shaping spatial structure of baboon groups might be underestimated. Collins (1984) similarly describes subordinate yellow baboons (*P. cynocephalus*) being more likely to feed on the periphery of the troop but instead suggests that predation risk might be a key factor influencing a dominant individual's preference for more central positions. Likewise, in very large groups, such as those formed by gelada, the physical position of an individual (or unit) within the group will also be a factor in determining the probability of the individual being captured as prey. It has been shown that individuals at the edge of a group are likely to be exposed to a greater risk of predation (Hamilton, 1971; Collins, 1984; Ron *et al.*, 1996; de Ruiter, 1986), as are those at the front of a progressing group (Robinson, 1981; Busse, 1984; Collins, 1984; Rhine *et al.*, 1985; Cowlishaw, 1993; Steenbeek & van Schaik, 2001). If such factors are at play in the foraging ecology of gelada, and units differ in competitive abilities or dominance, then the size of a unit might determine its ability to maintain a more desirable central position within the herd. Analyses in the current chapter will be driven by the following hypotheses:

1) If a correlation exists between gelada group size and day journey length, the relationship is predicted to be influenced by levels of food availability. More specifically, it is predicted that gelada day journey length will correlate most strongly with group size in periods when food availability is lower and therefore a stronger limiting factor on foraging activities.

2) Since the fission-fusion nature of the gelada social system is thought to be an adaptation to fluctuations in their resource base, the degree to which gelada groups undergo fission and fusion is predicted to be negatively correlated with levels of food availability.

3) If larger units dominate more central foraging positions (in order to gain greater access to prime feeding patches), this pattern is predicted to be more prominent in periods or habitats in which the distribution of food is most clumped and therefore promotes higher levels of competition. Alternatively, if larger units are occupying central positions within the herd to lower their risk of predation relative to more

peripheral units, the level of visibility within a habitat, as a measure of predation risk, might predict the strength of the 'unit-position' patterns.

In light of the above hypotheses, section 6.2 will focus on variation in gelada group size and day journey length individually at Sankaber over the entire study. The possible ecological factors affecting these 2 variables will then be examined, before the strength of the relationship between group size and day journey length is linked to certain measures of variation in food availability which may underpin it (section 6.2.4). Section 6.3 will focus on the characteristics of the fission-fusion system in gelada group dynamics and its ecological correlates. Finally, section 6.4 will describe the nature and variation of the spatial positioning of units within the larger herd, and discuss the possible consequences in terms of differential predation risk and competition for food resources.

6.2 Group size and day journeys

Although the multi-level social system of the gelada has already been described by a number of authors (Crook, 1966; Dunbar & Dunbar, 1975; Kawai *et al.*, 1983), a brief outline of definitions used in the current analyses is required here.

Ohsawa (1979) noted that while individual units might range extensively they tended to utilise a relatively small core area and units that shared a common 'core range' typically foraged together and were thus classified as a '*band*'. Although they are the most commonly observed higher level of aggregation, bands often split into smaller associations of units or join to form '*mixed-band herds*'. In the present study, the term '*herd*' is used following Crook's (1966) original usage, referring to any temporary aggregation of units whether constituting a 'band' or not. Both Ohsawa (1979) and Dunbar & Dunbar (1975) have pointed out that associations of units within a band are not random and certain units show especially strong tendencies to associate together. These strongly linked groups of units usually remain together when the band splits and are presumably the result of a single unit splitting in the past. These associations (intermediate between 'bands' and 'units') will be referred to in the current study as '*teams*', following Kawai *et al.* (1983). Ohsawa (1979) even extends the classification of the gelada social system to include the '*gelada community*', which he defines as all units of all herds that ever encounter each other. However it is doubtful whether this level of association realistically constitutes a "network of social relationships" as Ohsawa (1979) suggests. (p78). Basically, the only element of gelada society that remains constant is the one-male, or 'family' unit and very little is known about the causes or patterns of higher level group dynamics.

An analysis of gelada group size or dynamics beyond the family unit is faced with two immediate problems. Firstly, the sheer number of individual gelada that move through the study site means that while identification is possible for a number of units, this often only provides suggestive evidence regarding the make up of an entire foraging herd on any one day. Secondly, identification of larger groups (and indeed even family units) is confounded by the extensive fission and fusion occurring within and between bands. In other words, even if a known individual or unit is present little can be concluded about the identity of all other units in the herd from day to day.

It was estimated that the 'main study band' at Sankaber, referred to throughout the current study, numbered approximately 253 individuals and contained approximately 17 units (see Chapter 2, section 2.2.1) However, given that an extensive investigation into patterns of group dynamics is far beyond the capacities of a one-person field study, the following analyses, by necessity, centre mostly on one 'team' within the main study band. Three units ('SM2', 'SM6' and 'SM7'), which were never observed apart, formed the core of the 'main study team'. This association usually incorporated 4 to 10 well known units, and formed the basis on which both the field-based decisions were made regarding which section of gelada to follow when group fission occurred, and the basis on which all 'group data' (e.g. group sizes, day journeys etc.) were collected.

6.2.1 Variation in group size

As described in Chapter 3, a count was made of all individuals (excluding infants attached to their mothers) to obtain a record of herd size at hourly intervals throughout the day on ten days per month (except for July, n = 6 days; and August, n = 5 days) and averaged to provide a mean daily group size. The mean group size of the main study band throughout the study was 238 individuals (sd = 101.15, min = 35, max = 651). As noted above, this range in group size centres on that experienced by the 'core study team' and incorporates both fractions of the main study band and affiliations with other bands, and will hereafter be referred to simply as a 'herd' or 'group' which bares no connotation regarding membership. Although the maximum group size recorded at Sankaber was 651 individuals, a group of 853 gelada, which did not include the main study band, was counted from video footage taken during the current study approximately 3 km west of the field site. The mean group size within each month is displayed in Figure 6.1.

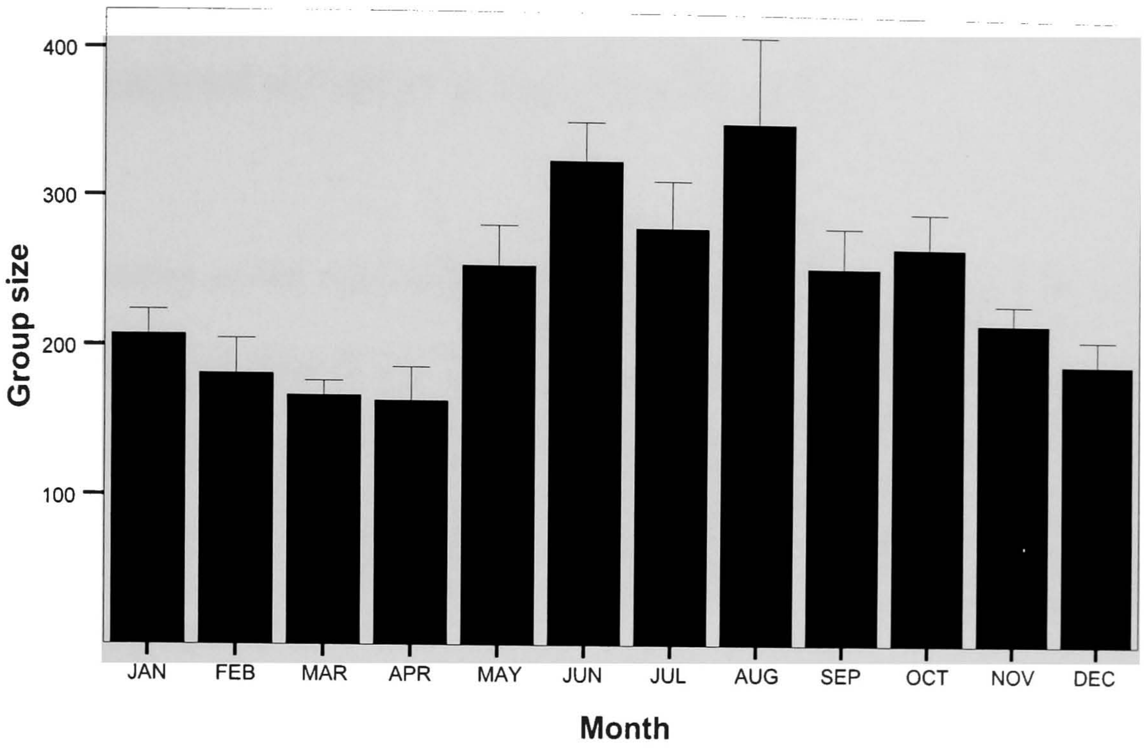


Figure 6.1 *Mean (and standard error) group size, incorporating the main Sankaber study 'team' in each month (July, n = 6; August, n = 7 days; n = 10 days for all other months).*

There is significant variation in mean group size between months, as displayed in Figure 6.1 (**ANOVA**: $F_{(11,119)} = 5.054$, $p < 0.001$), with post hoc analyses revealing that the variation lies between the two months of highest mean group sizes, June and August, and the six months of lowest mean group size (January, February, March, April, November and December; Tukey $p < 0.05$ in all cases). A clear feature of the results presented in Figure 6.1 is the relatively smaller groups observed in the first four months of the year before group size increases substantially from May to October. When group sizes are examined seasonally, the mean wet season group size of 289 (sd = 110, n = 60) is significantly higher than that recorded in the dry season; 188 (sd = 58, n = 60)(t = -6.332, df = 118, $p < 0.001$).

6.2.2 Seasonal variation in day journey length

The day journey of the main gelada study band was marked as accurately as possible on a 1:6250 map during all day follows, using a continuous line drawn in reference to easily demarcated physical features. A planimeter was then used to trace the line and calculate the full distance travelled throughout the day from morning sleeping site to evening sleeping site.

Kawai and Iwamoto (1979) found that the gelada at Gich typically travelled between 1.82 - 1.96 km, while Iwamoto and Dunbar (1983) report mean day journeys of 600m, 2160m and 1008m for gelada populations at Bole, Sankaber and Gich respectively. However, it is unclear in which months or seasons these records were collected and no previous study has presented day journey data over a full annual cycle. The mean day journey length travelled by gelada in the current study was 2056.0m (sd = 569.8, n = 111), ranging between a minimum of 1015m and a maximum of 3523m. The mean (and standard error) of day journey lengths within each month is displayed in Figure 6.2.

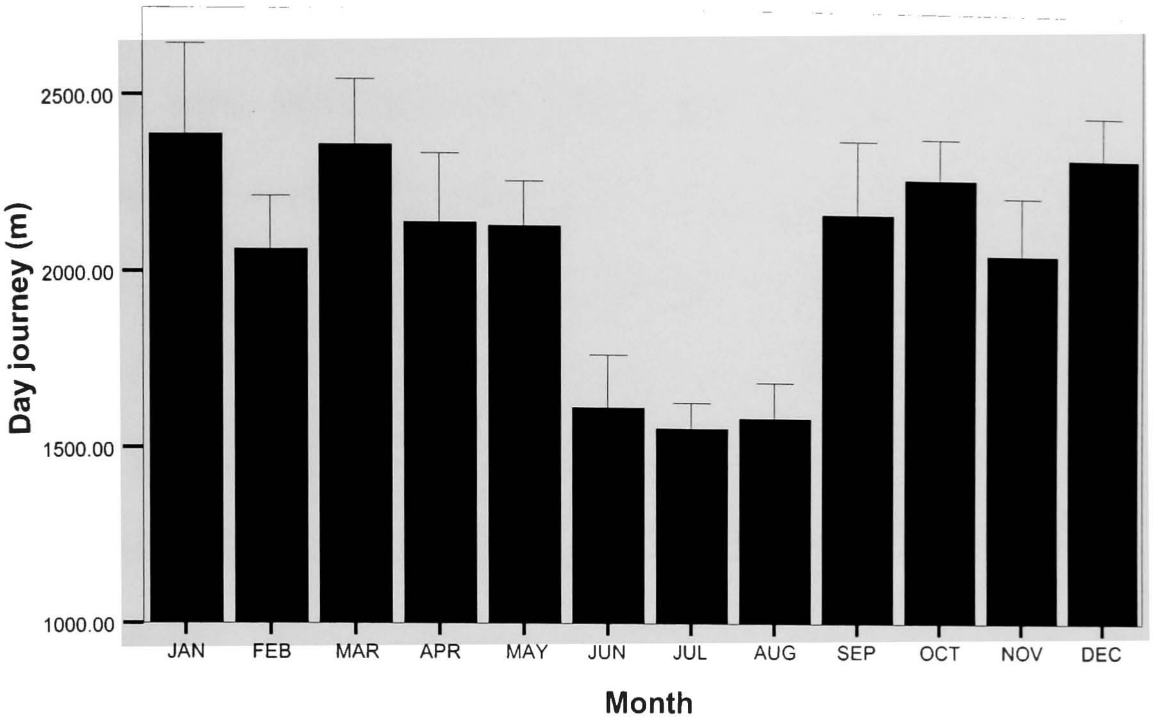


Figure 6.2 *Mean (and standard error) monthly day journey length in metres, based on n = 10 days per month, except for July (n = 6 days) and August (n = 5 days).*

There is a significant difference in day journey length between months (**ANOVA**: $F_{(11,111)} = 3.514$, $p < 0.001$) and the post hoc analyses indicate that all the variance exists between the two months of longest day journey lengths - January (mean = 2387 m, sd = 812) and March (2359 m, sd = 584), and the two months of shortest day journey lengths - July (mean = 1555 m, sd = 235) and August (mean = 1587 m, sd = 320)(Tukey: $p < 0.05$, in all cases). Such variation between months also underpins a significant difference between the length of day journeys travelled by gelada in the dry season (mean = 2224.3, sd = 573.4, n = 60) and that travelled in the wet season (mean = 1887.8, sd = 518.1, n = 51)(t = 3.372, df = 109, $p < 0.01$).

6.2.3 The relationship between group size and day journey

One of the most straightforward relationships involving day journey length, demonstrated for a number of primate species, has been that journey length is a linear function of group size (Waser, 1977; Sharman & Dunbar, 1982). The general assumption is that larger groups need to cover greater areas to obtain the same amount of food per individual (Altmann & Altmann, 1970; Steenbeck & van Schaik, 2001). Gelada provide an interesting opportunity to examine this relationship as their group sizes vary greatly. Kawai and Iwamoto (1979) suggested that mixed gelada herds (comprising more than one band) at Gich travelled approximately twice as far single bands, although no data were presented on the size of the groups actually effecting the day journeys reported. Similarly, Iwamoto and Dunbar (1983) report mean day journeys of 1.33 km for small gelada bands (less than 100 animals) and mean day journeys of 2.25 km for 'larger' bands. The daily distance travelled by the herd over the entire current study is plotted against the size of the foraging herd on the corresponding day in Figure 6.3.

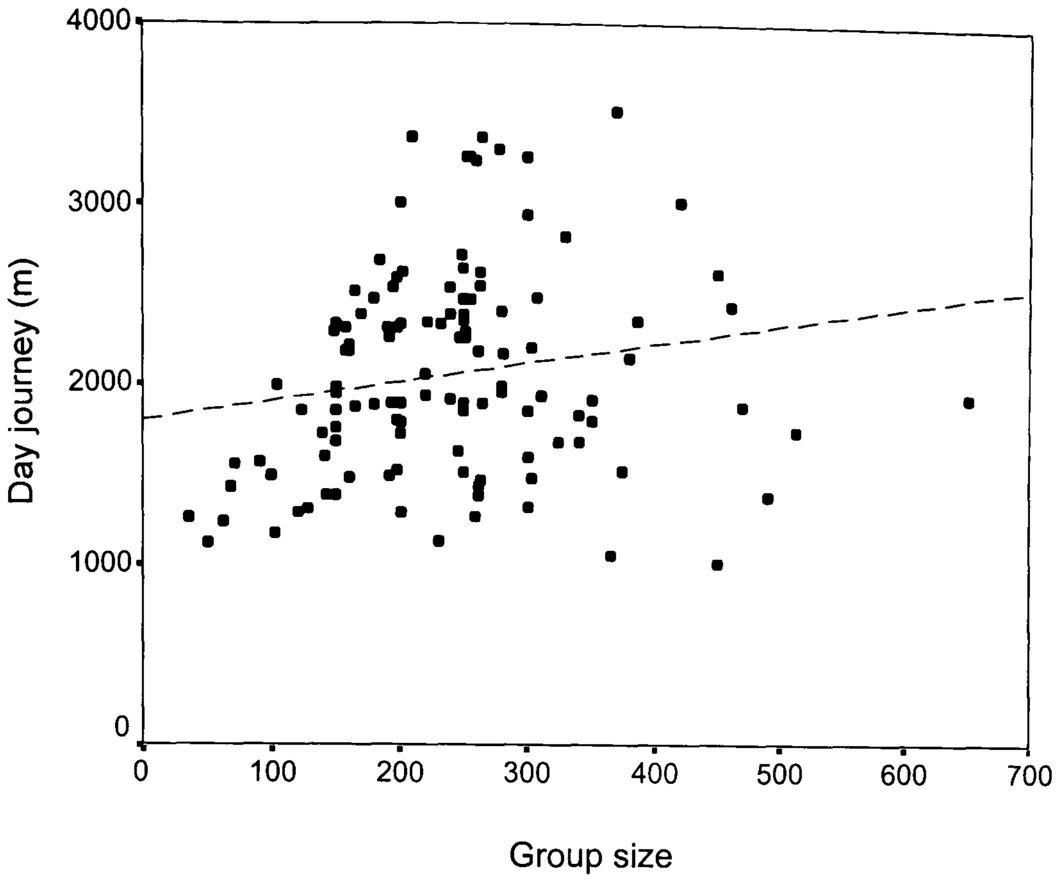


Figure 6.3 *Distance travelled per day in metres plotted against corresponding number of individuals (excluding infants) in foraging herd that day, throughout the study.*

A significant positive correlation was found between group size and day journey length across the entire year ($r = 0.189$, $n = 111$, $p < 0.05$), suggesting that each animal needs to cover a roughly constant amount of unforaged ground each day and that an increase in group size must be countered by travelling further. However, when the relationship between group size and day journey length was examined within each month, not all months were significant. The mean monthly group size and length of day journey travelled by the main study herd are shown in Table 6.1, along with their respective correlations. For the first five months of 1998 the distance the gelada travelled in a day was strongly positively correlated to the size of the group travelling. However, from May onwards there is no significant correlation between day journey and group size in any wet season month other than September. In other words, the relationship between group size and day journey length is stronger on average during the dry season months. The seasonality of the relationship can be tested further by plotting daily group size against day journey length for dry season (Figure 6.4) and wet season days (Figure 6.5) independently.

Table 6.1 *Mean monthly group size, day journey length and Pearson's correlation between the two variables. Wet season months in italics.*

Month	Mean group size	Mean day journey (m)	r	p
January	206.6	2387.4	0.965	< 0.01**
February	181.0	2064.6	0.956	< 0.01**
March	166.7	2359.4	0.933	< 0.01**
April	163.2	2139.3	0.942	< 0.01**
May	254.7	2130.2	0.877	< 0.01**
June	325.6	1613.8	0.513	0.143
July	280.4	1555.3	0.568	0.087
August	351.4	1587.4	0.484	0.156
September	253.8	2169.6	0.882	< 0.01**
October	267.9	2270.7	0.446	0.197
November	217.3	2057.8	0.507	0.137
December	169.3	2337.1	0.747	0.05*
Total	238.2	2056.0	0.189	< 0.05*

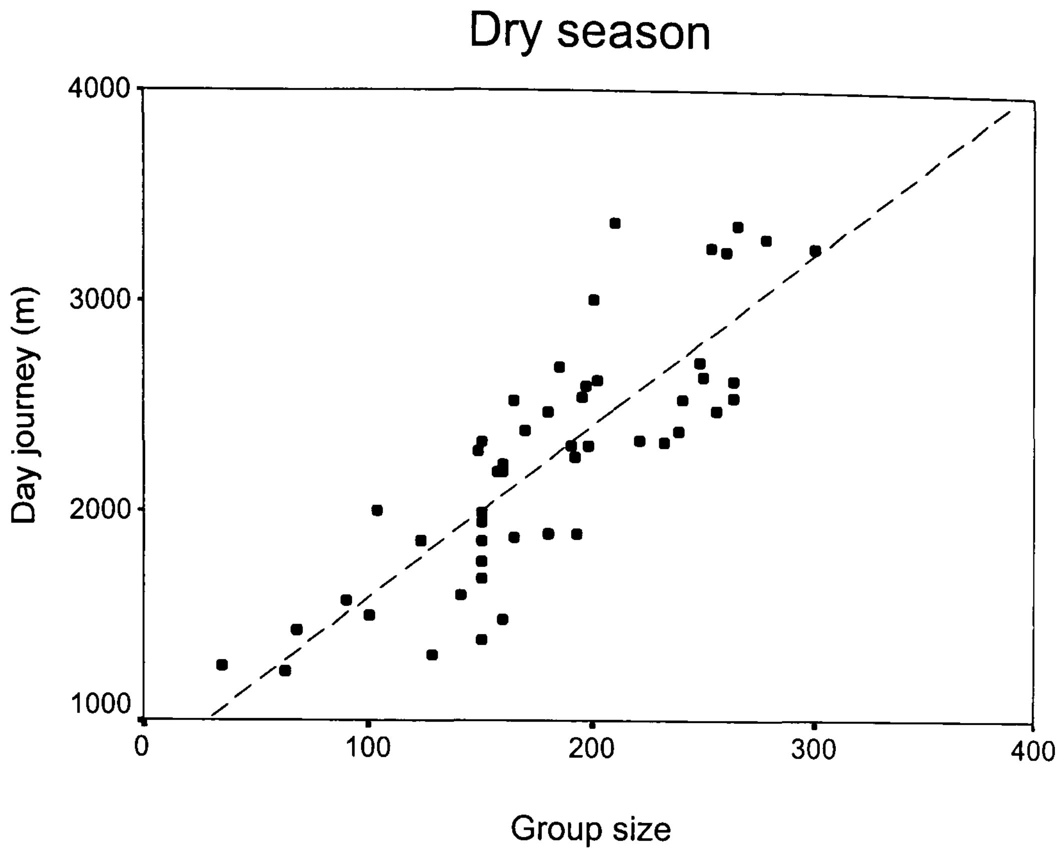


Figure 6.4 *Daily day journey length in metres plotted against group size for dry season months (N = 60 days).*

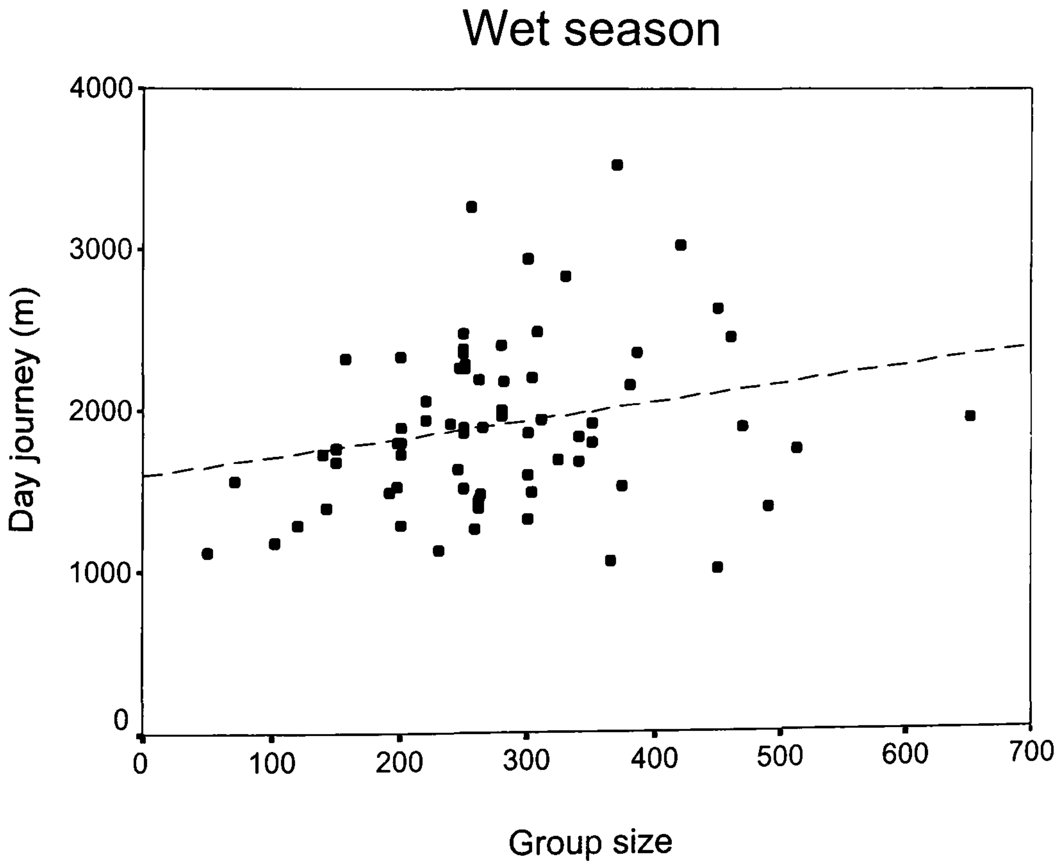


Figure 6.5 *Daily day journey length in metres plotted against group size for wet season months (N = 60 days).*

In line with the results presented in Table 6.1, there is a stronger positive correlation between day journey length and group size in the dry season (**r** = 0.736, n = 60, $p < 0.001$) than in the wet season (**r** = 0.263, n = 60, $p < 0.05$) The assumed underlying influence of food availability on this relationship will be examined in the following section.

6.2.4 Ecological correlates of day ranging

The preceding sections have demonstrated the large variation found in gelada group sizes at Sankabar and the nature of the relationship between group size and day journey length. However, the direction and distance that a group of primates travels in any one day will be influenced by a number of concomitant factors. The current analyses will now shift to examine in more detail how certain ecological parameters such as rainfall (a common estimate of habitat quality) and green vegetation cover are related to variation observed in group size and day journey length.

6.4.2.1 Rainfall and day ranging

The mean monthly day journey length recorded in the current study is plotted against monthly rainfall in Figure 6.6. The correlation is significant in the negative direction (**r** = -0.891, n = 12, $p < 0.01$) primarily reflecting the shorter distances travelled by the gelada in the main wet season months of June, July and August (see Figure 6.1).

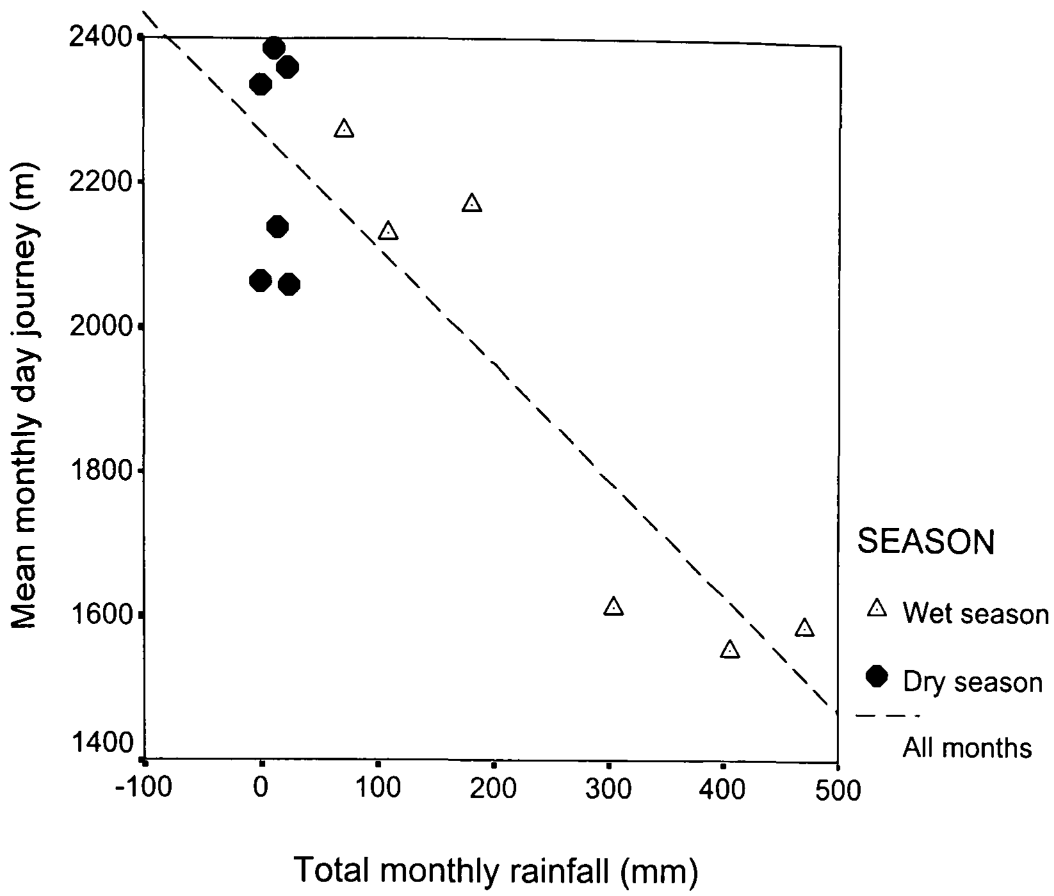


Figure 6.6 *Mean monthly day journey (in metres) plotted against total monthly rainfall (in mm) during the corresponding month.*

In section 6.2.3, a strong positive correlation was found between daily group size and day journey length. Whereas in Figure 6.6 a negative correlation was found between day journey length and monthly rainfall. We might therefore predict mean monthly group size to show a similar negative correlation to monthly rainfall. Indeed, a significant correlation does exist between mean monthly group size and rainfall in the corresponding month (**r** = 0.880, n = 12, $p < 0.01$), but the relationship is positive (Figure 6.7).

Graphically, the relationship displayed in Figure 6.7 is best represented by a quadratic regression line (**Rsq** = 0.815, df = 9, $p < 0.01$), reflecting the fact that an upper limit exists to the maximum possible group size formed by gelada regardless of the amount of monthly rainfall. The opposite directions of the relationships displayed in Figure 6.6 and 6.7 respectively, indicate that while day journey length might vary in response to the foraging constraints imposed by group size on a daily basis over the entire study, the relationship is not as straightforward on a monthly or seasonal scale, as was shown in Table 6.1.

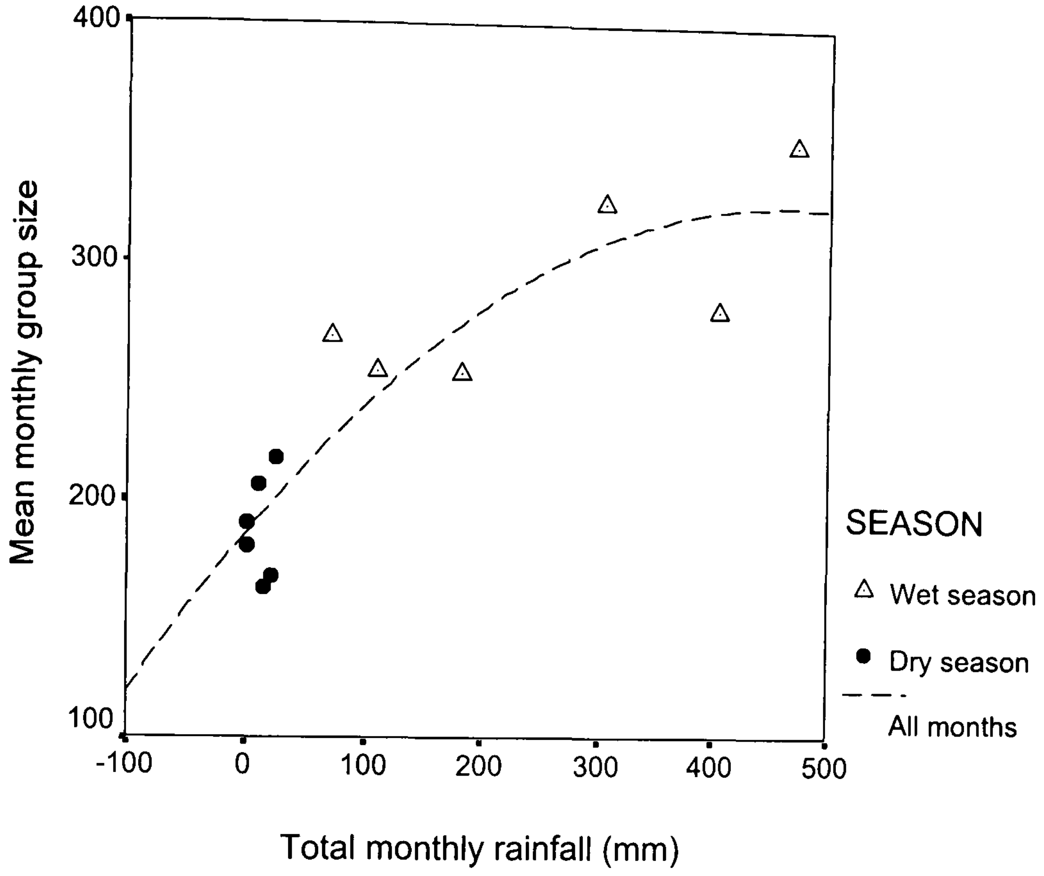


Figure 6.7 *Mean monthly group size plotted against total monthly rainfall (in mm) during the corresponding month.*

6.2.4.2 Green cover and day ranging

Dunbar and Dunbar (1975) found that gelada band size was significantly positively correlated with the amount of grass available within its respective home range. However, their calculation included a combination of two bands on the grounds that they 'used the same area for much of the study period' (p135). Given that the home ranges of gelada bands commonly overlap extensively, it may be problematic to combine certain bands and not others when comparing groups. In the current study, a positive correlation was found between mean monthly group size and the mean percent of green cover in all quadrats during those months (**r** $= 0.649$, $n = 12$, $p < 0.05$). The relationship is plotted in Figure 6.8. It thus appears that larger congregations of animals were possible during periods of greater green grass cover as presumably this constituted richer grazing conditions. This is supported by the fact that the relationship between green cover and mean group size is even stronger when examining quadrats of the key grass grazing habitat type, P-open, alone (**r** $= 0.766$, $n = 12$, $p < 0.01$), as plotted in Figure 6.9. As day journey length is commonly assumed to be influenced by the levels of food available to the animals that day, it is perhaps surprising that no correlation was found between the mean percent green cover and the mean monthly day journey even when controlling for variation in group size ($\mathbf{r}_{\mathbf{partial}} = 0.1878$, $n = 12$, $p = 0.580$), as plotted in Figure 6.10.

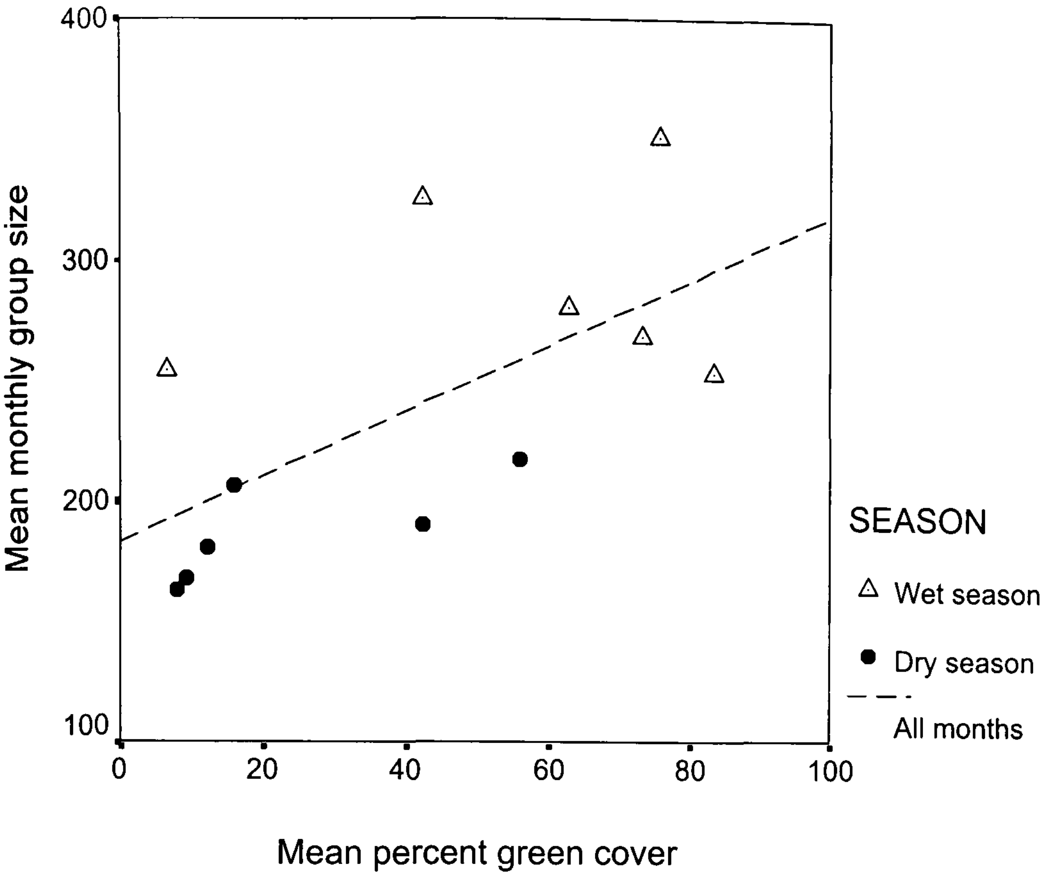


Figure 6.8 *Mean monthly group size plotted against mean monthly percent of green cover across all 20 quadrats, in the corresponding month.*

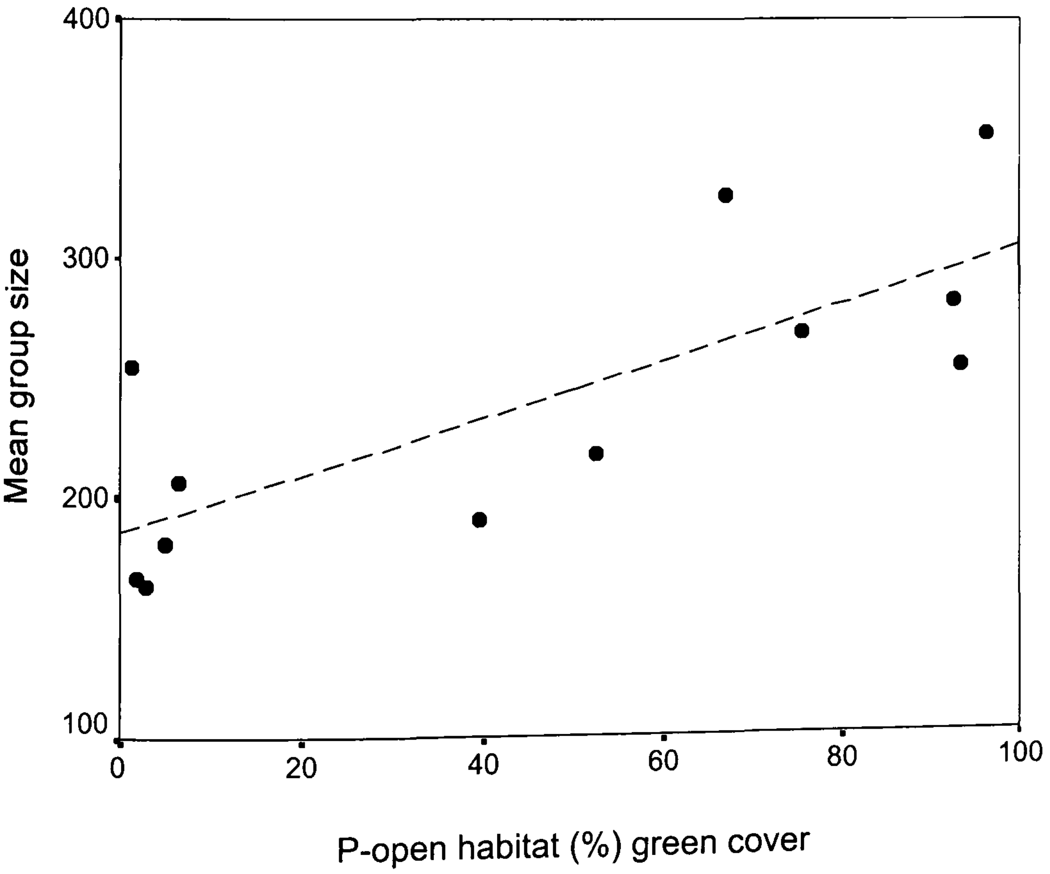


Figure 6.9 *Mean monthly group size plotted against mean monthly percent of green cover in P-open quadrats (n = 14), in the corresponding month.*

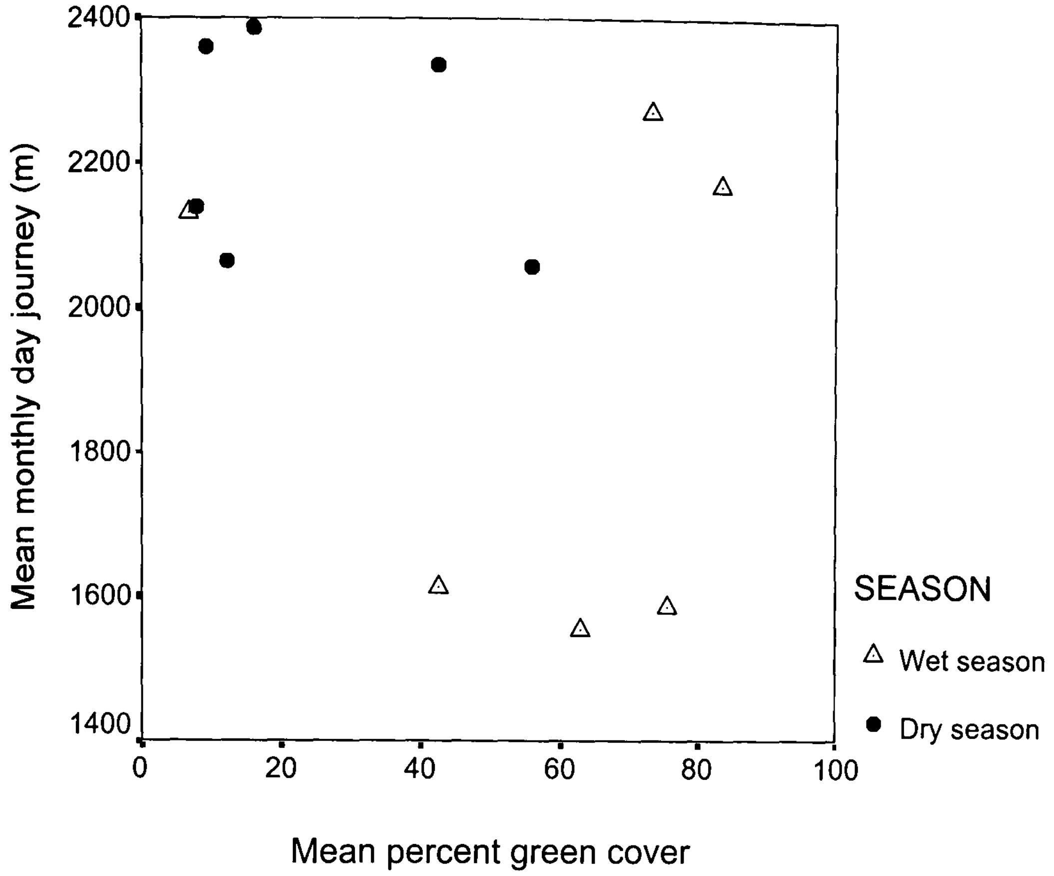


Figure 6.10 *Mean monthly day journey (in metres) plotted against mean monthly percent green cover across all 20 quadrats, during the corresponding month.*

However, monthly means provide only a crude measure of the variables being considered and it is important to bear in mind the large within-month variation existing in both percent of green cover (Figure 4.1; see also CVs in Table 6.3 below) and day journey length (see error bars in Figure 6.2). Furthermore, variation in day journey has been shown to correlate strongly with group size in most months (Table 6.1) and it would thus appear to exert a stronger influence on the length of day journeys throughout a month than the mean levels of green cover.

Given the assumption that the relationship between group size and day journey length is based on food availability (Clutton-Brock & Harvey, 1977), it is interesting that the monthly correlations presented in Table 6.1 bear the least significance in the months during which the gelada home range supports the highest levels of green vegetation. It appears that variation in different ecological conditions not only affects group size and day journey independently, but also the strength of the relationship between these 2 variables. This was also shown when comparing the day to day correlations in the dry season (Figure 6.4) with those in the wet season (Figure 6.5). Therefore, the strength of the monthly correlations between day journey length and group size (i.e. the Pearson's r values in Table 6.1) were compared firstly with monthly rainfall totals (Figure 6.11).

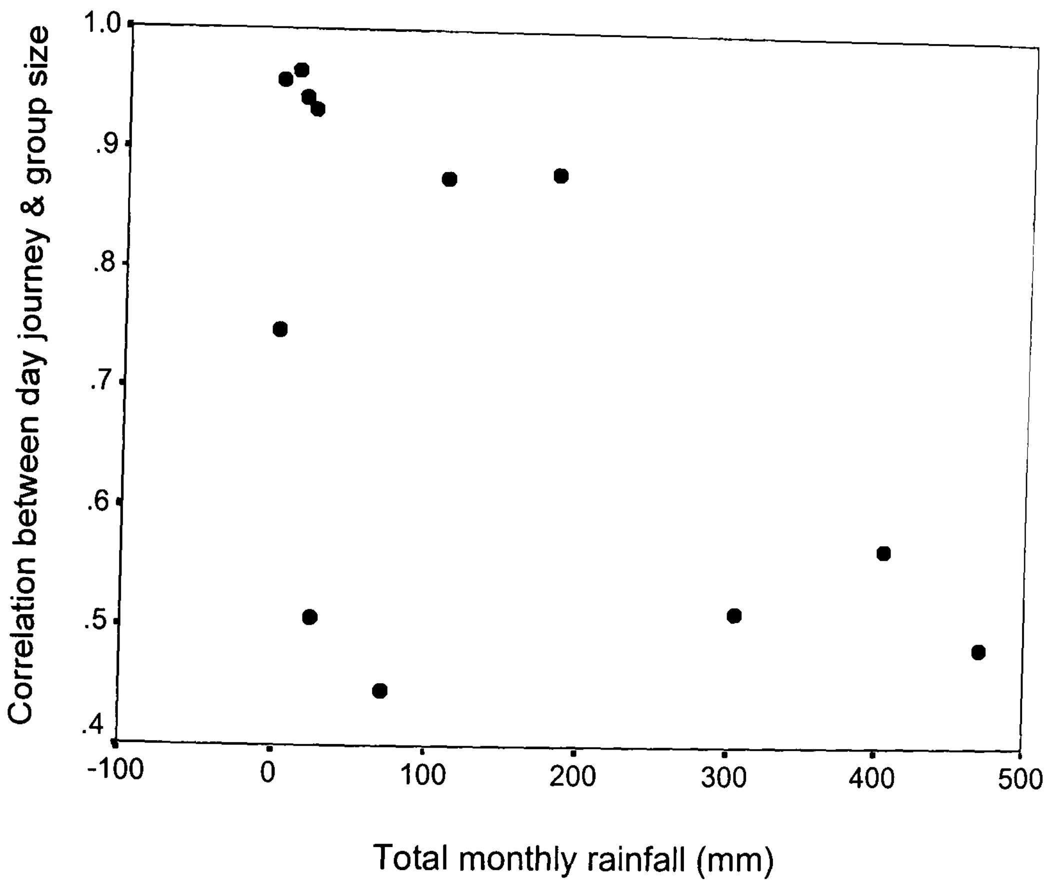


Figure 6.11 *The Pearson's r value for the correlation between day journey and group size plotted against total rainfall per month (mm).*

A negative trend appears to exist between monthly rainfall and the strength of the correlation between day journey and group size within that month, and the correlation only just fails to reach significance (**r** = -0.574, n = 12, p = 0.051). The same

Pearson's r values were then plotted against the mean monthly level of green cover in Figure 6.12 and found to be significantly negatively correlated (**r** = -0.715, n = 12, p < 0.01).

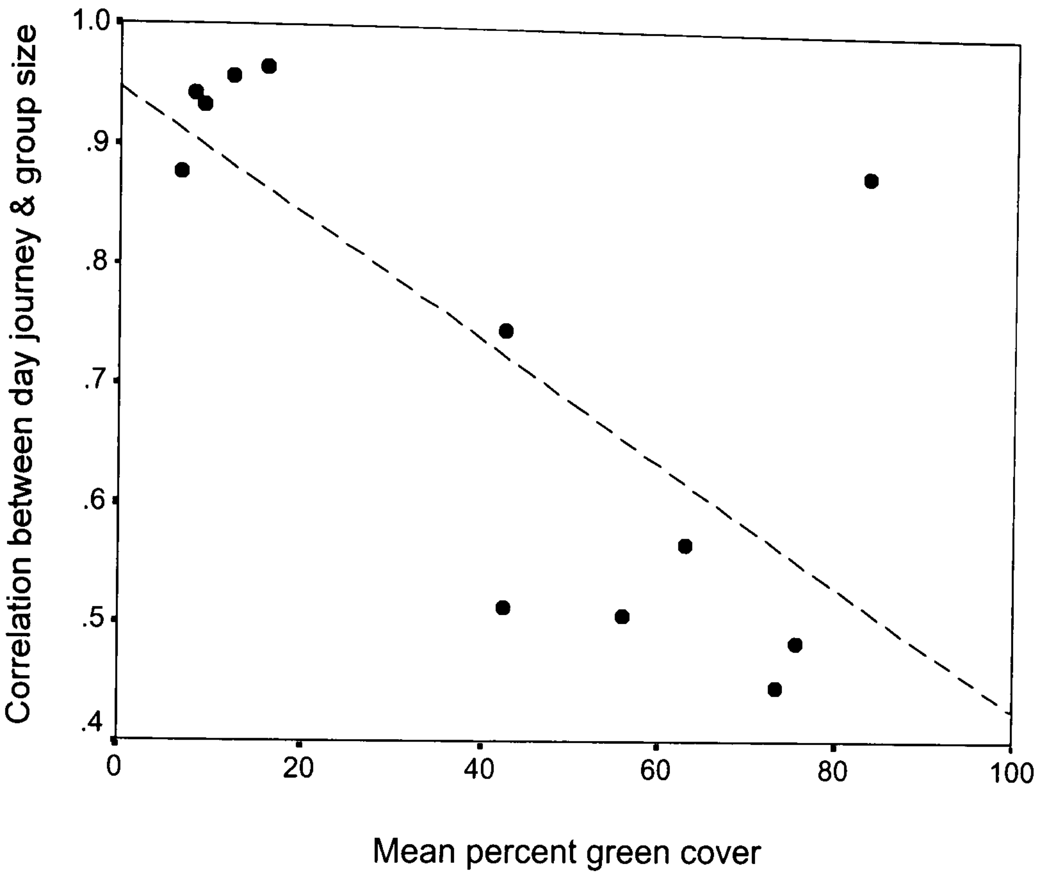


Figure 6.12 *The Pearson's r value for the correlation between day journey and group size plotted against the mean percent of green grass cover per month.*

The correlation is even stronger when comparing the strength of the Pearson's correlation between day journey and group size within each month and the mean level of green cover within the P-open habitat alone (**r** = -0.753, n = 12, p = 0.005). These results provide further evidence that the strength of the relationship between group size and day journey length is dependant on levels of food availability. However, caution must be exercised when using percent green cover as a measure of food availability during all months, as the results presented in Chapter 5 demonstrated that not only does the gelada diet shift markedly to underground food items in the dry season months, but that the dry season diet (when levels of green cover are very low) does not appear to represent a period of nutritional shortfall. Furthermore, it is important to note that a significant relationship between group size and day journey was not found in five months, four of those being in the wet season. These results provide strong evidence in support of the first prediction of this chapter; namely that a correlation does exist between gelada group size and the distance they travel that day, but that the influence of group size on day journey length is only strong in the dry season when food availability is lowest.

6.3 Group fission and fusion

Encounters between different gelada bands were common due to the high level of overlap between each band's home range and the high density at which gelada exist throughout the Simen Mountains. Dunbar and Dunbar (1975) calculated the density of gelada at Sankaber to be in the region of 78 individuals per km^2, which is far higher than the density at which most other terrestrial primates are found (see Melnick & Pearl, 1987 for a review). Inter-band encounters usually resulted in the two bands joining and forming a mixed-band herd when occupying similar areas. The herd usually separated when one of the bands moved back into regions of their home range that were unfamiliar to other bands. Although gelada herds would often react with alarm calls at the first detection of another herd, gelada are not territorial (Crook, 1966) and there was rarely ever any antagonism when bands or herds joined. Dunbar and Dunbar (1975) suggest that familiarity between units of different bands reduces initial antagonism upon meeting. In light of this, it is interesting to note that when in mixed-band herds, units from the same band remain together spatially, suggesting possible benefits from maintaining proximity to familiar units while foraging. This will be examined further in section 6.4.

The previous section highlighted the massive variation in group size experienced by gelada throughout the study, and the error bars displayed in Figure 6.1 indicate substantial variation in group size even within months. Clearly, to effect such changes in group size, large numbers of individuals must merge and separate from the main study band on a regular basis. To obtain a more detailed picture of the patterns underlying the fission and fusion of gelada groups, data were collected on the size of groups merging or departing, the habitat location and daily rate at which changes occur. In a similar fashion to collecting group size records (see section 3.2.2), group fission and fusion events were only recorded once the gelada were clearly off the sleeping sites. This allowed for the nightly dispersion of units along the sleeping ledges, and subsequent morning reunification, without these being counted as fission-fusion events, and meant that almost all group fission-fusion data was collected roughly between the hours of 10:00 to 16:00. The results are summarised in Table 6.2.

Over 110 full days, 69 fission-fusion events (34 merges and 35 splits) were recorded considering the 'core study team' as the base group. On some occasions the merging or departing party could be identified, but given the large number of unidentifiable units it was not possible to obtain reliable records of movement and associations between known bands. An important piece of information contained in Table 6.1 is the remarkably high mean rate at which groups merge (0.31 times/day) and depart from (0.32 times/day) the main study band throughout the study (January can be excluded from the current analysis as fission-fusion data are only available for one day).

Table 6.2 *Mean size of groups merging with, or departing from, main study band during all day follows in each month, and mean daily rate at which fission-fusion events occurred. Wet season months in italics.*

Month	mean no. merges per day	mean merging group size	mean no. departures per day	mean departing group size	mean no. all fission-fusion events / day	no. days (N)
Jan.	0.0	0.0	0.0	0.0	0.0	1
Feb.	0.20	73.1	0.40	48.0	0.60	5
Mar.	0.70	57.7	0.60	56.7	1.30	10
Apr.	0.22	80.0	0.22	80.0	0.44	9
May	0.90	132.2	1.20	117.1	2.10	10
Jun.	0.38	97.5	0.25	115.0	0.63	8
Jul.	0.17	88.3	0.17	90.0	0.30	6
Aug.	-	-	-	-	-	0
Sep.	0.19	78.1	0.13	95.0	0.31	16
Oct.	0.08	86.8	0.12	72.5	0.20	25
Nov.	0.20	62.0	0.10	90.0	0.30	10
Dec.	0.50	59.3	0.40	59.3	0.90	10
overall	0.31	88.6	0.32	82.1	0.63	110

There is no significant difference between the mean rate at which groups join the main study band and the mean rate at which groups depart from the main study band (**Mann Whitney U**: z = -0.151, n = 10, p = 0.880). Similarly, there is no significant difference in the mean size of joining and departing groups (**Mann Whitney U**: z = -0.131, n = 10, p = 0.895). All fission-fusion events were therefore pooled in the penultimate column of Table 6.2. There is, however, a significant difference between the mean size of groups merging and departing in the wet season and the mean size of groups merging and departing in the dry season (**Mann Whitney U**: $z = -2.402$, $n = 5$, $p < 0.05$). This might be expected, due simply to the significantly larger size of the main study group in the wet season, as shown in section 6.2.1. However, the fact that merging and departing groups are likewise larger in the wet season is an important corollary, indicating that the patterns of group size variation observed for the main band of the current study are likely to apply to the size of other gelada groups throughout the Simien Mountains, at least on a seasonal scale. In other words, not only was the main study band larger on average in the wet season, but neighbouring gelada groups were as well.

Although no significant difference was found in the mean daily rate of fission-fusion events between seasons (**t** $= 0.003$, df $= 5$, $p = 0.997$) there is substantial difference between months. The highest monthly rate (2.1 events/day) was recorded in May when a total of 21 fission-fusion events were observed during ten full observation days. In contrast, only 5 fission-fusion events were recorded during 25 days in October, at a mean rate of 0.20 events/day.

6.3.1 Factors affecting the rate of fission-fusion events

In order to test Crook's (1966) hypothesis that the ability of the gelada social system to merge and split so readily is a response to declining food availability, the monthly rate of fission-fusion events was correlated against the mean monthly percent green cover within established vegetation quadrats (Figure 6.13). A negative trend exists between the mean percent of green cover in a month and the rate at which groups of gelada merged with or departed from the main study band, but the correlation is not significant (r = -0.510, n = 10, p = 0.109). This appears to run against the second prediction of this chapter, in that levels of fission and fusion do not appear related to levels of food availability. However, an important feature of the levels of green cover presented in chapter 4 (Figure 4.1) was the large error bars associated with the means. This indicated that in certain months percent green cover varied greatly between quadrats even within one habitat type (as discussed in section 4.2.1), and suggested that above ground food resources, especially green grasses, may be patchily distributed in space.

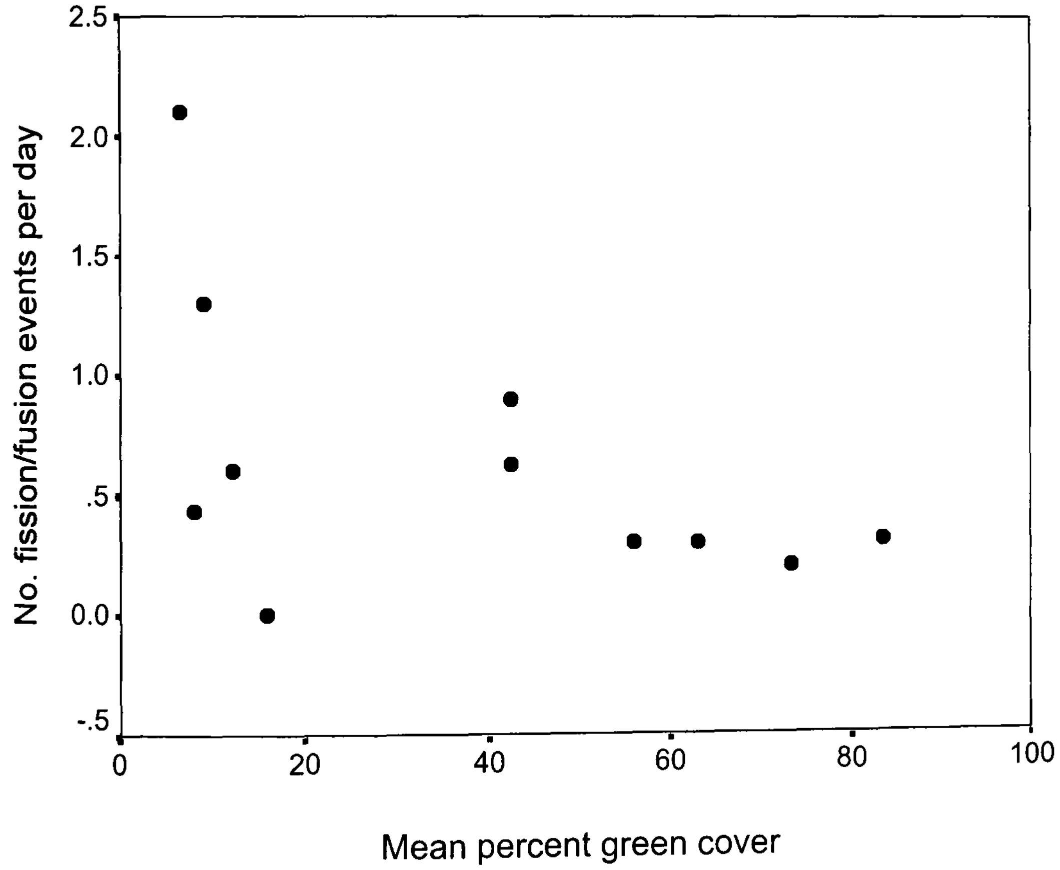


Figure 6.13 *Mean daily rate of fission-fusion events per month involving the main study group plotted against mean monthly percent green vegetation cover in established quadrats.*

A rudimentary measure of the unevenness of gelada food distribution between quadrats is provided by the coefficient of variation (CV) of percent green cover. This was calculated from the mean and standard error (CV = sd/mean) of percent green cover across all quadrats in each month, and is displayed as a percentage in Table 6.3.

Table 6.3 *Mean (and standard error) percent green cover across all quadrats (n = 20) within each month, corresponding monthly coefficient of variation (CV) and the mean daily fission-fusion rate for each month. Percent green cover was taken from the data presented in Figure 4.1. Wet season months in italics.*

Month	Percent green cover		Coefficient of Variation (%CV) = sd/mean	Mean no. fission-fusion events per day
	Mean (%)	sd		
January	16.00	16.34	102	0.0
February	12.30	12.86	105	0.60
March	9.20	10.88	118	1.30
April	7.95	3.36	42	0.44
May	6.70	6.76	101	2.10
June	42.50	27.72	65	0.63
July	62.90	27.93	44	0.30
August	75.55	22.43	30	-
September	83.40	15.77	19	0.31
October	73.30	18.62	25	0.20
November	55.90	25.66	46	0.30
December	42.50	28.47	67	0.90

The coefficient of variation (for mean percent of green vegetation cover) is high in most months, reflecting the large variation that exists when values are pooled for all 20 quadrats across five habitat types. Nonetheless, this does represent a measure of the variation in patchiness of green forage throughout the home range, and was therefore plotted against the mean daily rate of fission-fusion events in Figure 6.14. The mean monthly rate at which fission-fusion events occur is positively correlated to the coefficient of variation for percent green cover in the corresponding month ($r = 0.752$, $n = 10$, $p < 0.05$).

In other words, during months in which the gelada experienced the most uneven distribution of food resources, the main study group was more likely to undergo fission or fusion. However, this pattern is based on vegetation data from all 20 established quadrats, which were distributed across five habitat types and varied greatly in their importance to gelada foraging. Therefore, the analyses were repeated using data specific to each of the four habitat types for which sufficient records are available (P-open, P-bushy, G-open and E-heather, see Figure 4.1).

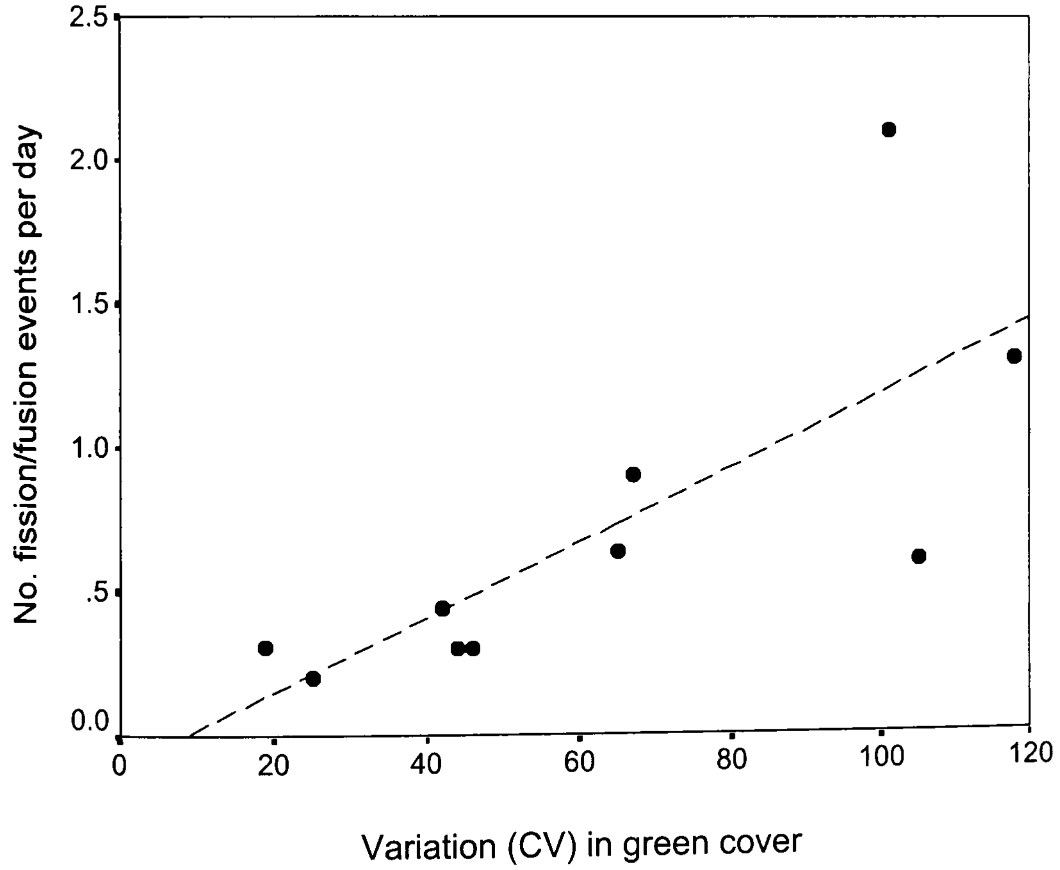


Figure 6.14 *Mean daily rate at which the main study band experienced group fission or fusion events per month plotted against the coefficient of variation (expressed as a percentage) for levels of green cover for all quadrats (n = 20).*

The monthly rate of fission-fusion events was found to correlate significantly with the coefficient of variation (CV) of green cover in the P-open (**r** = 0.797, n = 10, p < 0.01) and P-bushy (**r** = 0.779, n = 10, p < 0.01) habitat types but not the G-open (**r** = 0.293, n = 10, p = 0.411) and E-heather (**r** = 0.122, n = 10, p = 0.738) habitat types.

The strongest relationship was found in the P-open habitat and CV of green cover for quadrats in this habitat type is plotted against fission-fusion rate in Figure 6.15. Given that the P-open and P-bushy habitat types are by far the most important habitat types to the gelada in terms of foraging (see sections 4.3.1), it is perhaps even more striking that it is only within these two habitat types that the degree of variation in green cover correlates so strongly with the amount of fission and fusion of the main gelada group.

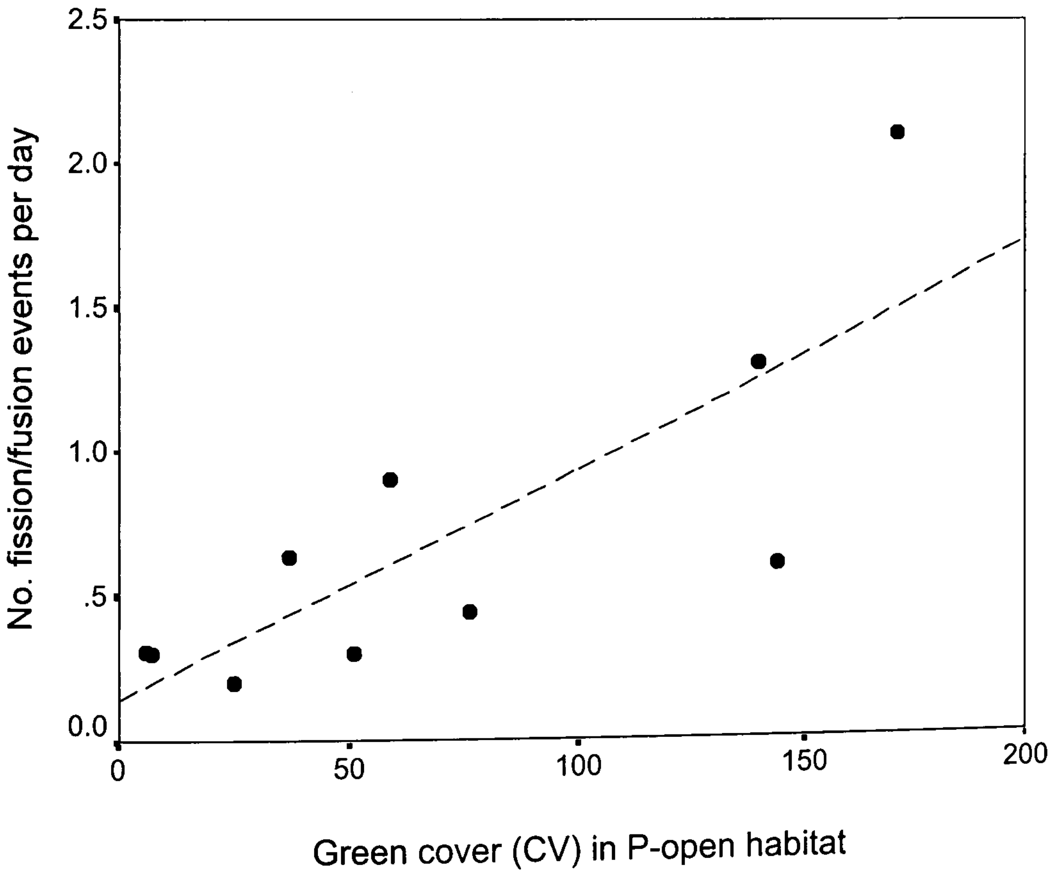


Figure 6.15 *The mean daily rate at which the main study band experienced group fission or fusion events per month (n = 10) plotted against the coefficient of variation (expressed as a percentage) for levels of green cover in P-open quadrats.*

6.4 Spatial patterns of units

It has already been shown in section 6.2.3 that an increase in gelada group size leads to longer day journeys, indicating that an individual's foraging efficiency is diminished when larger numbers seek to exploit the same resources. Mori (1979) noted that gelada units maintain spatial integrity through any herd size in any habitat, and that certain "teams" of units were usually contiguous in space, while units of different bands remain discrete even when they are present in the same herd. The fact that units within bands and bands within herds remain remarkably discrete implies that benefits derive from familiarity with neighbours. Mori (1979) also described gelada units fighting over access to a watering hole (p85), and used artificial provisioning to incite agonistic interactions between units, demonstrating that larger units are significantly more likely to dominate smaller units in terms of spatial supplantation.

During October (11 days) and November (23 days) 2000, data were collected on the positional location of 17 known units within the herd. When a unit was present during hourly scans, its position was assigned to one of three equal portions of the herd in terms of 'leadership' (with regards to the direction the herd were generally moving), and 'centrality', depending on how close to the outer edge of a herd it was (see Figure 3.1). A total of 250 position records were collected from group scans; a mean of 15 per unit (min = 6, max = 29). Unit-position scans were conducted on the hour and only when the herd was primarily in foraging mode, between 10:00 and 15:00, and the general direction of herd movement was clear.

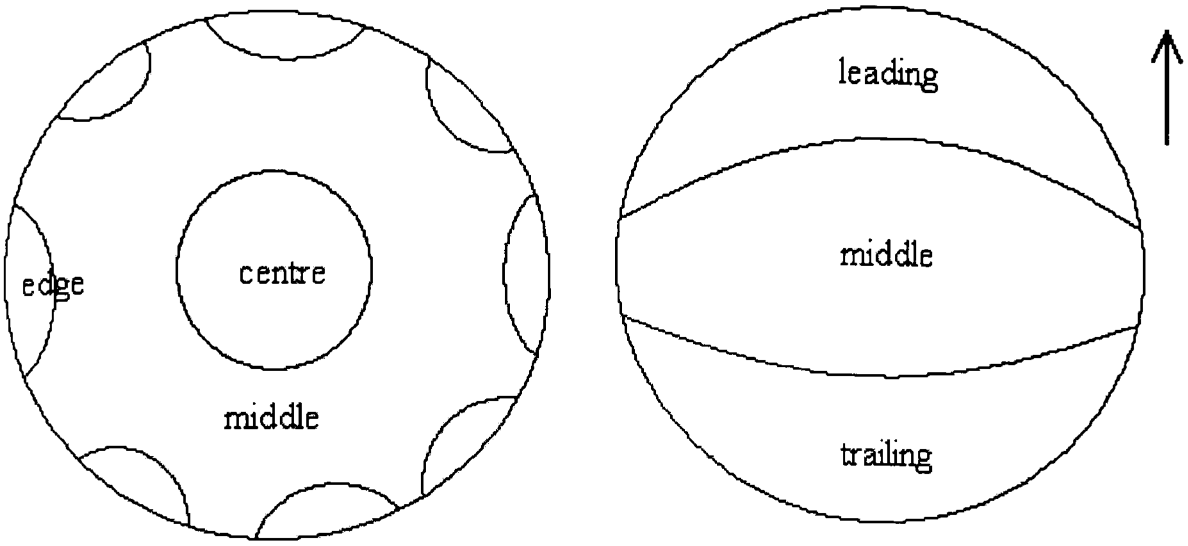


Figure 6.16 *Diagrammatic representation of; a) the location ('centrality') of units with regards to the centre '1' or edge '3' of the herd. {N.B. '3' only assigned when unit was on the* extreme *periphery of the group}, and b) the location of units with regards to the direction of movement of the grazing herd – does not include full group 'marches', as described in Chapter 6 .*

It is important to note that almost all studies cited in this section relate to the position of *individual* animals, whereas the current analyses focus on the spatial patterns of individuals grouped into units. Comparisons and conclusions will therefore be limited. Nevertheless, gelada units remain spatially discrete within the larger herd, and individuals within a single unit can thus be assumed to face essentially the same conditions with regards to foraging and predation risk, when compared with individuals in other units. Therefore, the analyses that follow will investigate inter-unit differences within the gelada herd in a similar broad ecological context to that which underpinned other (primarily baboon) field studies examining inter-*individual* differences within troops (e.g. Post *et al.*, 1980; Whitten, 1983; Johnson, 1989; Amat & Obeso, 1991; Mitchell *et al.*, 1991).

6.4.1 Unit position and leadership

Dunbar and Dunbar (1975) found that one gelada unit (out of 6 for which data were available) was found to lead herd progressions significantly more than expected by chance. However, as mentioned above, such 'progressions' or marches were not the focus of the current study, and spatial data presented here were instead collected when the gelada herd was engaged in 'travel-feeding' as defined by Crook (1966). Table 6.4 displays the number of times each of the 17 focal units in the current study was recorded as being in the leading, middle or trailing zones of the progressing herd (see diagram, Figure 3.1). The number of adult females in the unit is listed as a measure of unit size.

Given that the three zones were of approximately equal size within a herd at any one time, a random distribution of positions should result in a unit being recorded in each zone in roughly equal number (33.3%) of records. This is clearly not the case. Although all but one unit was observed in all three zones of the herd, significant variation was found between units in the proportion of records they were located in the three zones ($\chi^2 = 16.62$, df = 2, $p < 0.001$). It therefore appears that some units are not found randomly positioned throughout the herd. Dunbar and Dunbar (1975) similarly describe 'leader' and 'follower' units within their gelada study band. From the results presented in Table 6.4, it appeared that some units, such as SM-8 (n = 5 ♀♀), were predominantly observed in the leading third of the herd, while others, such as SM-6 (n = 2 ♀♀) were not. Given that the leading edge of a foraging herd might present better foraging opportunities to grazers (Jarmen, 1974), and that larger units might be spatially dominant over smaller units (Mori, 1979), the mean size of all units recorded in each of the three zones was compared (Figure 6.17).

Table 6.4 *Individual unit ID, number of adult females and number of occasions the unit was observed in the leading middle or trailing third of the herd.*

Unit ID	Number of females	Number (and percent) of records in progression positions			No. cases
		Leading third	middle	Trailing third	
SM-5	2	5 (38.5%)	7 (53.8%)	1 (7.7%)	13
SM-6	2	1 (10.0%)	6 (60.0%)	3 (30.0%)	10
SM-1	2	7 (29.2%)	12 (50.0%)	5 (20.8%)	24
DM-3	2	3 (37.5%)	4 (50.0%)	1 (12.5%)	8
DM-2	2	3 (37.5%)	3 (37.5%)	2 (25.0%)	8
SM-16	3	8 (61.5%)	3 (23.1%)	2 (15.4%)	13
SM-12	3	6 (46.2%)	5 (38.5%)	2 (15.4%)	13
SM-3	3	7 (30.4%)	9 (39.1%)	7 (30.4%)	23
SM-2	4	11 (39.3%)	8 (28.6%)	9 (32.1%)	28
SM-9	4	5 (27.8%)	9 (50.0%)	4 (22.2%)	18
SM-10	4	2 (20.0%)	6 (60.0%)	2 (20.0%)	10
J-4	4	2 (33.3%)	2 (33.3%)	2 (33.3%)	6
SM-8	5	22 (75.9%)	6 (20.7%)	1 (3.4%)	29
J-1	5	3 (33.3%)	6 (66.6%)	0 (0.0%)	9
DM-5	6	3 (25.0%)	5 (41.7%)	4 (33.3%)	12
SM-15	7	4 (30.8%)	4 (30.8%)	5 (38.5%)	13
SM-13	8	5 (38.5%)	6 (46.2%)	2 (15.4%)	13
total counts		88	102	60	250

Although units observed in the leading third of the herd were slightly larger than those in the middle or trailing third, the difference was not significant (**ANOVA**: $F_{(6,249)} = 1.329$, $p = 0.245$). Nonetheless, in the interest of testing the third prediction of this chapter it is an important observation that certain individual units are significantly more likely to be found in certain areas of the herd than others.

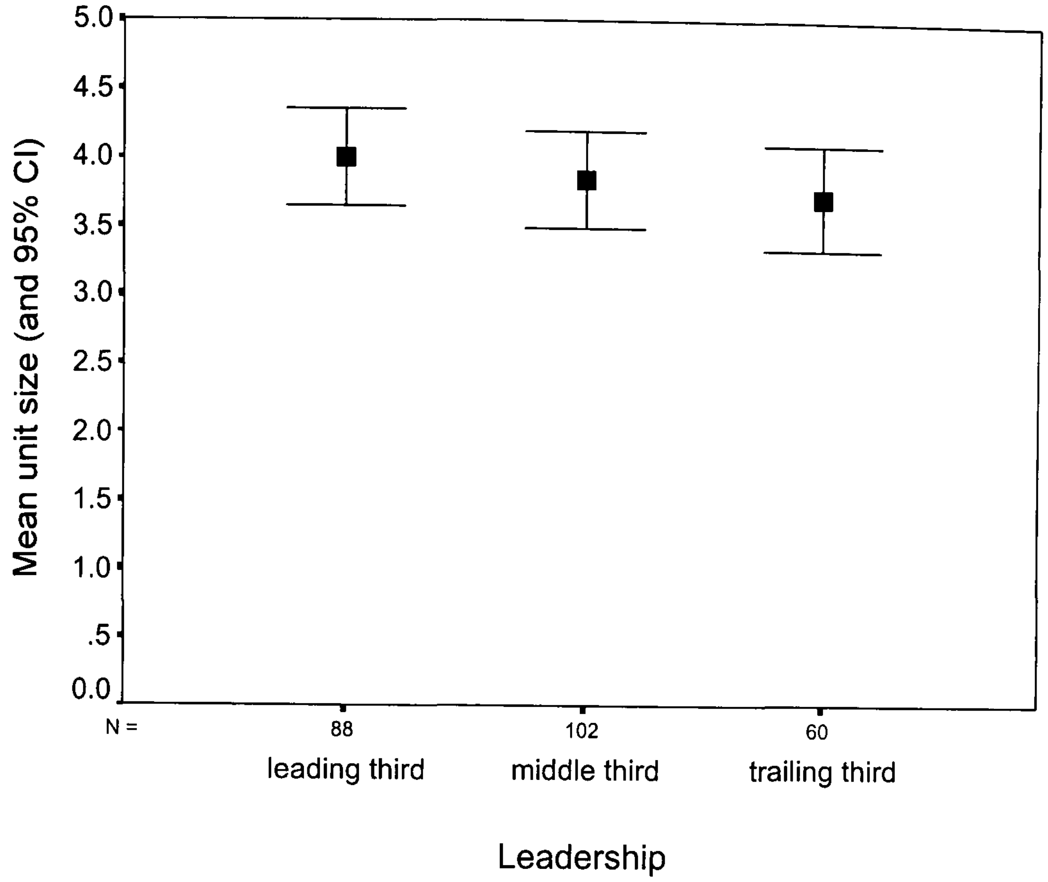


Figure 6.17 *The mean number (and 95% CI) of adult females in units recorded in the leading, middle and trailing zones of the herd. See Figure 6.16, for diagrammatic representation.*

6.4.2 Unit position and centrality

The mean distance travelled by gelada in a day is relatively short compared with other terrestrial primates (see section 6.3.1) and herd movement is commonly slow, steady and a secondary artefact of small individual foraging movements. Therefore, another perspective from which to examine the location of units within the foraging herd is their position in reference to the centre or edge of the group. For reasons outlined in the introduction of this chapter, it is assumed that a central position may be more favourable in terms of lowering individual exposure to predation risk, while size of a unit might predict its ability to maintain a more desirable central position within the herd.

The mean sizes of the units recorded in three concentric zones (central, middle/outer and extreme edge; see diagram, Figure 3.1) of the herd are displayed in Figure 6.18. Although the mean size of units did not vary significantly in relation to their proximity to the edge of the herd (**ANOVA**: $F_{(6,249)} = 1.950$, $p = 0.074$) the p value approaches significance and warrants further examination. When the central and middle zones are pooled, the units at the extreme outer edge of the herd are significantly smaller than units not on the edge (**Mann Whitney U**: $Z = -3.374$, $n = 250$, $p < 0.01$).

In line with the third prediction, it may be that larger units dominate more central foraging positions as this affords them greater access to prime feeding patches (Rutberg, 1986; Harcourt, 1987). If this were the case, we might expect the pattern of smaller units being located on the periphery of the herd to be more prominent in periods or habitats in which the distribution of food was most clumped. It is not possible to test this directly as the positional data presented here were collected in October and November 2000, while ecological data are only available for 1998. Nonetheless, the strength of the relationship between unit size and centrality is presented in Table 6.5, along with the appropriate measures of the evenness of food distribution (coefficient of variation, CV%, see section 5.2.1), and a measure of habitat-specific predation risk, namely the percent of visibility under 10 metres distance.

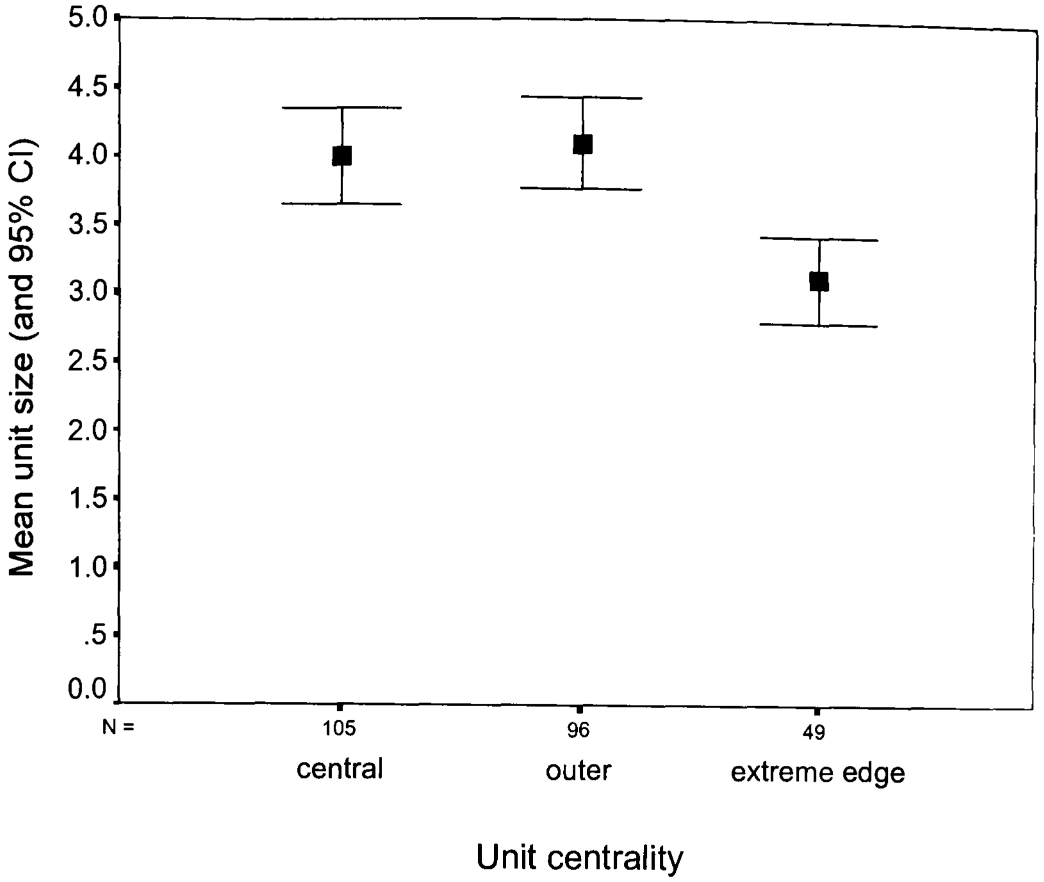


Figure 6.18 *The mean number (and 95% CI) of adult females in units recorded in the central, outer and extreme edge zones of the herd. See Figure 6.16, for diagrammatic representation.*

Table 6.5 *The strength of the relationship between unit size and centrality in each habitat type (data collected in Oct/Nov 2000), the coefficient of variance (CV%) of green cover in the corresponding months in 1998 and the percent of visibility under 10 m each habitat type.*

Habitat	CV (%) green cover; Oct/Nov. (*from Figure 6.1*)	% visibility under 10 m (*from Table 5.1*)	Smaller unit size at edge (**Mann Whitney** U test) Z	p	cases (N)
E-heather	18.5	37.5	-0.461	0.717	19
P-open	38	4.5	-2.419	**0.016***	159
P-bushy	85	92.3	0.697	0.735	31
G-open	42.5	3.2	-1.167	0.286	23
G-bushy	-	51.5	-1.031	0.616	18
Total/mean	42.7	29.8	3.374	**0.001****	250

A bivariate correlation between the strength of the above relationship (Mann Whitney test p values for unit size at edge vs. unit size not at edge) and the coefficient of variation of green cover in each habitat type was not found to be significant ($r = 0.381$, $n = 4$, $p = 0.527$). However, the key feature of Table 6.5 is that significantly smaller units were only found at the edge when the herd was in their primary foraging area, P-open, and no other habitat type, lending support to the hypothesis that patterns of unit positioning might be based in a context of foraging profitability.

As outlined in the introduction, the alternative hypothesis to explain the results in Figure 6.17 is that if larger units are occupying central positions within the herd to lower their risk of predation relative to more peripheral units, then the level of visibility within a habitat, as a measure of predation risk, might predict the strength of the relationship. As the herd moves into habitats with higher levels of visibility under 10 metres (found to be a significant predictor of the rate of alarm responses, see Chapter 7, section 7.5) the competitive advantage to units maintaining a central position might increase. However, not only is the correlation not significant ($r = -0.856$, $n = 5$, $p = 0.064$) but the trend is in the opposite direction to what might be expected. Indeed, given that the effect of unit size on edge location does not materialize in 4 out of 5 habitat types, it is impossible at this stage to draw any clear conclusions on the environmental factors influencing it. Nonetheless, the present analyses do suggest that the size of a unit might affect its ability to avoid extreme edge locations within a herd, and that this pattern is most pronounced when gelada are in their key feeding habitats.

6.5 Discussion

The current chapter has focused on testing a number of predictions based on inter-unit levels of association within the gelada social system and some of the possible factors affecting herd dynamics and ranging behaviour. In section 6.2.1 the highly flexible nature of gelada group size was highlighted by the large variation in herd size observed within and between months. Crook (1966) originally hypothesised that the tendency for gelada herds to vary so greatly in size was an adaptation to a seasonal deficiency in food resources, and supported this by pointing out that larger gelada herds were more common at Amba Ras (Crook's fieldsite, see map, Figure 2.1) in the wet season than dry season. In line with Crook's (1966) original report, gelada herds in the current study at Sankaber were significantly larger in the wet season than in the dry season. Furthermore, mean monthly group size was positively correlated to both monthly rainfall and levels of green vegetation cover (section 6.2.4), suggesting that more verdant conditions allowed gelada to form larger herds.

Lower levels of food availability are also thought to exert a positive influence on day journey length, since a group of animals will be forced to travel further to obtain the same amount of food per individual (Davidge, 1978; Stacey, 1986). Again, in agreement with Crook's (1966) proposition that the dry season offered sparser levels of food for the gelada, the mean daily travel distance per month in the current study was significantly longer in the dry season than in the wet season (section 6.2.2), and found to be negatively correlated to monthly rainfall. This seems to support Crook's (1966) hypothesis that reduced gelada herd size was a response to periods of diminished dry-season foraging opportunities. However, a more detailed analyses indicated that the patterns in which these factors are related might not be so straightforward. Firstly, the aforementioned trend for mean monthly group size to be positively correlated to rainfall, while mean monthly day journey length is *negatively* correlated to rainfall, appears to contradict the commonly cited positive effect that primate group size has on day journey length (see Waser, 1977; Sharman & Dunbar, 1982). However, when these data were examined on a daily basis, group size and day journey length were indeed found to be significantly positively correlated (section 6.2.3). Although this correlation was true for days in both wet and dry seasons, the relationship was weaker in the wet season and further analyses revealed that group size was not correlated to day journey length in 5 months; 4 of those being in the wet season. This result suggests that the actual number of gelada in the dry season herd places greater pressure on an individual's foraging returns and therefore has a more direct influence on the distance the herd needs to travel during a dry season day, thus providing strong evidence in support of the first prediction of this chapter. These results also highlight the fact that the relationship between group size and day journey length may vary depending on the temporal scale upon which it is analysed.

Although it appears that the size of a gelada herd exerts a far stronger influence on daily travel distance in dry season months than wet season months, the strength of the relationship was not found to correlate with monthly rainfall. Instead, the results suggest that the relationship between group size and day journey length is dependant on levels of food availability (section 6.2.4.2), an important caveat being that if the amount of food available to the gelada reaches a certain threshold, group size might no longer constitute a key determinant of day journey length.

Although seasonal fluctuations in food resources might be a key factor influencing seasonal variation in group size, it does not explain why group size was found to vary greatly within months. This variation is effected by high rates of groups joining and splitting from the main study band on a daily basis (section 6.3). Therefore, the theory that the fission-fusion nature of gelada society is an adaptation to seasonal levels of food availability only offers an explanation on a crude temporal scale and factors affecting fission-fusion need to be examined on a much finer temporal scale (e.g. within months). Therefore, spatial constraints on fission-fusion were also investigated, although it was pointed out in section 6.3.1 that the rate at which the main band underwent fission or fusion could not be predicted by at least two measures of overall food availability; namely rainfall and mean levels of green forage cover. Instead, it appears that the amount of group fission and fusion is driven not by food availability *per se*, but by the degree to which that food is distributed unevenly. Thus, variation in food availability does appear to underpin the rate at which the main group undergoes fission-fusion, thereby substantiating the second prediction of the introduction. However, the confirmation of this hypothesis carries the important twist that the nature of the effect is not via overall levels of green food cover but by the patchiness of their distribution.

The third hypothesis to be tested in this chapter was that relating to the position of units of different size within the foraging herd. It was suggested that the physical position of a unit within the herd might convey costs or benefits with regards to access to prime feeding spots or exposure to predation risk. Also, competitive differentials between units (based on the size of the unit) might determine access to more favourable locations within the herd. Smaller (and presumably less dominant) units were significantly more likely to be found on the outer periphery of the herd, suggesting an advantage might exist to maintaining a more central position within the herd. Although, very little could be concluded from the limited data presented in section 6.4, the unit-position patterns outlined above were found to be specific to the gelada's main feeding habitat type, and no other, thus providing tentative support for the hypothesis that it is a spatial foraging advantage and not predation avoidance that is driving the pattern for smaller units to be peripheral.

CHAPTER SEVEN

Predation Risk and Alarm Responses

7.1 Introduction

In the previous chapters, the distribution of food resources, different habitat types, and some climatic and physical features were found to influence the foraging and ranging patterns displayed by gelada. However, as discussed in the introductory chapter, the foraging patterns of a primate may be concurrently shaped by a trade-off with the need to maintain the risk of predation at acceptably low levels (Houston *et al.*, 1993; Cowlishaw, 1997a). Hence, while the foraging aspects of gelada behavioural ecology constitute the central theme of the thesis, this chapter will shift focus to examine certain facets of the predation risk as faced by gelada at Sankaber.

Since predation pressure is generally assumed to exert strong selective pressure on the grouping behaviour of primates (Alexander, 1974; van Schaik, 1983; Terborgh, 1983; Terborgh & Janson, 1986; Dunbar, 1988; Hill & Lee, 1998; Janson, 1998), individual animals are expected to be sensitive to the risk of predation and adjust their behaviours accordingly. It has been proposed that gelada graze in such large herds as a response to predation pressure (Dunbar & Dunbar, 1975), although this hypothesis has never been examined in detail and does not account for the massive variation in group size observed even within a single band. Kawai and Iwamoto (1979) noted that larger gelada herds were more willing to forage further from the cliff refuges than smaller groups, but the increased foraging needs of larger groups may be a confounding factor here (see Chapter 6). Nonetheless, variation in habitat structure has been shown to be an important factor in determining different levels of predation risk for other species (Cowlishaw, 1994, 1997 a,b; Iwamoto *et al.* 1996) and therefore warrants consideration in the current study.

While previous research on predation avoidance has primarily focused on variation in the use of forest canopy by aboreal species (e.g. Robinson, 1981; de Ruiter, 1986), less is known about how predation risk affects the ranging patterns of terrestrial primates. Cowlishaw (1997a) found that desert baboons (*Papio cynocephalus ursinus*) at Tsaobis, Namibia, tended to avoid low-visibility, high-risk habitats except when feeding on plants specific to that habitat. Most other activity and movement was conducted in more open habitats in which it was suggested the risk of predation was mitigated by higher levels of visibility. In the same study, Cowlishaw (1997a) found that group size affected habitat use, in that larger groups were more likely to occupy the higher risk, lower visibility habitats. Cowlishaw (1993) also presented models to suggest that the degree of vegetation cover was the most important factor influencing the risk of predation attack. More specifically, Altmann & Altmann (1970) found that savannah baboons at Amboseli were more frequently attacked by predators and gave more alarm barks when in areas of denser vegetation in their home range.

Although ecological data on primate predators is scarce (Boinski & Chapman, 1985), leopards are considered the main predator of *Papio spp.* baboons (Cowlishaw, 1994).

Since leopards attack from ambush (Bertram, 1982; du Bothma & Le Riche, 1986) the probability of attack has been linked to the proportion of immediate visibility that falls below 10m – the critical attack distance for leopards (Kruuk & Turner, 1967; Schaller, 1972; Bertram, 1982). Hill (1999) also suggested that the degree of bush level cover was an important determinant of predation risk and the probability of attack across habitats. However, Byrne (1981) found that baboons might also be more nervous in exposed areas where they are far from large trees or suitable refuges. Also, researchers studying mandrills (*Mandrillus sphinx*) have noted the extremely large groups formed by the animals when crossing open expanses of grassland between areas of dense primary rainforest, suggesting this phenomenon is directly related to the increased risk of predation in these exposed areas (Hoshino, 1985). Therefore, a suggested compromise between these conflicting patterns is that predation risk may be positively correlated to the density of low-level vegetation from which ambush predators can attack, whilst negatively correlated to the density of large trees or appropriate refuges (see Dunbar, 1996). This is an important consideration with regards to gelada as their environment is considered open and exposed relative to most *Papio* baboon habitats and large trees are unavailable and therefore irrelevant to gelada as refuges. Instead, in response to danger gelada only flea directly to and over the escarpment edge, highlighting the importance of the location of the cliff edge in their day ranging patterns.

Despite the body of literature on predation risk outlined above, predator-prey relationships remain poorly understood, actual predation is rarely observed (Cheney & Wrangham, 1897; Isbell, 1994; Cowlishaw, 1997a), and many studies on predation risk are forced to rely on modelling techniques (Cowlishaw, 1993; Hill, 1999). While assuming that predation does exist in the present study it is important to recognise the difference between predation *rate*, which in itself is difficult to ascertain, and predation *risk*. These are fundamentally different concepts, as pointed out by Hill & Dunbar (1998), who describe predation rate as, "the level of successful predator attacks that the animals are unable to control *after* they have implemented their antipredation strategies". Predation risk on the other hand, represents the prey animals' perceived susceptibility to attack by a predator, and has been considered by Endler (1991) to consist of four key component probabilities; (i) Predator encounter, (ii) Predator attack, (iii) Prey capture, and (iv) Individual capture probability. Although a detailed examination of the dynamics of predation risk facing gelada was beyond the scope of the current study, rates of predator encounter (i above) are not considered insignificant at Sankaber, and habitat-specific levels of visibility directly affect the probability of predation attack (ii above). Furthermore, the probability of individual prey capture (iv above) is a direct function of group size (Hamilton, 1971), a parameter of gelada socioecology already examined in some detail in Chapter 6. In light of this, I will briefly investigate one aspect of the anti-predator behaviour exhibited by gelada, namely their flight response. Assuming that the rate of alarm response exhibited by the main gelada study group provides some measure of their perceived levels of threat, it is predicted that;

1) Flight responses will be positively correlated to distance from the nearest refuge but negatively correlated with mean visibility.

2) Real predators will provoke a significantly greater proportion of the group into a full flight response, and the gelada will flee significantly further, than in response to alarm caused by other stimuli.

3) In order to test the hypothesis that ambush predators (such as jackals and leopards) represent the main threat to gelada at Sankaber, it is predicted that levels of visibility under 10m will be a stronger determinant of flight response than overall mean levels of visibility.

Section 7.2 will examine the levels of visibility experienced by gelada in different habitat types along with the distance gelada range from safe refuges. Section 7.3 will provide a description of the response gelada groups exhibit when encountering different threat stimuli, whether real or perceived, before section 7.4 will examine these alarm responses in more detail. Primarily, the cause of the alarm will be related to the distance fled and the size and proportion of the gelada group responding. Finally, in section 7.5, the effect of visibility levels in different habitat types will be examined in relation to the alarm responses shown by the main study group.

7.2 Habitat characteristics

7.2.1 Habitat-specific visibility

Although gelada are considered to inhabit one of the most open and treeless environments of any primate species (Crook, 1966; Napier & Napier, 1967), certain areas at the Sankaber field site, such as the P-bushy and G-bushy habitat types, include areas of thick low-level vegetation. Visibility at gelada eye-level was recorded within each habitat (see Chapter 3, section 3.4, for methodology), and the mean visibility levels for different habitat types are shown in Table 7.1. The E-cliff quadrats were excluded due to their inaccessible nature, but visibility in this habitat type is assumed to be of little relevance as the cliff quadrats, almost by definition, constitute a complete and unambiguous refuge from predators. Cleary, the cultivated fields and 'open' areas of the gorge and plateau offer high levels of visibility, while the 'bushy' component of the gorge and especially the plateau represent areas of relatively very low visibility.

Table 7.1 *Mean (and standard deviation) visibility distances within each habitat type, and the proportion of visibility under 10 metres.*

HABITAT	mean visibility (m)	sd	vis <10m (%)	N
Escarpment - cliff	-	-	-	34
Escarpment - heather	12.55	(4.36)	37.5	56
Plateau – open	66.95	(41.20)	4.5	50
Plateau – bushy	4.46	(2.90)	92.3	15
Gorge – open	45.68	(29.75)	3.2	31
Gorge – bushy	9.94	(4.51)	51.5	33
Fields	93.38	(35.68)	0	13

In over 51% of G-bushy quadrats, and over 92% of P-bushy quadrats, the mean visibility fell below the 10m distance considered critical to the risk of attack by leopards (Bertram, 1982; Cowlishaw, 1993).

7.2.2 Distance from refuges

Although it is assumed that high levels of visibility are advantageous to the gelada in detecting and avoiding predators, the advantage might be reduced if the animals are a relatively long way from any form of cliff refuge (as noted earlier, the gelada at Sankaber have no other form of refuge other than cliffs). Although no relationship was found between the use of a quadrat and its distance to the nearest refuge (section 4.2), the use of a quadrat was shown to correlate negatively with its distance from the nearest sleeping site in a number of habitats, including the most used habitat type, P-open. The mean distance of quadrats (in each habitat type) from the nearest refuge is shown in Figure 7.1.

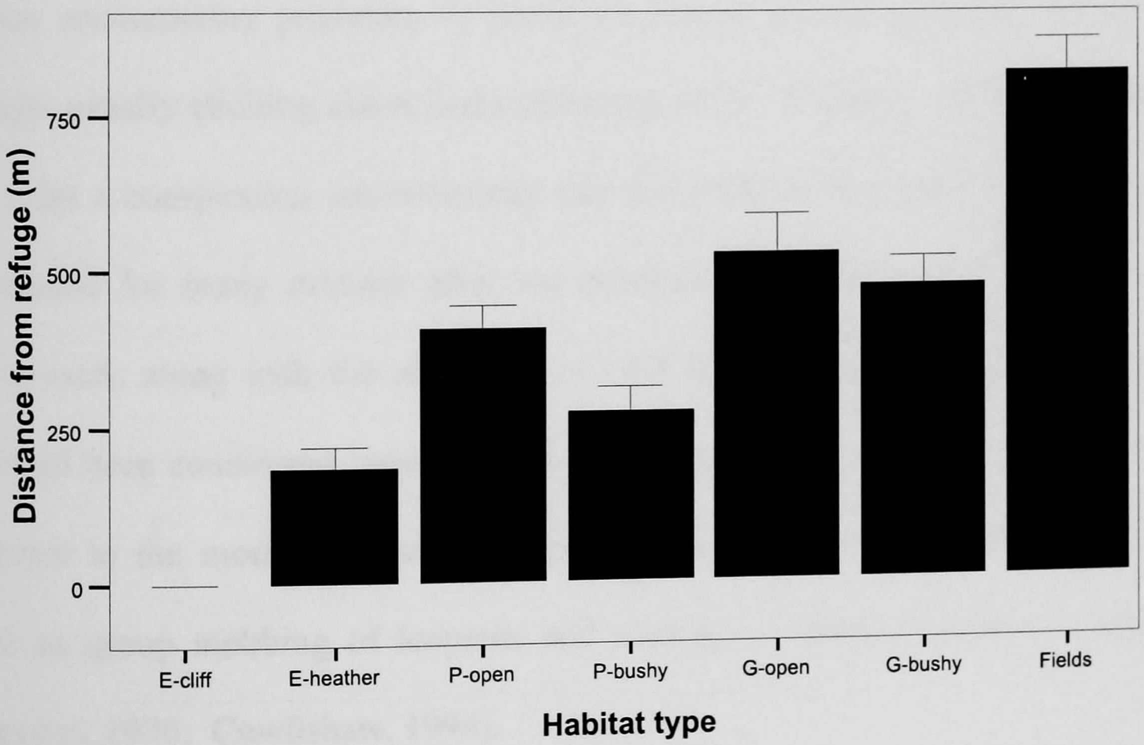


Figure 7.1 *Mean (and standard error) distance of quadrats in each habitat type from nearest cliff refuge.*

The mean distance of each quadrat from the nearest refuge varied significantly between habitat types (**ANOVA**: $F_{(6,231)} = 32.92$, $p < 0.01$), and although visibility levels were high throughout the Field habitat-type, post hoc analyses reveal that Field quadrats were significantly further away from the nearest refuge than quadrats in all other habitat types (Tukey; $p < 0.01$ in all cases). Obviously, as all cliff quadrats represent a refuge, the distance is taken as zero, and accordingly the above results vary little when these quadrats are excluded from the analyses (**ANOVA**: $F_{(5,197)} = 21.19$, $p < 0.01$).

7.3 Anti-predator behaviour

When encountering predators or perceived threats gelada typically flee towards a refuge, usually eliciting alarm barks (Ohsawa, 1979; Iwamoto, 1993). Alarm calling provides a conspicuous advertisement that the predator has been detected, and often continued for many minutes after the predator had disappeared from site. Such behaviours, along with the utilisation of cliff refuges and the large foraging herds, have all been considered 'passive' anti-predator strategies (Iwamoto, *et al.*, 1996), in contrast to the more aggressive anti-predator behaviours found in *Papio* baboons, such as group mobbing of leopards and chasing of smaller predators (Altmann & Altmann, 1970; Cowlishaw, 1994).

A number of predator species are present at Sankaber, and although little is known of their relative densities, strong evidence was presented in Chapter 2 (section 2.1.4) to suggest that at least three species (hyena, jackal and leopard) predate on gelada at the current field site. After leopards, hyena are considered the second most common predator of *Papio* baboons (Cowlishaw, 1994), and spotted hyena (*Crocuta crocuta*) exist at very high densities throughout the gelada's geographical distribution in the Ethiopian highlands (Kingdon, 1997). Hyena hunt primarily between dusk and dawn, highlighting the importance of the sheer cliff sleeping sites to gelada, and predation by hyena is probably restricted to individual gelada who are injured or sick and thereby unable to descend to the sleeping sites overnight.

On four occasions during daylight hours jackals were observed to make ambush attacks on the gelada. Typically, a pair of jackals was observed ambushing gelada from a short distance and chasing the herd over 30 metres, before the jackals were repelled when adult male geladas turned on them abruptly at a distance of approximately 5 metres. On one occasion a leopard was observed stalking the gelada herd, although none of these cases resulted in actual prey capture. In fact, the aggressive response shown by the gelada, especially adult males (see 2.1.4) in the current field study, differs markedly from the 'passive' behaviour described by Ohsawa (1979), and instead confers with the anecdotal accounts of gelada 'systematically mobbing' a leopard, as described by Iwamoto *et al.* (1996). This is an important observation in that the overall size of the foraging herd will have a direct impact not only on the ability to detect predators early but on the ability of the group to form a proactive, defensive coalition, especially as more adult males are present (see also, Busse, 1977; van Schaik & van Noordwijk, 1989, Boesch, 1991).

7.4 Alarm responses

On 89 full days spread across 6 months (Feb-Jun 1998, Oct-Nov 1998, and Jan 1999), all flights or alarms in response to threats or perceived threats were noted, including the cause (if known), location, group size, percent of group dislocated and distance dislocated. In total, 151 incidents were recorded, giving a mean rate of 1.66 flights (or 'scares') per day, in which the gelada fled a mean distance of 47.9m (sd = 71.7m, range: 0-700m). In almost all cases the flight involved some or all of the individuals in the herd suddenly running away from the source of the perceived 'threat'. Just over 29% of flights involved the entire herd (i.e. 100% of the individuals present), while on average 64.1% (sd = 32.1, range 0-100%) of the herd engaged in the flight response (when discussing percent of group showing flight response, '0%' represents cases of alarm call only, i.e. no movement). In 5.2% of cases the gelada elicited alarm calls but remained where they were. On two such occasions a low-flying bird of prey triggered a sudden crouching response from many of the gelada under its flight path. It should also be noted that on a number of occasions, what appeared to be alarm calls were given in response to the first detection of another gelada herd. While technically any 'alarm' call or response was recorded, these instances are omitted from the current data set as it assumed the gelada are responding to a fundamentally different stimulus.

7.4.1 Cause of alarm responses

The gelada showed an alarm response to a wide variety of different stimuli (19 were identified). These ranged from an aggressive ambush by predators and being chased by stone-throwing shepherd boys, to being startled into flight by thunder or even a low flying flock of rock martins (*Hirundo fuligula*).

Although 20 different stimuli of flight were recorded, these could be grouped into five broad categories: 1) Humans (passive or aggressive), 2) Other species' alarm responses (bushbuck, klipspringer, Francolins, Hamadryas baboons, Wattled Ibis), 3) Real predators (jackals, dogs, leopard, birds of prey), 4) Startled response (horses, thunder, fog, flocks of small birds and rock hyrax), and 5) unknown. The data are summarised in Table 7.2.

Table 7.2 *Alarm responses grouped by category of stimulus; showing the mean percent and size of the herd dislocated, and the mean distance of the flight.*

	Alarm response						
Alarm stimulus	Mean percent of group moved	sd	Mean group size	sd	Mean flight distance	sd	**N**
Humans	69.9	(28.7)	235.2	(83.4)	41.7	(29.4)	72
Other prey alarms	65.4	(34.5)	189.0	(96.4)	34.7	(40.8)	27
Predators	56.3	(37.7)	249.6	(74.8)	102.3	(147.9)	21
Startle-stimuli	70.0	(36.9)	210.0	(47.8)	24.5	(38.5)	6
unknown	50.0	(31.0)	306.4	(94.3)	52.5	(105.7)	25
TOTAL	64.4	(32.1)	237.2	(90.1)	47.9	(71.7)	151

7.4.2 Flight distances

There was significant variation in the distance fled by gelada in response to the different stimuli categories (**ANOVA**: $F_{(4,130)} = 4.957$, $p < 0.05$), with post hoc analyses revealing that all variation existed between the distance fled in response to 'real predators' (mean = 102.3m, sd = 147.9, n = 21) and the distance fled in response to all other stimuli categories (mean = 49.9, sd = 70.1, n = 128) (Tukey, $p < 0.05$ in all cases). The mean distances fled in response to different stimuli are shown in Figure 7.2.

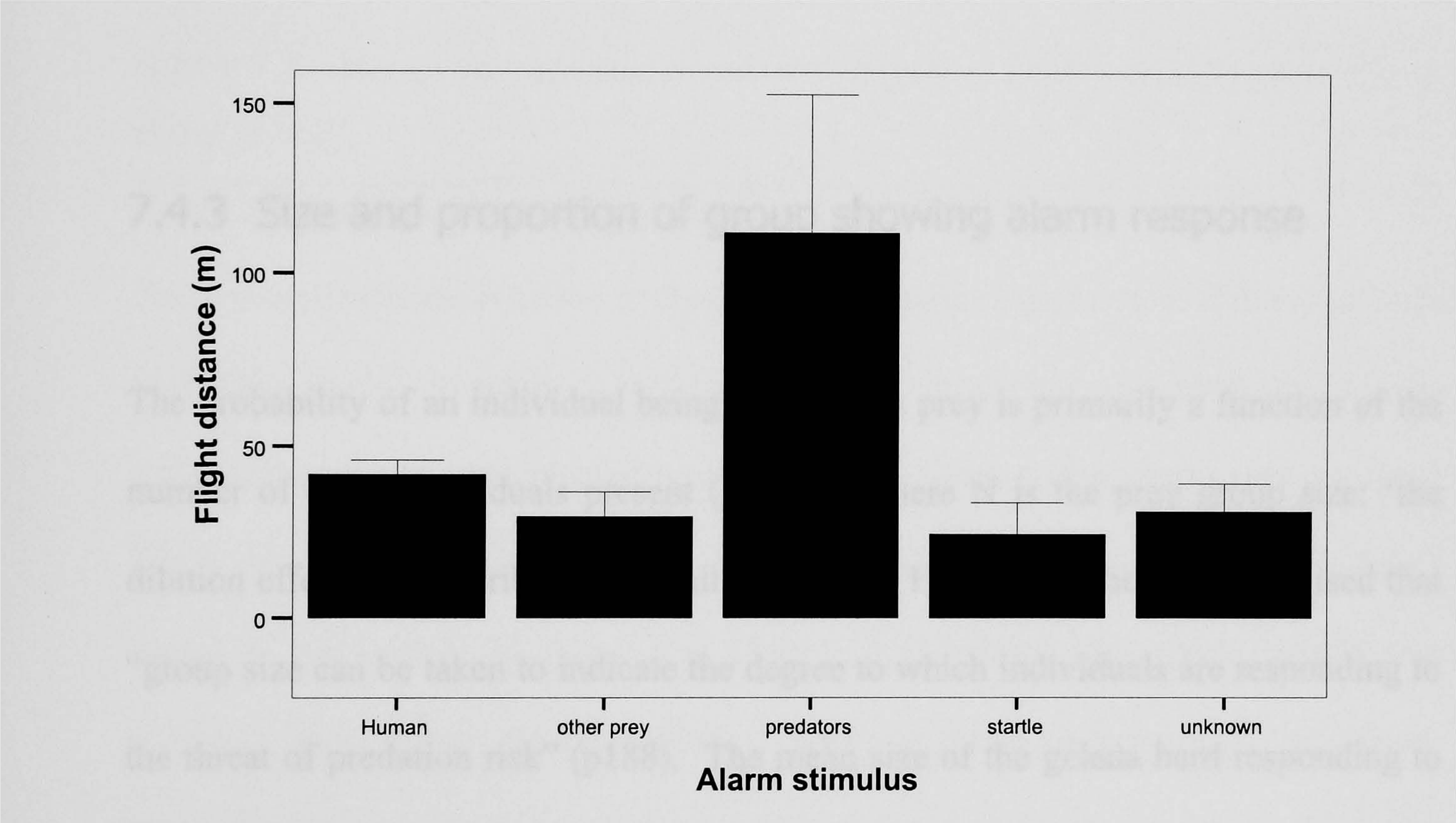


Figure 7.2 *Mean (and standard error) flight distance in response to different alarm stimuli.*

Although it is clear that an encounter with a real potential predator dislocates the gelada herd significantly more on average than other stimuli, the relatively large error bar associated with the mean suggests large variation in flight distance in response to predators, and it is important to note that not all encounters with predators lead to large dislocations of the herd. During six of the 21 encounters with predators (28.6%) the gelada did not move at all, and on those occasions when jackals or dogs were either detected early or moving through high-visibility areas, the gelada would often do little more than alarm bark, suggesting that jackals pose little threat other than as a short range ambush predator. In contrast, on the four occasions when jackals were observed to ambush and run at the gelada at high speed, the mean flight distance was 247.5m (sd = 176.9). Furthermore, the single encounter with an active leopard in the gorge led to the group rapidly moving 700m, the largest single distance gelada were observed dislocated during any of the recorded alarm responses.

7.4.3 Size and proportion of group showing alarm response

The probability of an individual being captured as prey is primarily a function of the number of other individuals present (i.e. 1/N, where N is the prey group size: 'the dilution effect', as described by Hamilton, 1971). Hill (1999) therefore surmised that "group size can be taken to indicate the degree to which individuals are responding to the threat of predation risk" (p188). The mean size of the gelada herd responding to each category of alarm stimuli is displayed in Figure 7.3.

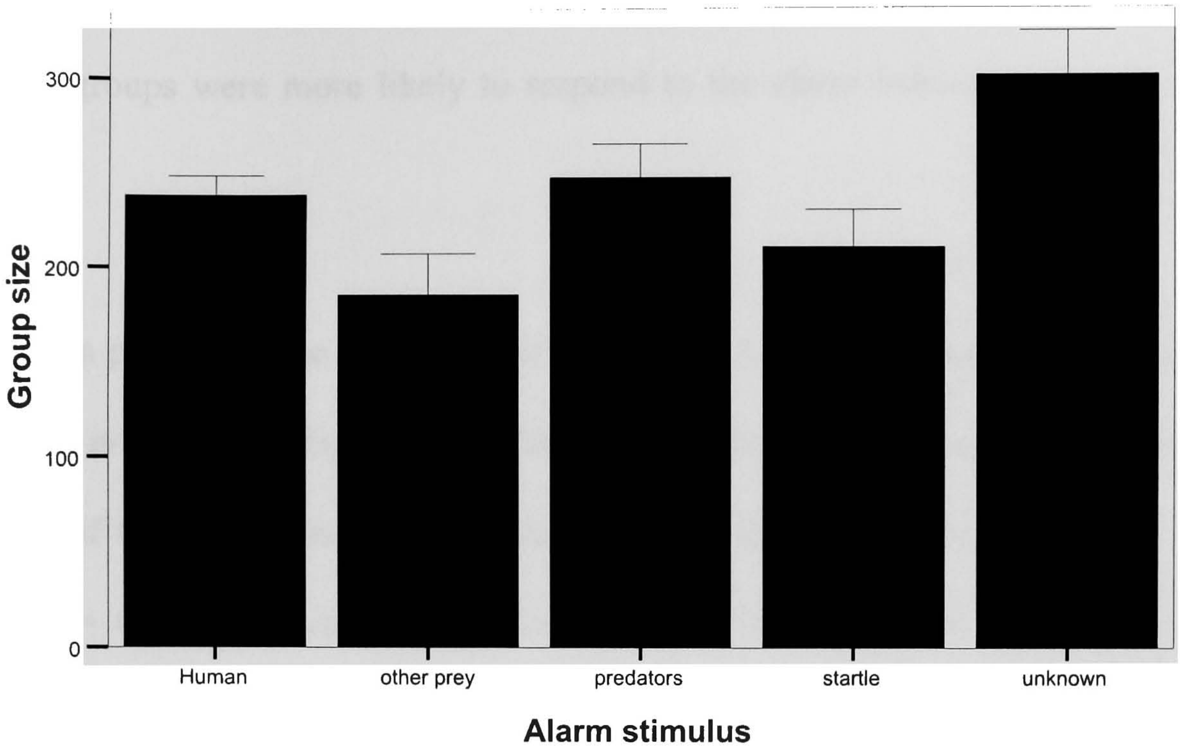


Figure 7.3 *Mean (and standard error) size of gelada herd responding to different alarm stimuli.*

There was significant variation in the size of the group responding to different stimuli (**ANOVA**: $F_{(4,126)} = 4.854$, $p < 0.01$), with all variation being explained by the difference in group sizes responding to 'other prey species alarm responses' (mean = 189.0, sd = 96.4, n = 23) and the size of groups responding to 'unknown' stimuli (mean = 306.4, sd = 94.3, n = 24) (Tukey, $p < 0.05$). This result suggest that relatively larger groups are more likely to show an alarm response to an 'unknown' stimulus, while relatively smaller groups were more likely to respond to the alarm behaviour or call of other species. In the first scenario, an individual gelada might be more likely (simply due to the sheer numbers in larger herds) to respond to the alarm behaviour of others around them rather than the stimulus itself, thus leading to 'false alarms'. Conversely, smaller groups might be more attuned to the threat detection of sympatric species, either because they are noticed more easily or because the gelada are more nervous in smaller groups. This result suggest that relatively larger groups are more likely to show an alarm response to an 'unknown' stimulus, while relatively smaller groups were more likely to respond to the alarm behaviour or call of other species.

The mean percent of the group that actually moved rapidly in response to each alarm category is shown in Figure 7.4. While there was no significant difference in the percent of the group dislocated by the different alarm stimuli (**ANOVA**: $F_{(4,130)} = 2.07$, $p = 0.088$) the variance approaches significance largely due to the smaller relative proportion of the herd responding to an 'unknown' stimulus. This might be explained by the fact that individuals on the far side of a herd, especially if the herd is well spread, are less likely to be roused into flight unless the real cause of the alarm becomes apparent. However, this line of reasoning is problematic simply because an alarm stimuli recorded by an observer as 'unknown' is not necessarily 'unknown' to the gelada.

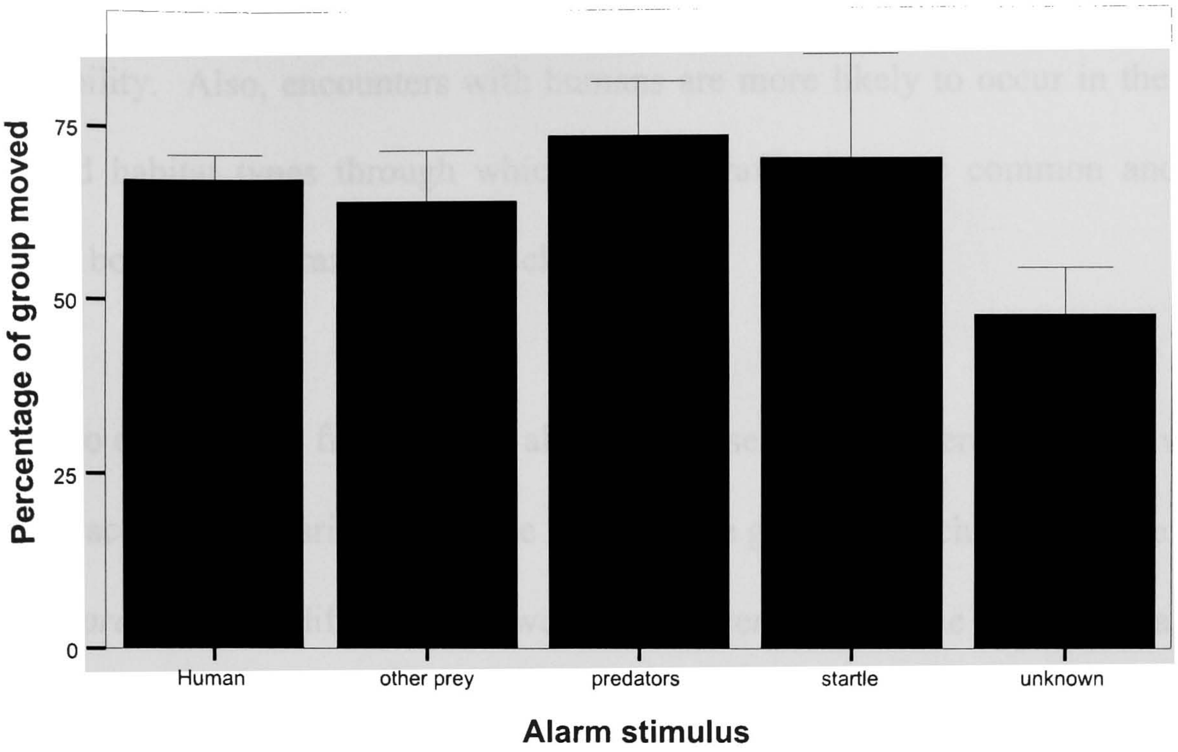


Figure 7.4 *Mean (and standard error) percentage of the gelada herd moving in flight response to different alarm stimuli categories.*

7.4.4 Habitat-specific alarm responses

The above analyses focus on variation in the alarm responses shown by the gelada to different causes of perceived threat, real or otherwise. However, the degree or frequency of responses shown to a particular stimulus might be confounded by the habitat in which the 'threat' is encountered. Although it is impossible to ascertain the density of specific predators or threats within each habitat type it is possible to examine variation in the stimuli of gelada alarm responses on a habitat by habitat basis. Although no significant difference was found in the habitat type in which different stimuli were encountered (**ANOVA**: $F_{(5,140)} = 2.147$, $p < 0.064$), this relationship approaches significance and warrants further investigation. As some of the most important predators of gelada, such as leopard and jackal, rely on ambush, one might expect encounters with ambush species to be higher in habitats of relatively low visibility. Also, encounters with humans are more likely to occur in the P-open and Field habitat types through which human traffic is more common and where shepherd boys attend grazing liverstock.

In order to examine the frequency of alarm responses in the different habitats we must take into account the variation in time spent by the gelada in each habitat type. To do this, the *proportional* difference between the percentage of time occupying a habitat type and the percentage of alarm responses within that habitat was calculated (as per the Electivity Index presented in Chapter 4, section 4.3). The Index varies between +1 (strongly selected) and –1 (strongly avoided), and was calculated on the basis of the following formula:

$$\mathrm{AI} = \frac{(h_i - p_i)}{(h_i + p_i)}$$

where AI is the Alarm index, h_i, is the observed proportion of all alarms occurring in habitat i, and p_i, is the relative proportion of time the gelada spent in habitat i. The Alarm indices for each habitat type are displayed in Figure 7.5. Clearly the gelada are displaying more alarm responses in certain habitats than would be expected given the amount of the time they spend there. This is especially pronounced in the P-bushy and G-bushy habitats where the gelada experience low levels of visibility.

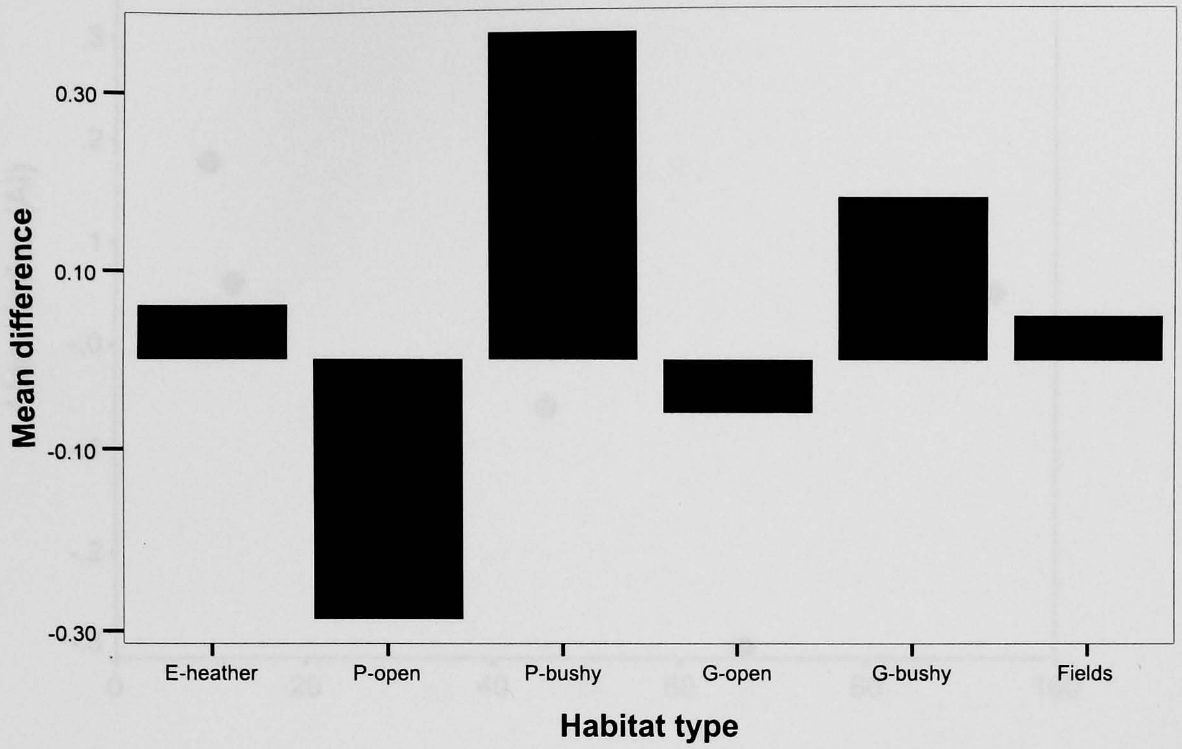


Figure 7.5 *Alarm index for each habitat type based on the proportion of time spent in that habitat.*

7.5 The effect of visibility on alarm rates

Given the striking variation in alarm response rate shown between habitats (Figure 7.5), and the variation in visibility described between habitats (section 7.2.1), we might predict that the frequency of alarm responses shown by gelada within a habitat might be related to the level of visibility available to the gelada within that habitat type. The Alarm index for each habitat is plotted against the mean visibility of the corresponding habitat in Figure 7.6.

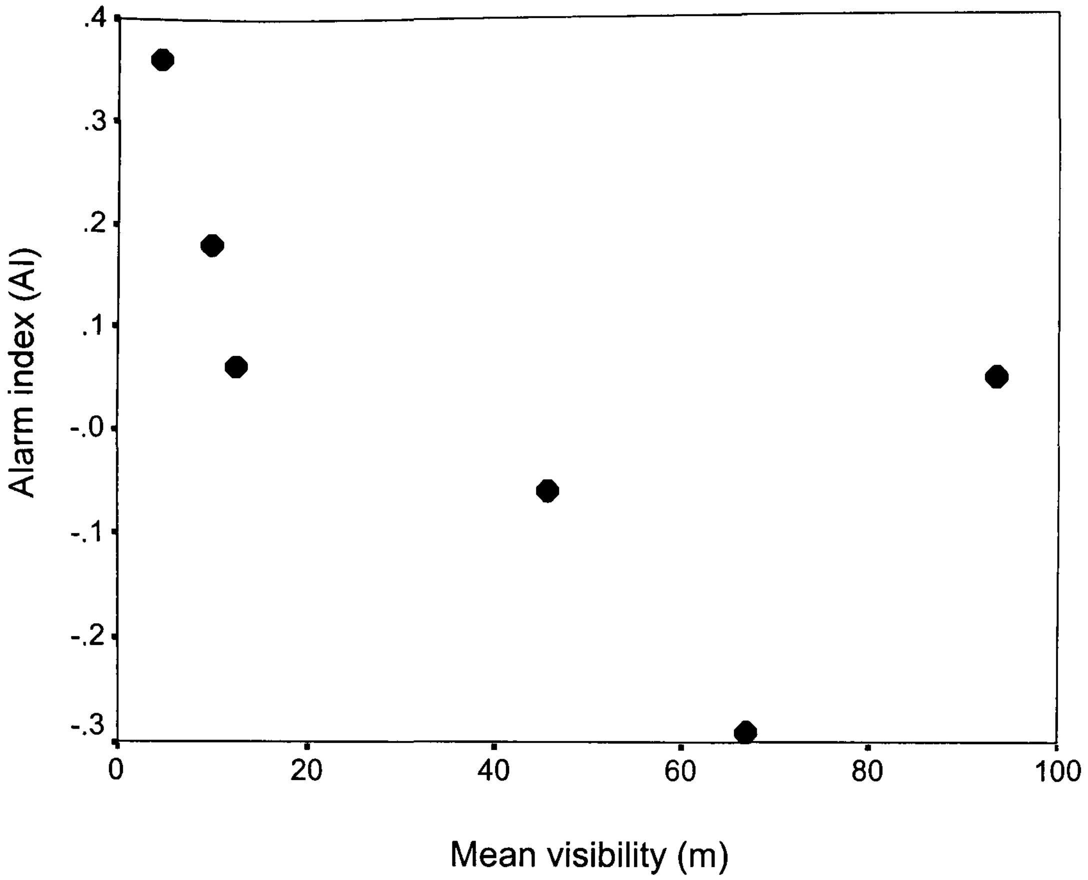


Figure 7.6 *Mean visibility (m) within each habitat type plotted against the relative alarm index (AI).*

While the relationship is not significant (r = -0.631, n = 6, p = 0.179), it is in the predicted negative direction suggesting that the gelada are showing a higher rate of alarm response when in areas of lower mean visibility. The mean distance of quadrats from cliff refuges within each habitat type was also not found to correlate significantly with the alarm index (r = -0.205, n = 6, p = 0.698). However, it is worth noting that when the gelada are in the habitat with the highest mean visibility, Fields (see outlying point in Figure 7.6), they are more likely to be chased or disturbed by humans until they are off the fields. As the anecdotal evidence suggests that geladas main serious threats might come from ambush predators, the percentage of visibility under ten metres within each habitat type is plotted against the Alarm index for that habitat in Figure 7.7

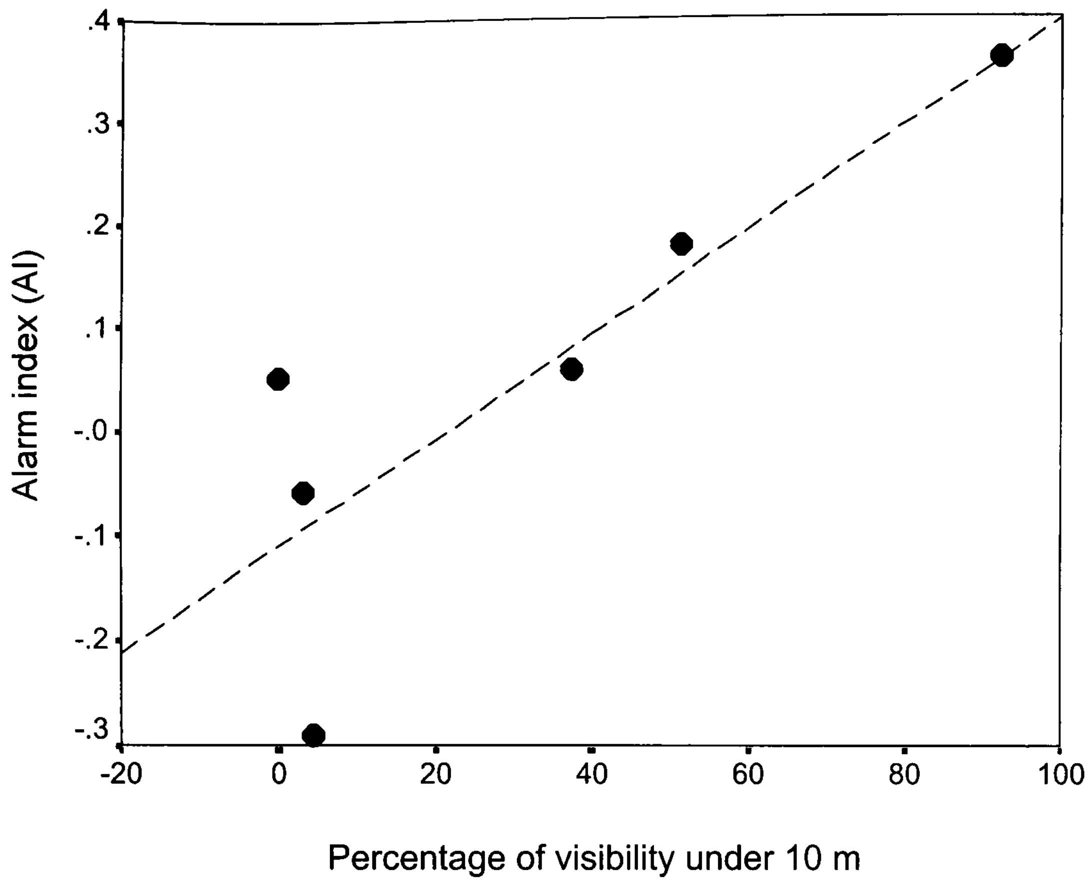


Figure 7.7 *The relationship between the relative alarm rate indices for each habitat and the percentage of visibility under ten metres within that habitat.*

The correlation is significant ($r = 0.844$, $n = 6$, $p < 0.05$), indicating that the gelada are stimulated into a flight response more often when in areas with higher relative levels of visibility under 10 metres. A partial correlation shows that this relationship is significant even when controlling for the mean distance from refuges ($\mathbf{r_{partial}} = 0.927$, $n = 6$, $p < 0.05$). It appears therefore, that the percentage of visibility under 10 metres is a stronger predictor of the rate of alarm responses than is the mean visibility of that habitat.

7.6 Discussion

The large foraging herds created by gelada are thought to be a response to the risk of predation (Crook, 1966; Dunbar & Dunbar, 1975; Kawai & Iwamoto, 1979), especially since the gelada's general habitat is considered to be open grassland with few refuges. However, it was shown in Chapter 4, and section 7.2 above, that the seven habitat types at Sankaber differ substantially in the both the mean levels of visibility at gelada eye level and the percent of visibility under 10 metres. In a series of papers, Cowlishaw (1994, 1997a,b) has suggested that lower levels of visibility raise the risk of predation significantly. In the current study, quadrats within the different habitat types also differ in their mean distance from cliff refuges, but this is primarily driven by the cultivated barley fields located on the edge of the gelada's home range furthest from the escarpment. Alarm rates were not found to correlate with the mean distance of quadrats (within each habitat type) from cliff refuges, which is contrary to prediction 1 of this chapter. However, a habitat-specific 'mean distance from cliff refuges' is a problematic measure and of little meaning given the mosaic pattern of habitat types (see map, Figure 2.3). In future, what is needed to accurately test the gelada's flight response against the their distance from genuine refuge is data on *quadrat*-specific alarm responses. Prediction 1 was also not upheld in that mean visibility levels of a habitat did not correlate to the alarm index calculated for that habitat type (Figure 7.6). However, the correlation approached significance and suggested that visibility might play a role in alarm responses once the influence of the man-made habitat (Fields) and the associated encounters with humans were removed from the analysis (see below).

Although it has been claimed that actual mortality due to predation is not important (Hill & Dunbar, 1998; Cowlishaw, 1998), little quantifiable data exist to test variation in predation risk. Nonetheless, anecdotal evidence discussed in section 7.3 (see also section 2.1.3, Chapter 2) suggests that gelada are preyed upon by hyena, leopard and jackal at the fieldsite. In fact, 21 gelada-predator encounters were observed over 89 days (a mean rate of 0.24/day) and predators were observed to attack the gelada herd a number of times during the current study. As described in section 7.3, the gelada's response to encounters with threats (or perceived threats) ranged from no individual moving but many eliciting alarm calls, to the entire herd being dislocated 700 metres.

On average, gelada fled significantly further when scared by real predators (including domestic dogs) than other causes of alarm, supporting the second prediction of this chapter. However, they also showed the greatest variation in flight distance when responding to predators compared with other stimuli (section 7.4.2). This is primarily due to the dichotomous nature of gelada-predator encounters. On the one hand, high visibility, large herds and early detection of prey often lead to mass alarm calling but minimal flight. On the other hand, a genuine ambush, especially in habitats of low visibility, typically caused the entire herd to flee a few hundred metres. Ohsawa (1979) described how gelada at Gich noticed jackals but their reaction was limited. Since they usually continued grazing even when the jackal approached within 50 metres, Ohsawa concluded that there was 'little or no predation pressure" on gelada at Gich (p111). However, as noted by Kingdon (1997) it is erroneous to ascribe an apparent complacency exhibited by prey or predator species as evidence for absence of predator-prey relationship. Furthermore, the Gich fieldsite is almost entirely short open grassland where few opportunities exist for ambush predators, whereas visibility at Sankaber has been shown in this chapter to vary greatly between habitat types.

One of the more common alarm stimuli, typically causing an immediate flight reaction from the gelada, was the very distinctive alarm bark elicited by nearby bushbuck (*Tragelaphus scriptus*). Although bushbuck are very shy and would flee for cover at the first site of humans, they were often observed (through binoculars) to graze in and amongst gelada herds. Dunbar and Dunbar (1981) similarly described gelada forming mixed grazing herds with Walia Ibex at Sankaber. Although Walia were not present at Sankaber during this study, gelada-Walia mixed groups are still very common in areas of the Simien Mountains inhabited by Walia. Mixed-species herds are common among many grazing herbivores and thought to offer the species involved complimentary advantages in detecting predators (Terborgh, 1990). It is therefore not surprising that gelada would respond so readily to the alarm call of one of their most common grazing neighbours.

It was shown in section 7.4.4 that there is no significant relationship between the stimulus of an alarm and the habitat type in which the gelada encounter it, although disturbances caused by humans (by far the most common alarm stimulus) were more common in the P-open and Field habitat types. However, it is problematic to assume that an incident in which gelada flee from, or are dislocated by, humans is directly analogous to flight in response to the presence of a real or perceived predator. All analyses were therefore repeated with alarm in response to humans excluded. None of the above results changed significantly although, with the Field habitat now totally excluded, and fewer alarm responses in the P-open habitat (both high visibility habitats), the relationship between the relative Alarm Indices and the mean visibility of a habitat type (Figure 7.6) was also found to be significant ($r = -0.925$, $p < 0.05$), thus partially resurrecting a confirmation of prediction 1.

Caution is necessary in drawing any conclusions from the data on alarm response presented here, especially in the absence of more direct measures of predation rate and predation risk. Nonetheless, a clear relationship does exist between the visibility within a habitat and the likelihood that the gelada will be provoked into a flight response, regardless of the stimulus. More specifically, the key finding of the current chapter is that the rate of alarm responses within different habitat types correlates most strongly with the degree to which gelada are surrounded by levels of visibility under 10 metres. This result is consistent with the evidence suggesting that during daylight hours the most serious threat to the gelada is from ambush predators, notable leopards and jackals, and lends convincing support to the third prediction of the chapter. The results also provide another example of how variation in habitat-specific characteristics affects the behaviour and movement of gelada in the current study.

CHAPTER EIGHT

Discussion

8.1 Purpose of the study

In contrast to literature available on *Papio* baboons, previous field research on gelada is limited to a small number of intensive studies which focused primarily on fine-scale social dynamics and interactions (e.g. Dunbar & Dunbar, 1975; Kawai, 1979; Dunbar, 1984). Although the construction of gelada social organisation is well documented in these studies, far less research has been conducted on identifying the ecological parameters underlying it. For instance, a key characteristic of the gelada social system is the large herds formed by bands of units. These multi-unit groups provide the context within which ecological parameters shape the way gelada use the space and food resources around them. This represents an important deficit in our knowledge of gelada ecology since although their social interactions are limited beyond the scope of the 'unit', the costs, benefits, and factors effecting group living are key issues to any social animal (Clutton-Brock & Harvey, 1977; Terborgh & Janson, 1986). Furthermore, while some past studies have briefly described the unique ecological niche occupied by gelada (see Crook, 1966; Dunbar & Dunbar, 1975; Iwamoto, 1979), little quantitative data has been presented, and less attention has been paid to how fluctuations in the environment influence the foraging decisions of gelada groups as a whole. This thesis represents an attempt to fill some of these gaps. By focusing primarily on group-level phenomena, a number of ecological variables, such as predation pressure and food availability, have been examined in reference to the constraints they place on the grouping and ranging behaviour exhibited by a band of gelada in the Simen Mountains of Ethiopia.

In this concluding chapter I will briefly review the salient findings of each data chapter in turn, and discuss some key issues raised by these results and their contribution to what is currently known about gelada specifically and primate ecology in general.

8.2 Habitat use

In Chapter 4, a detailed description of the distribution of food resources and the physical and climatic environment at the Sankaber field site provided a background for examining the temporal and spatial patterns in which the gelada use their home range. Distinct 'wet' and 'dry' seasons were characterised by striking temporal differences in precipitation and levels of above-ground green vegetative cover. More direct measures of gelada food availability (obtained by clipping) were found to not only vary temporally, but spatially between habitat types. As predicted, the patterns in which food sources were distributed were found to underlie the gelada's habitat selectivity and ranging patterns. On a finer spatial scale, gelada also showed strong preference for individual (200 x 200m) quadrats over others, suggesting that food distribution might be less evenly distributed than is typically acknowledged for a 'grazing' species. Indeed, in the dry season, quadrats in the open areas of the plateau varied from supporting a minimum 5.6 g/m^2 dry-weight of underground food, to a maximum 165.7 g/m^2. Barton *et al.* (1992) similarly found that baboon food at Laikipia was also more concentrated in discrete patches during the dry season than the wet season.

The importance of different habitat types was also found to vary seasonally. Most notably, the gelada's use of gorge areas was significantly higher in the wet season than dry season. However, levels of food availability did not appear to underpin this shift in home range use since both the G-open and G-bushy habitat types offered the lowest levels of above-ground green vegetative food in the wet season. Instead, the gelada's avoidance of heavy and consistent mist in the wet season appears to predetermine their use of these more climatically sheltered habitat types. Further analyses revealed a preference for the G-open over G-bushy habitat type, suggesting that the influence of mist on ranging behaviour was not simply due to the avoidance of adverse weather conditions but was due to the dramatically reduced visibility it entails. This finding gains significance in light of the relationship between predation risk and visibility levels described in Chapter 7.

A subsequent prediction in Chapter 4, that above-ground food sources would determine ranging in seasons of adequate green cover, while the distribution of underground food sources would determine ranging in the dry season, was also upheld. More importantly however, was the finding that only the distribution of below ground food resources appeared to influence ranging patterns in the dry season. As far as I am aware, this is the first study to report a primate species' ranging behaviour determined solely on the distribution of below-ground food resources. This result highlights the great importance of underground food sources to gelada and the exploitation of these items represents an adaptation that allowed all the Theropithecenes to tap into a grassland food source (i.e. subterranean storage organs) that is unavailable to the gelada's main competitors, namely grazing ungulates (Jolly, 1972).

8.3 Feeding ecology

Byrne *et al* (1993) have shown that chacma baboons in the Drakensburg Mountains, gain significantly less nutrition from the same time invested in foraging during the late winter than early summer, and the winter conditions faced by mountain baboons are therefore thought to constitute a 'nutritional bottleneck' (Henzi *et al.*, 1992). In the same study, Byrne *et al* (1993) found that the baboons increased their feeding time during the 'nutritional bottleneck' of winter, but that this "made no effective compensation for the poorer food yields". As the rate of nutrient uptake fell in the winter, individuals were unable to compensate by feeding longer, suggesting that they were already at the extreme activity budgeting limits of time available for feeding (Whiten *et al.*, 1987).

The key aim of Chapter 5 was to test the long held assumption that the seasonal concentration of rainfall experienced by gelada leads to a seasonal differential in actual food intake (Crook, 1966; Dunbar & Dunbar, 1975). In testing this hypothesis a number of secondary predictions were tested relating to the ways in which gelada might deal with such seasonal constraints on their feeding ecology.

Gelada are indeed faced with a 'dry' season, similar to mountain baboons, and show a dramatic dietary shift to more subterranean items as green grasses become sparser. As noted, the gelada's ability to exploit underground food resources is paramount to their survival in an environment of such seasonal rainfall, and allows gelada to occupy the Sankaber home range at densities 3-4 times higher than sympatric *Papio spp.* and at a much higher faunal biomass than sympatric antelope (Dunbar & Dunbar, 1974). This seasonal shift in dietary profile is also accompanied by a significantly greater proportion of the gelada's dry-season time budget being devoted to feeding. This has prompted the hypothesis that the seasonal increase in feeding time is associated with the slower rate of processing (and therefore calorific intake from) underground food sources (see Whiten *et al*, 1991, 1992). In the current study, data were presented and analysed to test this prediction with regards to gelada, but it was not upheld. Instead it appears that the mean rate at which dry-season calories are ingested is limited chiefly by the lower calorific value of dry season grasses. In other words, the sparser spatial spread of individual green grass blades is what necessitates the significant increase in feeding time in the dry season, not the shift to a more subterranean diet.

Similarly, it was predicted that if the dry season handicap was merely an artefact of the longer processing time associated with subterranean foods, then the daily rate of actual nutrient intake is expected to be slower during the dry season, regardless of time invested in feeding. The gelada do increase both the time invested in feeding and the volume of their food intake during this time, while also gaining fewer calories per unit time.

However, the substantially greater time spent feeding in the dry season (66.9% of the activity budget) than the wet season (49.6% of the activity budget), not only appears to compensate for the lower intake of calories but suggest that the gelada are actually gaining a higher overall mean daily calorie intake during the dry season (2789.5 kcal/day) than the wet season (2506.8 kcal/day). These results throw considerable doubt on the long held assumption that the dry season represents a period of relative food scarcity for the gelada (see Crook, 1966; Crook and Aldrich-Blake, 1968, Dunbar, 1977; Iwamoto, 1979) and caution should be exercised before claiming the dry season a 'nutritional bottleneck'.

Despite the apparent lack of a nutritional shortfall, there appears to be strong selective pressure forcing the gelada to alter their activity budgets on a seasonal basis. The fact that gelada sacrifice so much time to feeding in the dry season in order to maintain their nutritional intake warrants further consideration. An initial point worth noting is that the calorific value of a food source is only one facet of its nutritional worth, and it is not known whether the gelada's dry-season nutrients might be less accessible due to an increased content of structural cellulose within the plant. Dougall *et al.* (1964) found that the crude fibre content of grass blades on the East African savannah increased in the dry season and Iwamoto (1979) reported that the digestibility of gelada food at Gich averaged 39.3% in the wet season but fell to 24.1% in the dry season. Furthermore, little is known of the fibre to protein ratios of gelada food. Whiten *et al.* (1991) found that protein content was the only nutrient that consistently predicted diet selection across all types of food plant for mountain baboons. A more detailed chemical analyses of gelada foods is clearly needed to illuminate the nutritional constraints associated with the different dietary profiles of the wet and dry seasons. For instance, practically nothing is known about intake levels of protein, lipid, alkaloid, fibre, phenolics, the nutrients' relative digestibility or the gelada's metabolic abilities. Although numerous studies have pointed to the complex nature of *Papio* baboon diets as evidence of a lack of gut specialisation to ferment leaves (e.g. Johnson, 1990; Whiten *et al.*, 1990, 1992; Byrne *et al.*, 1993), very little is known about the digestive capabilities of gelada and whether their predisposition to feeding on grass leaves is enabled by hindgut fermentation. While the results presented in this study contribute to the knowledge of what is ingested by gelada, it is important to recognise that less is known of what is *digested* by gelada.

It is interesting that the increase in dry-season feeding investment was more pronounced for female than male gelada. Although behavioural observations in the current study did not include the reproductive state of focal females, Dunbar and Dunbar (1988) have reported that 60% of gelada births at Sankaber occurred between November and March, meaning that significantly more females were engaged in lactation during the dry season. Moreover, lactation is considered the period of highest energy demands in a female primate's reproductive career (Portman, 1970; Silk, 1986), and lactating female gelada have been shown to spend approximately 30% more time feeding than non-lactating females (Dunbar & Dunbar, 1988). The energetic costs of lactation in the dry season are likely to be exacerbated by the thermoregulatory stress caused by extremely low night-time temperatures and thus might drive the striking increase in foraging efforts by females observed in the dry season.

A second consideration regarding the gelada's surprisingly high dry-season intake is the issue of thermoregulation. Iwamoto and Dunbar (1983) presented evidence to suggest that the gelada's energy requirements increase with altitude due to declining ambient temperature. Similarly, Dunbar (1979b) demonstrated that time spent feeding by klipspringer correlated with mean temperature at Sankaber, while Belovsky and Jordan (1978) found that time spent feeding by moose (*Alces alces*) was inversely related to ambient temperature. It was suggested in Chapter 4 (section 4.2.4) that the high precipitation experienced by gelada during the wet season represents a period of adverse weather conditions. However, the most severe thermal conditions faced by the gelada are the night time minima during the dry season (see Figure 4.3). Killick (1963) demonstrated that heat loss via radiation is especially pronounced on calm clear nights, such as those experienced by gelada in the dry season, and Henzi *et al.* (1992) found that a high altitude troop of Chacma baboons in the Drakensburg Mountains abandoned the most productive areas of their home range during the coldest months and only returned once ground temperatures had risen above 0°C. Henzi *et al.* (1992) also make the important observation that temperatures at ground level in a montane baboon habitat are consistently lower than those recorded from a standard-height weather station. Given that thermometers in the current study were positioned in sheltered locations and at a height of approximately one metre, the thermal conditions experienced by the gelada may be slightly more extreme than those listed in this study. Although the connection is only speculative at this stage, it appears that the increased energy requirements of gelada in the dry season might be related to the number of nights in which ambient temperatures drop the furthest below their thermoneutral zone.

8.4 Competition for resources

A key element of gelada social organisation, namely strong and stable matriarchal bonds, is at theoretical odds with traditional assumptions regarding their resource base, and a primary aim of this study has been to elucidate the ecological factors underlying this discrepancy. As grazers, gelada have traditionally been assumed to utilise widely and evenly distributed food resources (Crook & Aldrich-Blake; Iwamoto, 1975; Dunbar, 1977), yet the existence of firm hierarchical social bonds within the gelada social system produces somewhat of a conundrum. While a number of studies have suggested that such relationships between female primates are the result of contest competition for food resources (Wrangham, 1980; Janson & van Schaik, 1987; van Schaik, 1989; Gore, 1993; Pruetz & Isbell, 2000), it is commonly assumed that little if any intra-group competition exists for food resources among grazing herbivores (Geist, 1974; Rutberg & Greenberg, 1990; see Wittenberger, 1981, for a review). Resources are generally widespread and of low nutritional value. Therefore, the cost of conflict over such items is thought to outweigh the possible benefits (Geist, 1974), antagonistic encounters over food are rare (Clutton-Brock & Harvey, 1976), and there is little evidence that access to food is rank-related (Clutton-Brock & Harvey, 1976). Instead, competition within grazing groups for resources is considered to be indirect and occur when other animals have previously passed through and foraged in an area (Jarmen, 1974).

In the current study, day journey length was found to correlate to gelada group size, suggesting that the addition of extra units will add to travel costs via increased scramble feeding competition. But it is important to note that a significant relationship between group size and day journey was not found in five months, four of those being in the wet season, thus showing a seasonal variation in degree of scramble competition. This raises the possibility that if the amount of food available to the gelada reaches a certain threshold, group size might no longer constitute a key determinant of day journey length. Moreover, the relationship between day journey length and group size was found to be more affected by the patchiness of food resources than overall food availability.

Clearly the key to pinpointing what lies beneath the existence of the gelada's solid matrilineal social system is an understanding of the nature of their resource base. Importantly, this study has revealed a number of points indicating that the gelada's food sources, at least at Sankaber, might be more patchily distributed than previously thought. Not only did habitat selection vary significantly but it was shown that gelada strongly favour certain (200m x 200m) quadrats over others, suggesting that considerable variation exists in spatial preference for foraging on a finer spatial scale. Subsequent analyses were able to show this large variation existed in the fine-scale distribution of food sources; both temporally (days within months) and spatially (within specific habitat types). Larger food patches available to terrestrial primates are thought to facilitate larger groups (Terbough, 1983), but a species may only be able to sustain this pattern seasonally if the size of their food patches varies seasonally. As the dry season begins, the location of green grass becomes restricted topographically to lower lying gullies, bowls and creek beds which may constitute a 'patch' size impossible for a group of many hundred gelada to share. The energetic costs of adding extra units to the herd may thus vary between months and habitats and the size of the patch will bear directly on the increase in scramble competition suffered by individuals. Furthermore, the only food source found to underpin gelada ranging in the dry season, underground items, showed the highest levels of patchiness of any food resource monitored. These findings raise important implications for the socioecology of gelada since, as noted above, the distribution of food resources has commonly been cited as a key factor underpinning the social system of a primate species (Wrangham, 1980; Janson & van Schaik, 1987). Data presented in this study point towards a more patchy distribution of gelada food resources than previously assumed and this new understanding of gelada ecology fits more harmoniously with models that predict advantages in contest competition between social cliques will drive the strong matrilineal bonds present within gelada units (Wrangham & Runbenstein, 1986; van Schaik, 1989).

8.5 The fission-fusion social system

As stated in the introduction to this thesis, the density and distribution of food patches is thought to determine the travel costs for a primate group of any given size, but the rate at which a group depletes a patch and must move on is also directly influenced by the size of the group (Charnov, 1976; Stephens & Krebs, 1986). MacDonald (1979) suggested that if a species has access to a non-depleting resource, as might be the case with grazers, then groups size will be unlimited by travel costs and therefore large. However, an animals diet might require secondary food sources not found at the non-depleting patch and their group size might thus be determined by the distribution of these rare but limiting resources (Chapman *et al*, 1993). It is unlikely that group size for primates can escape ecological constraints and thus species who show large variation in group size are prime candidates the test these relationships. It is important here, to recognise the difference between the one-off occurrences of group fission in baboons, discussed above, and true fission-fusion social systems. Although rare, studies of primate fission-fusion systems have been used to test general ecological models of group size by comparing group sizes across species and among different communities within a species (e.g. Chapman, 1990; Chapman *et al*, 1993; Wrangham *et al*, 1993; Chapman *et al*, 1995). Two prominent examples of fission-fusion social organisations are spider monkeys (*Ateles geoffrroyi*) and chimpanzees (*Pan troglodytes*). Chapman *et al* (1995) note that unlike most primate species, do not form spatially cohesive social groups but subgroups that differ frequently in their size and composition. The density, distribution and size of food patches is thought to constrain the size of spider monkey and chimpanzee subgroups, and thus underlie the overall patterns of fission and fusion in their social organisation. Furthermore, the above studies contrast with gelada and hamadryas, whose style of fission-fusion only operates at the level of family units and therefore conveys no significant changes within the social sphere.

Crook (1966) hypothesised that gelada herds habitually fissure and regroup in response to seasonal fluctuations in food availability. However, this does not explain the large variations in gelada herd composition observed within months (section 6.3). By monitoring the fission-fusion system of gelada in the current study on a finer scale it was possible to examine the ecological parameters driving it. Data have been presented in the present study to show that for gelada, the degree to which food is unevenly distributed is a better predictor of the rate at which gelada herds undergo fission or fusion events than overall food availability, as suggested by Crook (1966). However, the relationship revealed itself as more complex on a finer temporal scale. For example, it is worth considering the two months in which the gelada groups showed the highest levels of fission and fusion; March (1.30 events/day; see section 6.3) and May (2.10 events/day). Firstly, during March, in the height of the dry season, the gelada rely heavily on underground food resources. Although data are not available on the distribution of such items on a monthly basis, it was shown that the mean (32.2 g/m^2, and sd = 50.7 g/m^2) dry-weight distribution of underground food items in the dry season produced a coefficient of variation (CV = 157.5%) which is higher than any other food category in either wet or dry season (CVs calculated from Table 4.1). This measure of the degree to which resources are clumped is even high in comparison to the data available for spider monkeys (food patches/ha, CV = 85.6%, Robbins *et al*, 1991), and Chapman *et al* (1995) have been ale to show that the fission-fusion nature of spider monkey social organisation appears to be driven by constraints imposed by the patchiness of their resources. For gelada, the highly patchy nature of the distribution of subterranean food items (a key component of the diet in March) is consistent with the positive relationship between CV of food distribution and the amount of group fission-fusion activity, as shown in Figure 6.14. Therefore, in circumstances of high food density, the distribution of the main food resources may become less important as travel distance is greatly minimised. However, it does not need to be the gelada's key resource that is driving to nature of their fission fusion system. Instead, the patchy distribution of a secondary resource such as underground food items, might be enough to place short-term constraints on group size.

Secondly, during May the marked onset of the rains leads to the most dramatic single ecological change in the gelada's environment, namely the rapid flush of fresh green grass which prompts an almost instant and striking shift in the gelada's dietary profile. The new grass growth in May is more widely and uniformly spread in comparison to underground food items eaten in the preceding 'dry' months, and the increased group sizes recorded in the wet season begin in May (see Figure 6.1). Thus May appears to represent a prominent transitional period in the behavioural ecology of the gelada over an annual cycle and the relatively high rate at which the groups join and split during May might be considered a facet of the 'stuttering' seasonal shifts in mean group size and dietary profile. Therefore the fission-fusion system of gelada organisation appears to be a response to patterns of short term, immediate food distribution, especially in periods when food is difficult to find or process.

8.6 Predation risk and spatial patterns

Presumably, when a gelada unit decides to leave a large herd the costs of departing and foraging in a smaller group are less than the costs incurred by remaining. For instance, individuals that break away to form smaller groups might be more likely to find themselves positioned on the edge than when in larger herds, enabling easier access to new or richer food sources (Henzi *et al.*, 1997a). Conversely, the risk of predation to an individual has been shown to be inversely related to the number of animals in the group and might favour individuals in a safer more central location. A key feature of the spatial dynamics within gelada herds is that units remain integral in space. Thus the actual position of a unit within the gelada herd is expected to determine both an individual member's degree of access to unforaged food sources, and the levels of individual predation risk they are exposed to.

In addition to the possibility of feeding competition discussed in section 8.4 above, little is known about the possibility of competition for 'safety' amongst gelada. For example, social alliances among unit members might convey advantages in terms of access to prime sleeping ledges (e.g. van Schaik & van Noordwijk, 1987) or lower risk positions within the herd (Busse, 1984, Janson 1990). Indeed, gelada groups were found to be sensitive to variation in predation risk. The key finding of Chapter 7 was that, within a specific habitat type, the percentage of visibility under 10 metres is a stronger predictor of the rate of alarm responses than is the mean visibility of that habitat. Thus it is not visibility *per se* that is driving the gelada to show more alarm responses but the degree to which they are surrounded by vegetation from which they are vulnerable to an ambush predator. Along with these ecological factors, the potential social costs to primates living in groups should also be taken into account. For instance, a primate positioned on the outer edge of a group might be able to lower the costs of social vigilance and the likelihood of agonistic encounters with conspecifics (Silk *et al.*, 1981; Cowlishaw, 1999). Regardless of the competitive framework driving such patterns, it is an important observation that some units are not found randomly positioned throughout the herd.

In the current study, units at the extreme periphery of the gelada foraging herd were found to be significantly smaller than those in the middle. This is interesting given the evidence suggesting that the size of a one-male unit imparts a competitive advantage in terms of inter-unit competition. It is possible that larger units occupy more central positions in order to maximise foraging success or minimise predation risk, while sub-optimal positions might lose out on both. Although it is acknowledged that data in the current study are limited, it was worth noting that the prevalence of inter-unit spatial patterns was only observed when the gelada were in prime foraging habitats and not at all when in habitats of greatest predation risk. It appears that larger more dominant units may be monopolising central positions to diminish their vulnerability to predation but primarily to enable them greater access to discrete food patches.

8.7 Conclusion

The current study has tested a number of predictions to show that numerous group-level patterns of gelada behavioural ecology respond to certain ecological factors. Implicit in the above discussion, is the notion that gelada grouping behaviour may be concurrently shaped by the pressures resulting from an increased cost of foraging in larger groups versus the decreased cost of predation risk. Data were presented to illuminate both these ecological factors and how their influence on gelada ecology might vary in time and space. For instance, during the dry season, simply the fact that gelada appear forced into smaller groups entails a trade-off with predation risk, via a reduced dilution effect (Hamilton, 1971). During the same period, these smaller gelada groups avoid the E-heather habitat (with its high-risk, low-visibility) despite the significantly higher levels of green-grass to be found there, while being restricted to safer, more open habitats during the dry season necessitates a shift to underground food items which are patchily distributed in space. Gelada are able to deal with this short-term (patchy) variation in resource distribution by containing their social relations within the unit but joining and disbanding groups of units when the foraging cost of a multi-unit band can be sustained. Thus the well documented fission and fusion of gelada social structure appears pinned to a much finer spatiotemporal framework of resource distribution than the previously recognised more simplistic seasonal dichotomy. A more radical explanation could be that if the constraint that predation pressure places on minimal tolerable group size is habitat specific (as the results suggest) and gelada range between habitat types regularly, the fission-fusion system might also carry benefits relating to short-term variation in predation pressure. Future data on variation in foraging efficiency and vigilance of units in different group sizes and habitats should answer this question.

A number of previous gelada studies have utilised cross-population comparisons to stress the importance of rainfall and temperature as the pre-eminent factors shaping gelada socioecology (Dunbar & Dunbar, 1975; Iwamoto & Dunbar, 1983; Dunbar, 1984; Iwamoto, 1993b). However, simply the environmental differences between the two main gelada fieldsites, Sankaber and Gich, highlight the difficulty in formulating general models of gelada socioecology. For example, the dry season distribution of underground resources, so important to the gelada at Sankaber in this study, is practically irrelevant to the gelada at Gich whose habitat of longer Festuca grasses provides for a higher density of green blades to survive through the dry season, while on the other hand, the extremely open habitat at Gich should leave the gelada far less susceptible to attack from ambush predators, more common at Sankaber. Also, despite implicitly recognising that food patch size and distribution are significant determinant of primate socioecology, Iwamoto (1979) pointed out that measuring these variables accurately in the gelada's grassland environment remains difficult and time-consuming. Nonetheless, a theme running throughout this thesis has shown that the nature and distribution of gelada food resources is a more complex and influential selective force than previously acknowledged. This is an important development in our understanding since patterns of resource availability are directly effected by rainfall and altitude, yet represent a more proximal influence on the gelada's day to day ecology. Therefore, I suggest that the fresh understanding of the nature of gelada resources, presented in this study, may represent the ecological template underlying both the existence of the gelada's strong matriarchal bonds and their elaborate fission-fusion social system.

References

Alexander, R.D. (1974) The evolution of social behaviour. *Ann. Rev. Ecol. Syst.*, **5**: 325-383.

Altmann, J. (1974) Observational study of behaviour: sampling methods. *Behaviour* **49**: 227-267.

Altmann, J. (1980) *Baboon mothers and infants*. Harvard University Press, Cambridge.

Altmann, S.A. (1974) Baboons, space, time and energy. *Am. Zool.*, **14**: 221-248.

Altmann, S.A. (1979) Baboon progressions: order or chaos? A study in one-dimensional group geometry. *Anim. Behav.*, **27**: 46-80.

Altmann, S.A. (1991) Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. *Proc. Natl. Acad. Sci. USA*, **88**: 420-423.

Altmann, S.A. (1998) *Foraging for survival: yearling baboons in Africa*. University of Chicago Press, Chicago.

Altmann, S.A. & Altmann, J. (1970) *Baboon ecology*. Chicago University Press, Chicago.

Altmann, J. and Maruthi, P. (1988) Differences in daily life between semi-provisioned and wild-feeding baboons. *Amer. Journ. Primatol.*, **15**: 213-221.

Altmann, S.A., Post, D.G., & Klein, D.F. (1987) Nutrients and toxins of plants in Amboseli, Kenya. *Afr. J. Ecol.*, **25**: 279-293.

Amat, J.A. & Obeso, J.R. (1991) Black coots (*Fulica atra; Aves, Rallidae*) supplanting conspecifics from foraging sites. *Ethology*, **87**: 1-8.

Anderson, C.M. (1981a) Intertroop relations of chacma baboons (*Papio ursinus*). *Int. J. Primatol.*, **2**: 285-310.

Anderson, C.M. (1981b) Subtrooping in a chacma baboon (*Papio ursinus*) population. *Primates*, **22**: 445-458.

Appleby, M. C. (1983) Competition in a red deer stag social group: rank, age and relatedness of opponents. *Anim. Behav.*, **31**: 913-918.

Barrett, L. Dunbar, R & Dunbar, P. (1992) Environmental influences on play behaviour in immature gelada baboons. *Anim. Behav.* **44**:111-115.

Barton, R.A. (1989) Foraging strategies, diet and competition in Olive baboons. PhD Thesis, University of St. Andrews.

Barton, R.A. (1992) Allometry of food intake in free-ranging anthropoid primates. *Folia Primatol.* **58**: 56-59.

Barton, R. A. (1993) Sociospatial mechanisms of feeding competition in femal olive baboons, *Papio anubis. Anim. Behav.* **46**: 791-802.

Barton, R.A. & Whiten, A. (1993) Feeding competition among female olive baboons, *Papio anubis. Anim. Behav.*, **46**: 777-789.

Barton, R.A., Byrne, R.W. & Whiten, A. (1996) Ecology, feeding competition and social structure in baboons. *Behav. Ecol. Sociobiol.*, **38**: 321-329.

Barton, R.A., Whiten, A., Strum, S.C., Byrne, R.W. & Simpson, A.J. (1992) Habitat use and resource availability in baboons. *Anim. Behav.*, **43**: 831-844.

Barton, R.A., Whiten, A., Byrne, R.W. & English, M. (1993) Chemical composition of baboon plant foods: implications for the interpretation of intra- and interspecific differences in diet. *Folia Primatol.*, **61**: 1-20.

Belovsky, G.K. & Jordan, P.A. (1978) The time-energy budget of a moose. *Theoretical Population Biology*, **14**: 76-104.

Bernstein, I.S. (1972) Daily activity cycles and weather influences on a pigtail mokey group. *Folia Primatol.*, **18**: 390-415.

Bernstein, I.S. (1976) Activity patterns in a sooty mangabey group. *Folia Primatol.*, **26**: 185-200.

Bertram, B. (1982) Leopard ecology as studied by radio-tracking. *Symp. Zool. Soc. Lond.*, **49**: 341-352.

Black, J.M., Carbone, C., Wells, R.L. & Owen, M. (1992). Foraging dynamics is goose flocks: the cost of living on the edge. *Anim. Behav.* **44**: 41-50.

Boesch, C. (1991) The effects of leopard predation on grouping patterns in chimpanzees. *Behaviour.* **117**: 220-242.

Boinski, S. and Chapman, C.A. (1995) Predation on primates: Where are we and what's next? *Evol. Anthrop.* **4**: 1-3.

du Bothma, J. & Le Riche, E.A.N. (1984) Aspects of the ecology and the behaviour of the leopard *Panthera pardus* in the Kalahari desert. *Koedoe* (suppl.), **27**: 259-279.

du Bothma, J. & Le Riche, E.A.N. (1986) Prey preference and hunting efficiency of the Kalahari leopard. In: Miller, S.D. & Everett, D.D. (eds.) *Cats of the world: biology, conservation and management.* pp. 389-414. National Wildlife Federation, Washington DC.

Boutton, T.W., Tieszen, L. L., & Imbamba, S.K. (1988) Seasonal changes in the nutrient content of Est African grassland vegetation. *Afr. J. Ecol.* **26**: 103-115.

Brain, C. (1990) Spatial usage of a desert environment by baboons (Papio ursinus). *Jrn. Arid Ecol.* **18**: 67-83.

Bronikowski, A.M. & Altmann, J. (1996) Foraging in a variable environment: weather patterns and the behavioural ecology of baboons. *Behav. Ecol. Sociobiol.*, **39**: 11-25.

Busse, C. D. (1977) Chimpanzee predation as a possible factor in the evolution of red colobus social organization. *Evolution* **31**: 907-911.

Busse, C. D. (1984) Spatial structure of chacma baboon groups. *Int. J. Primatol.*, **5**: 247-261.

Byrne, R.W. (1981) Distance vocalizations of Guinea baboons (*Papio papio*) in Senegal: an analysis of function. *Behaviour*, **78**: 283-312.

Byrne, R.W., Whiten, A., Henzi, S.P. and McCulloch, F.M. (1993) Nutritional constraints on mountain baboons (*Papio ursinus*): implications for baboon socioecology. *Behav. Ecol. Sociobiol.*, **33**: 233-246.

Casperd, J.M. & Dunbar, R.I.M., (1996) Asymmetries in the visual processing of emotional cues agonistic interactions by gelada baboons. *Behav. Processes.* **37**: 57-65.

Chagnon, N.A. (1975) Genealogy, solidarity, and relatedness: Limits to local group size and patterns of fissioning in an expanding population. *Yearb. Phys. Anthrop.*, **19**: 95-110.

Chapman, C.A. (1990) Association patterns of spider monkeys: the influence of ecology and sex on social organisation. *Behav. Ecol. Sociobiol.*, **26**: 409-414.

Chapman, C.A., Chapman, L.J. & McLaughlin, R.L. (1989) Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. *Oecologica.* **79**: 506-511.

Chapman, C.A., Wrangham, R.W. & Chapman, L.J. (1995) Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behav. Ecol. Sociobiol.* **36**: 59-70.

Charnov, E. L. (1976) Optimal foraging; the marginal value theorm. *Theor. Popul. Biol..*, **9**: 129-136.

Cheney, D.L. & Seyfarth, R.M. (1987) The influence of intergroup competition on the survival and reproduction of female vervet monkeys. *Behva. Ecol. Sociobiol.* **21**: 375-386.

Cheney, D.L. & Wrangham, R.W. (1987) Predation. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wranham, R.W. & Struhsaker, T.T. (eds.) *Primate societies*. pp. 227-239. University of Chicago Press, Chicago.

Chivers, D.J. and Hladik, C.M. (1980) Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. *Journal of Morphology*. **166**: 337-386.

Clutton-Brock, T.H. (1977) Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In: Clutton-Brock, T.H. (ed.) *Primate ecology*. pp. 557-579. Academic Press, New York.

Clutton-Brock, T.H. & Harvey, P.H. (1976) Evolutionary rules and primate societies. In: *Growing Points in Ethology* (Ed. by P.P.G. Bateson & R.Hinde), pp. 195-237. Cambridge: Cambridge University Press.

Clutton-Brock, T.H. & Harvey, P.H. (1977) Primate ecology and social organisation. *J. Zool., Lond.*, **183**: 1-39.

Coe, M.J., Cumming, D.H. & Phillipson, J. (1976) Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, **22**: 341-354.

Collins, D.A. (1984) Spatial pattern in a troop of yellow baboons (*Papio cynocephalus*) in Tanzania. *Anim. Behav.*, **32**: 536-553.

Cowlishaw, G.C. (1993) Trade-offs between feeding competition and predation risk in baboons. Ph.D. Thesis, University College London.

Cowlishaw, G.C. (1994) Vulnerability to predation in baboon populations. *Behaviour*, **131**: 293-304.

Cowlishaw, G.C. (1997a) Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim. Behav.*, **53**: 667-686.

Cowlishaw, G.C. (1997b) Refuge use and predation risk in a desert baboon population. *Anim. Behav.*, **54**: 241-253.

Cowlishaw, G.C. (1998) The role of vigilance in the survival and reproductive strategies of desert baboons. *Behaviour*, **135**: 431-452.

Cowlishaw, G.C. (1999) Ecological and social determinants of spacing behaviour in desert baboon groups. Behav. Ecol. Sociobiol., **45**: 67-77

Crook, J.H. (1966) Gelada baboon herd structure and movement, a comparative report. *Symp. Zool. Soc. Lon.* **18**: 237-258.

Crook, J.H. (1970) The socio-ecology of primates. In: Crook, J.H. (ed.) *Social behaviour in birds and mammals*. pp. 103-166. Academic Press, London.

Crook, J.H. & Gartlan, J.S. (1966) Evolution of primate societies. *Nature*, **210**: 1200-1203.

Crook, J.H. & Aldrich-Blake, F.P.G. (1968) Ecological and behavioural contrasts between sympatric ground dwelling primates in Ethiopia. *Folia Primatolgia*. **8**: 192-227.

Davidge, C. (1978) Ecology of baboons (*Papio ursinus*) at Cape Point. *Zool. Afr.*, **13**: 329-350.

Deshmuhk, I.K. (1984) A common relationship between precipitation and grassland peak biomass for East and southern Africa. *Afr. J. Ecol.*, **22**: 181-186.

Devore, I. & Hall, K.R.L. (1965) Baboon ecology. In: Devore, I. (ed.) *Primate behaviour*. pp. 20-52. Holt, Rinehart & Winston, New York.

Dittus, W.P.J. (1987) Group fusion among wild toque macaques: an extreme case of intertroop resource competition. *Behav.* **100**: 247-291

Dougall, H.M., Drysdale, V.M. and Glover, P.E. (1964) The chemical composition of Kenya browse and pasture herbage. E. Afr. Wildl. J. 2: 82-125.

Dunbar, R.I.M., (1977). Feeding ecology of gelada baboons: a preliminary report. In: *Primate Ecology*, Clutton-Brock, T. H. (ed.), Academic Press, London, pp 250-273.

Dunbar, R.I.M. (1978) Competition and niche separation in a high altitude herbivore community in Ethiopia. *E. Afr. Wildl. J.* **16**: 183-200

Dunbar, R.I.M. (1979a) Structure of gelada baboon reproductive units I: Stability of social relationships. *Behaviour*. **69**: 72-87

Dunbar, R.I.M. (1979b) Energetics, thermoregulation and the behavioural ecology of klipspringer. *Afr. J. Ecol.*, **17**: 217-230.

Dunbar, R.I.M. (1980) Demographic and life history variables of a population of gelada baboons (Theropithecus gelada). *J. Anim. Ecol.* **49**: 485-506.

Dunbar, R.I.M. (1983a) Structure of gelada baboon reproductive units II: Social relationships among reproductive units. *Anim. Behav.* **31**: 556-564.

Dunbar, R.I.M. (1983b) Structure of gelada baboon reproductive units III: The males relationship with his females. *Anim. Behav.* **31**: 565-575.

Dunbar, R.I.M. (1983c) Structure of gelada baboon reproductive units IV: Integration at group level. *Zeitschrift fur Tierpsychologie*. **63**: 265-282.

Dunbar, R.I.M. (1983d) Relationships and social structure in gelada and hamadryas baboons. In: Hinde, R.A. (ed.) (1983) *Primate social relationships*. pp. 299-307. Blackwell Scientific Publications, Oxford.

Dunbar, R.I.M. (1984) *Reproductive decisions: an economic analysis of gelada baboon social strategies*. Princeton University Press, Princeton.

Dunbar, R.I.M. (1988) *Primate social systems*. Chapman & Hall, London.

Dunbar, R.I.M. (1992) Time: a hidden constraint on the behavioural ecology of baboons. *Behav. Ecol. Sociobiol.*, **31**: 35-49.

Dunbar, R.I.M. (1993a) Ecological constraints on group size in baboons. *Physiol. Ecol. Japan*, **29**: 221-236.

Dunbar, R.I.M. (1993b) Social organisation of the gelada. In: Jablonski, N. G. (ed.) *Theropithecus: The rise and fall of a primate genus*. pp. 425-441, Cambridge University Press, Cambridge.

Dunbar, R.I.M. (1996) Determinants of group size in primates: a general model. In: Runciman, W.G., Maynard Smith J. & Dunbar, R.I.M. (eds.) *Evolution of social behaviour patterns in primates and man*. pp. 33-57. Oxford University Press, Oxford.

Dunbar, R.I.M. & Dunbar, P. (1974) Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. *Folia Primatol.*, **21**: 36-60

Dunbar, R. & Dunbar, P. (1975) *The social dynamics of gelada baboons*. S. Karger.

Dunbar, R.I.M. & Dunbar, P. (1981) The grouping behaviour of male walia ibex with special reference to the rut. *Afr. J. Ecol.* **19**: 251-263.

Dunbar, R.I.M. & Dunbar, P. (1988) Maternal time budgets of gelada baboons. *Anim. Behav.*, **36**: 970-980.

Dunbar, R.I.M. & Bose, U. (1991) Adaptation to grass-eating in gelada baboons. *Primates*, **32**: 1-7.

Dunbar, R.I.M. & Sharman, M. (1984) Is social grooming altruistic? *Z. Tierpsychol.* **64**: 163-173.

Eisenberg, J.F., Muchenhirm, N.A. and Rudran, R. (1972) The relation between ecology and social structure in primates. *Science* **176**: 863-874.

Elgar, M.A. (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.* **64**: 13-33

Endler, J.A. (1991) Interactions between predators and prey. In: Krebs, J.R. & Davies, N.B. (eds.) *Behavioural ecology: an evolutionary approach*, 3rd Ed. pp. 169-196. Blackwell Scientific Publications, Oxford.

Fa, J.E. (1986) Use of time and resources by provisioned troops of monkeys: social behaviour, time and energy in the Barbary macaque (*Macaca sylvanus* L.) at Gibraltar. *Contributions to Primatology*, Vol. 23. Karger, Basel.

Fraser, D.F. and Huntingford, F.A. (1986) Feeding and avoiding predation hazard: the behavioural response of the prey. *Ethology*, **73**: 56-68.

Gartlan, J.S. and Brain, C.K. (1968) Ecology and social variability in Ceropithecus aethiops and C. mitis. In: Jay, P.C. (ed) *Primates: studies in adaptation and variability*. pp 253-292. Holt, New York.

Gaynor, D. (1994) Foraging and feeding behaviour of chacma baboons in a woodland habitat. Ph.D. Thesis, University of Natal.

Geist, V. (1974) On the relationship of social evolution and ecology in ungulates. *Am. Zool.*, **14**: 205-220.

Gore, M. A. (1993) Effects of food distribution on foraging competition in rhesus monkeys, Macaca mulatta and Papio hamadryas. *Anim. Behav.*, **45**: 773-786.

Groves, C.P. (1993) Order Primates. In Wilson, D.E. & Reader, D.M. (eds), *Mammalian Species of the world: A taxonomic and geographical reference*, 2nd Ed. pp. 243-277. Smithsonian Institute Press, Washington D.C.

Hall, K.R.L. (1963) Variations in the ecology of the chacma baboon, *Papio ursinus*. *Symp. Zool. Soc., Lond.*, **10**: 1-28.

Hamilton, W.D. (1971) Geometry for the selfish herd. *J. Theor. Biol.*, **31**: 295-311.

Hamilton, W.J. III (1986) Namib desert chacma baboon (*Papio ursinus*) use of food and water resources during a food shortage. *Madoqua*, **14**: 397-407.

Hamilton, W.J. and Watt, K.E.F. (1970) Refuging. *Ann. Rev. Ecol. Syst.*, **1**: 263-286.

Hamilton, W.J. III & Bulger, J.B. (1993) Origin and fate of a one-male savannah baboon group formed by fissioning. *Int. J. Primatol.*, **14**: 131-143.

Hamilton, W.J. III, Buskirk, R.E.R. & Buskirk, W.H. (1976) Defence of space and resources by chacma (*Papio ursinus*) baboon troops in an African desert and swamp. *Ecology*, **57**: 1264-1272.

Harcourt, A. H. (1987) Dominance and fertility among female primates. *J. Zool. Lond.*, **213**: 471-497.

Harding, R.S.O. (1976) Ranging patterns of a group of baboons (*Papio anubis*) in Kenya. *Folia Primatol.*, **25**: 143-185.

Harding, R.S.O. (1977) Patterns of movement in open country baboons. *Am. J. Phys. Anthrop.* **53**:, 203-216.

Hawkins, D.M. (1999) Individual time budgets of yellow baboons in Mikumi National Park, Tanzania: Group size and environment. PhD Thesis. University of Liverpool.

Henzi, S.P., Dyson, M.L. & Deenik, A. (1990) The relationship between altitude and group size in mountain baboons (*Papio cynocephalus ursinus*). *Int. J. Primatol.*, **11**: 319-325.

Henzi, S.P., Byrne, R.W. & Whiten, A. (1992) Patterns of movement by baboons in the Drakensberg mountains: primary responses to the environment. *Int. J. Primatol.*, **13**: 601-629.

Henzi, S.P., Lycett, J.E., Weingrill, T., Byrne, R.W. & Whiten, A. (1997a) The effect of troop size on travel and foraging in mountain baboons. *S. Afr. J. Sci.*, **93**: 333-335.

Henzi, S.P., Lycett, J.E. & Piper, S.E. (1997b) Fission and troop size in a mountain baboon population. *Anim. Behav.*, **53**: 525-535.

Hill, R.A. (1999) Ecological and demographic determinants of time budgets in baboons: implications for cross-populational models of baboon socioecology. PhD Thesis, University of Liverpool.

Hill, R.A. & Dunbar, R.I.M. (1998) An evaluation of the roles of predation risk and predation rate as selective pressures on primate grouping behaviour. *Behaviour*, **135**: 411-430.

Hill, R.A. & Lee, P.C. (1998) Predation risk as an influence on group size in Cercopithecoid primates. *J. Zool., Lond.*, **245**: 447-456.

Hinde, R.A. (1976) Interactions, relationships and social structure. *Man*, **11**: 1-17.

Hinde, R.A. (1983) A conceptual framework. In: Hinde, R.A. (ed) *Primate social relationships*. pp. 1-7. Blackwell Scientific Publications, Oxford.

Hladik, C.M. (1977) A comparitive study of the feeding strategies of two sympatric leaf monkeys: Presbytis senex and Presbytis entellus. In: Clutton-Brock, T.H. (ed) *Primate Ecology*, pp. 324-353. Academic Press, London.

Hoshino, J. (1985) Feeding ecology of Mandrills (*Mandrillus sphinx*) in Campo Animal Reserve, Cameroon. *Primates* **26**(3): 248-271.

Hopkins, W.D. and Bard, K.A., (1993) Hemispheric specialization in infant chimpanzees (Pan troglodytes): evidence for a relation with gender and arousal. *Develop. Psychobiol.*, **26**: 219-235.

Houston, A.I., McNamara, J.M. & Hutchinson, J.M.C. (1993) General results concerning the trade-off between gaining energy and avoiding predation. *Proc. Roy. Soc. Lond. B*, **341**: 375-397.

Hurni, H. (1982) Climate and the Dynamics of Altitudinal Belts from the Last Cold Period to the Present Day. Simen Mountains – Ethiopia, Vol. II. Pro Simen Foundation.

Inglis, I. R. & Lazarus, J. (1981) Vigilance and flock size in brent geese: the edge effect. *Z. Tierpsychol.*, **57**: 193-200.

Isbell, L.A. (1991) Group fusions and minimum group sizes in vervet monkeys (*Cercopithecus aethiops*). *Am. J. Primatol.*, **25**: 57-65.

Isbell, L.A. (1994) Predation on primates: ecological patterns and evolutionary consequences. *Evol. Anthropol.*, **3**: 61-71.

Iwamoto, T. (1975) Food resources and the feeding activity. Studies of the gelada society (III). *Contemporary Primatology.* 5th Int. Congr. Primat. Karger, Basel. pp 475-480.

Iwamoto, T. (1978) Food availability as a limiting factor on population density of the Japanese Monkey and Gelada Baboon. In: *Recent advances in Primatology.* Ed: Chivers, D. Herbert, J. Vol. J. Behaviour (Academic Press, NY & London).

Iwamoto, T. (1979) Feeding ecology. In: Kawai (ed.) *Sociological and Ecological studies of Gelada baboons.* pp 280-339. Karger, Basel.

Iwamoto, T. (1993a) Food digestion and energetic conditions in *Theropithecus gelada.* In: Jablonski, N. G. (ed.) *Theropithecus: The rise and fall of a primate genus.* pp. 453-463, Cambridge University Press, Cambridge.

Iwamoto, T. (1993b) The ecology *of Theropithecus gelada.* In: Jablonski, N. G. (ed.) *Theropithecus: The rise and fall of a primate genus.* pp. 441-452, CambridgeUniversity Press, Cambridge.

Iwamoto T. & Dunbar, R.I.M. (1983) Thermoregulation, habitat quality and the behavioural ecology in gelada baboons. *J. Anim. Ecol.*, **53**: 357-366.

Iwamoto, T., Mori, A., Kawai, M. & Bekele, A. (1996) Anti-predator behaviour of gelada baboons. *Primates*, **37**(4): 389-397.

Jablonski, N.G. (1986) The hand of Theropithecus brumpti. Primate Evolution. *Proceedings of the 10th Congress of the International Primatological Society*, vol 1. pp 173-182. Cambridge: Cambridge Universtiy Press.

Janis, C. (1976) Evolutionary strategy of the equids and the origins of rumen and caecal digestion. *Evolution*, **30**: 757-774.

Janson, C.H. (1985) Aggressive competition and food consumption in the brown capuchin monkey (Cebus apella). *Anim. Behav.*, **40**: 922-934.

Janson, C.H. (1986) The mating system as a determinant of social evolution in capuchin monkeys, (*Cebus*). In: Else, J.G. & Lee, P.C. (eds.) *Primate ecology and conservation*. pp. 169-179. Cambridge University Press, Cambridge.

Janson, C.H. (1990) Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella. Anim. Behav.*, **40**: 922-934.

Janson, C.H. (1992) Evolutionary ecology of primate social structure. In: Smith, E.A, Winterhalder, B. (eds) *Evolutionary ecology and human behaviour.* pp 131-164, Aldine de Gruyter, New York.

Janson, C.H. (1998) Testing the predation hypothesis for vertebrate sociality: prospects and pitfalls. *Behaviour*, **135**: 289-410.

Janson, C.H. (2000) Primate socio-ecology: The end of a Golden Age. *Evol. Anthropol.* **9** (2): 73-86.

Janson, C.H. & van Schaik, C.P. (1987) recognizing the many faces of primate feeding competition: methods. *Behaviour*, **105**: 165-186.

Jarmen, P. J. (1974) The social behaviour of antelope in relation to their ecology. *Behaviour*, **48**: 213-267

Johnson, J.A. (1989) Supplanting by olive baboons: dominance rank differences and resource value. *Behav. Ecol. Sociobiol.*, **24**: 277-283.

Johnson, R.B. (1990) The effect of plant chemistry on food selection by adult male yellow baboons (Papio cynocephalus). In: De Mello, M.T., Whiten, A. & Byrne, R.W. (eds.) *Baboons: behaviour and ecology, use and care.* pp. 5-22. University of Brasilia Press, Braslia.

Jolly, C.J. (1970) The large African monkeys as an adaptive array. In: Napier and Napier; *Old World Monkeys*. pp. 139-174 Academic Press, London.

Jolly, C. J. (1972) The classification and natural history of Theropithecus, baboons of the African Plio-pleistocene. *Bull. Brit. Mus. Nat. Hist.* **22**: 1-123

Kawai, M., ed. (1979) *Ecological and Sociological Studies of Gelada Baboons.* Karger, Basel, and Kondansha, Tokyo.

Kawai, M. and Iwamoto, T. (1979) Nomadism and activities. In: Kawai (ed.) *Sociological and Ecological of studies of Gelada baboons*. pp 251-275. Karger, Basel.

Kawai, M. and Mori, U. (1979) Spacing within units and unit integrity. In: Kawai (ed.) *Sociological and Ecological of studies of Gelada baboons*. pp 200-214. Karger, Basel.

Kawai, M., Dunbar, R.I.M., Ohsawa, H., and Mori, U. (1983) Social organization of gelada baboons: social units and definitions. *Primates* **24**: 1-13.

Keverne, E.B., Leonard, R.A., Scruton, D.M & Young, S.K. (1978). Visual monitoring in social groups of talapoin monkeys (Miopithecus talapoin). *Anim. Behav.* **26**: 933-944.

Kildaw, S.D. (1995) The effect of group size manipulations on the foraging behaviour of black-tailed prairie dogs. *Behav. Ecol.* **6**: 353-358.

Killick, D.J.B. (1963) An account of the plant ecology of Cathedral Peak area of the Natal Drakensburg. Bot. Surv. S. Afr. Mem. No 34. Government Printer, Pretoria.

Kingdon, J. (1997) *The Kingdon field guide to African mammals.* Natural World, Academic Press. Harcourt Brace & Company.

Kirkpatrick, R.C. (1998) Ecology and Behaviour in Snub-nosed and Douc Langurs. In: *The Natural History of the Doucs and Snub-nosed Monkeys.* Edited by Nina G. Jablonski. pp 155-190. World Scientific Publishing.

Klotzli, F. (1986) Integration of a world heritage site in an agricultural environment in the Simen Mountains of Ethiopia. *Symb. Bot. Ups.* **26** (2): 94-100.

Krebs, C. (1989) *Ecological methodology.* Harper & Row, New York.

Kruuk, H. & Turner, M. (1967) Comparative notes on predation by lion, leopard, cheetah and hunting dog in the Seregeti area, East Africa. *Mammalia,* **31**: 1-27.

Kummer, H. (1968) *Social organisation of hamadryas baboons.* Karger, Basel.

Kummer, H. (1971) *Primate societies.* Aldine-Atherton, Chicago.

Malik, I., Seth, P.K. & Southwick, C.H. (1985) Group fission in free-ranging rhesus monkeys of Tughlaqabad, Northern India. *Am. J. Primatol.* **6**: 411-422.

Meier, C. Baumann, P., Scmid, J., Steck, P. & Demeke, Y. (1998) A Preliminary study of the butterfly fauna (*Lepidoptera, Papilionoidea, Hesperiodea*). In: Neivergelt, B., Good, T, & Guttinger, R. (eds) *A Survey on the Flora and Fauna of the Simen Mountains National Park, Ethiopia.* pp74-78. Institute of Zoology, University of Zurich, Switzerland.

Melnick, D.J. & Pearl, M.C. (1987) Cercopithecines in multimale groups: genetic diversity and population structure. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wranham, R.W. & Struhsaker, T.T. (eds.) *Primate societies.* pp. 121-134. University of Chicago Press, Chicago.

Melton, D.A. (1987) Habitat selection and resource scarcity. *Sth. Afr. J. Science.* **83**: 646-651.

Messerli, B. & Aerni, K. (1978) Cartography and its Application for Geographical and Ecological Problems. Simen Mountains - Ethiopia, Vol. I. Pro Simen Foundation.

Milton, K. (1979) Factors affecting leaf choice by howler monkeys: a test for some hypotheses of food selection by generalist herbivores. *Am. Nat.*, **14**: 362-377.

Mitchell, C.L., Boinski, S. & van Schaik, C.P. (1991) Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedi* and *S. sciureus*). *Behav. Ecol. Sociobiol.*, **28**: 55-60.

Mori, A. (1979) Individual relationships within a unit. In: Kawai, M. (ed.) *Sociological and Ecological studies of Gelada baboons,* pp 94-124. Karger, Basel.

Mori, A. and Belay, G. (1990) The distribution of baboon species and a new population of gelada baboons along the Wabi-Shebeli River, Ethiopia. *Primates.* **31** (4): 495-508.

Nagel, U. (1973) A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatol.*, **19**: 104-165.

Napier, J.R. and Napier, P.H. (1967) *A handbook of living primates.* London: Academic Press.

Nash, L. (1976) Troop fission in free-ranging baboons in the Gombe Stream National Park, Tanzania. *Am. J. Phys. Anthropol.*, **44**: 63-78.

Nievergelt, B., Good, T. & Guttinger, R. (1998) A Survey of the Flora and Fauna of the Simen Mountains National Park, Ethiopia. *Walia*, 1998, Special Issue.

van Noordwijk, M. A. & van Schaik, C. P. (1987) Competition among female long tailed macaques. *Anim. Behav.* **36**: 577-589.

Norton, G.W. (1986) Leadership: decision processes of group movement in yellow baboons. In: Else, J. & Lee, P.C. (eds.) *Primate ecology and conservation.* pp. 145-156. Cambridge University Press, Cambridge.

Norton, G.W., Rhine, R.J., Wynn, G.W. & Wynn, R.D. (1987) Baboon diet: a five-year study of stability and variability of the plant feeding and habitat of the yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. *Folia Primatol.*, **48**: 78-120.

Oates, J.F. (1987) Food distribution and Foraging behaviour. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wranham, R.W. & Struhsaker, T.T. (eds.) *Primate societies.* pp. 197-210. University of Chicago Press, Chicago.

Oftadel, O.T. (1992) The nutritional consequences of foraging in primates: the relationship of nutrient intakes to nutrient requirements. In: Whiten, A. & Widdowson E.M. (eds.) *Foraging strategies and natural diet of monkeys, apes and humans.* pp 161-170. Clarendon Press, Oxford.

Ohsawa, H. (1979) The local gelada population and environment of the Gich area. In: Kawai, M. (ed.) *Sociological and Ecological studies of Gelada baboons.* pp. 4-46. Karger, Basel.

Portman, O.W. (1970) Nutritional requirements (NRC) of nonhuman primates. In: R.S.Harris (ed.) *Feeding and Nutrition of Nonhuman primates*, pp. 87-115. Academic Press, New York.

Post, D.G. (1978) Feeding and ranging behaviour of the yellow baboon (*Papio cynocephalus*). Ph.D. Thesis, Yale University.

Post, D.G. (1982) Feeding behaviour of yellow baboons in Amboseli National Park. *Int. J. Primatol.*, **3**: 403-430.

Post, D.G., Hausfater, G. & McCuskey, S.A. (1980) Feeding behaviour of yellow baboons (*Papio cynocephalus*): relationship to age, gender and dominance rank. *Folia Primatol.*, **34**: 170-195.

Powell, G. V. N. (1974) Experimental analysis of the social value of flocking by starlings (Sturnus vulgaris) in relation to predation and foraging. *Anim. Behav.* **22**: 501-505.

Pulliman, H.R. & Curaco, T. (1984) Living in groups: is there an optimal size? In Krebs, J.R. & Davies, N.B. (eds) *Behavioural Ecology: an Evolutionary Approach*, 2nd Edition. pp 122-147.

Pruetz, J.D. & Isbell, L.A. (2000) Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behav. Ecol. Sociobiol.* **49**: 38-47.

Rasmussen, D.R. (1978) Environmental and behavioural correlates of changes in range use in a troop of yellow (*Papio cynocephalus*) and a troop of olive (*Papio anubis*) baboons. Ph.D. Thesis, University of California, Riverside.

Rasmussen, D.R. (1983) Correlates of patterns of range use of a troop of yellow baboons (*Papio cynocephalus*). II. Spatial structure, cover density, food gathering, and individual behaviour patterns. *Anim. Behav.*, **31**: 834-856.

Richard, A. (1978) Behavioural Variation: Case study of a Malagasy Lemur. Lewisburg, Pa.: Bucknell University Press.

Rhine, R.J. & Westlund, B.J. (1981) Adult male positioning in baboon progressions: order and chaos revisited. *Folia Primat.*, **35**: 77-116.

Rhine, R.J., Bloland, P. & Lodwick, L. (1985) Progressions of adult male chacma baboons (*Papio ursinus*) in the Moremi Wildlife Reserve. *Int. J. Primatol.*, **6**: 115-122.

Robbins, D., Chapman, C.A. & Wrangham, R.W. (1991) Group size and stability: Why do gibbons and spider monkeys differ? *Primates*, **32**(3): 301-305.

Robinson, J.G. (1981) Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus*. *Anim. Behav.*, **29**: 1036-1056.

Robinson, J.G. (1988) Group size in wedge-capped capuchin monkeys *Cebus olivaceous* and the reproductive success of males and females. *Behav. Ecol. Sociobiol.*, **23**: 187-197.

Ron, T., Henzi., S.P. & Motro, U. (1996) Do female chacma baboons compete for safe spatial position in a southern woodland habitat? *Behaviour*, **133**: 475-490.

Rosenzweig, M.L. (1968) Net primary productivity of terrestrial communities: prediction from climatological data. *Am. Nat.*, **102**: 67-74.

Rowell, T.E. (1969) Long-term changes in a population of Ugandan baboons. *Folia Primatol.*, **11**: 241-254.

de Ruiter, J.R. (1986) The influence of group size on predator scanning and foraging behaviour of wedge-capped capuchins (*Cebus olivaceus*). *Behaviour*, **98**: 240-258.

Rutberg, A.T. (1986) Dominance and its fitness consequences in American bison cows. *Z. Tierpsychol.* **63**: 206-212.

Rutberg, A.T. and Greenberg, S.A. (1990) Dominance, aggression frequencies and modes of aggressive competition in feral pony mares. *Anim. Behav.* **40**: 322-331.

van Schaik, C.P. & van Hooff, J.A.R.A.M. (1983) On the ultimate causes of primate social systems. *Behaviour*, **85**: 91-117.

van Schaik, C.P. (1983) Why are diurnal primates living in groups? *Behaviour*, **87**: 120-144.

van Schaik, C.P. (1989) The ecology of social relationships among female primates. In: Standen, V. & Foley, R.A. (eds.) *Comparative socioecology: the behavioural ecology of humans and other mammals.* pp. 195-218. Blackwell Scientific Publications, Oxford.

van Schaik, C.P. (1996) Social evolution in primates: the role of ecological factors and male behaviour. In: Runciman, W.G., Maynard Smith J. & Dunbar, R.I.M. (eds.) *Evolution of social behaviour patterns in primates and man.* pp. 9-31. Oxford University Press, Oxford.

van Schaik, C.P., Noordwijk, M.A., de Boer, R.J. & den Tonkelaar, I. (1983) The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behav. Ecol. Sociobiol.*, **13**: 173-181.

van Schaik, C.P. & Noordwijk, M.A. (1986) The hidden costs of sociality: intra-group variation in feeding strategies in Sumatran long-talied macaques (*Macaca fascicularis*). *Behaviour* 99: 296-319.

van Schaik, C.P. & Noordwijk, M.A. (1988) Scramble and contest in feeding competition among female long-talied macaques (*Macaca fascicularis*). *Behaviour* **105**: 77-98.

van Schaik, C.P. & Noordwijk, M.A. (1989) The special role of male Cebus monkeys in predation avoidance and its effect on group composition. *Behav. Ecol. Sociobiol.* **24**: 265-276.

Schaller, G.B. (1972) *The Serengeti Lion.* University of Chicago Press, Chicago.

Schoener, T.W. (1971) Theory of feeding strategies. *Ann. Rev. Ecol. Syst.*, **2**: 369-404.

Schoener, T.W. (1987) A brief history of optimal foraging theory. In: Kamil, A.C., Krebbs, J.R. & Pulliam, H.R. (eds.) *Foraging behaviour.* pp. 5-67. Plenum Press, New York.

Seyfarth, R.M. (1978) Social relationships among adult male and female baboons. II. Behaviour throughout the female reproductive cycle. *Behaviour*, **64**: 227-247.

Sharman, M. & Dunbar, R.I.M. (1982) Observer bias in selection of study group in baboon field studies. *Primates*, **23**: 567-573.

Sharman, M. (1981) Feeding, ranging and social organisation of the guinea baboon. Ph.D. Thesis, Yale University.

Sigg, H. and Stolba, A. (1981) Home range and daily march in a hamadryas baboon troop. *Folia Primatol.*, **36**: 40-75.

Silk, J.B. (1986) Eating for two: Behavioural and environmental correlates of gestation length among free-ranging baboons (*Papio cynpcephalus*). *Int. J. Primatol.* **7** (6): 583-602.

Silk, J.B., Samuels, A., and Rodman, P. (1981) The influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macacques (Macaca radiata). *Behaviour*, **78**: 111-177.

Sokal, R.R. and Rohlf, F.J. (1995) *Biometry.* W.H. Freeman & Company, New York.

Stacey, P.B. (1986) Group size and foraging efficiency in yellow baboons. *Behav. Ecol. Sociobiol.*, **18**: 175-187.

Steenbeck, R. and van Schaik, C.P. (2001) Competition and group size in Thomas's langurs (Presbytis thomasi): the folivore paradox revisted. *Behav. Ecol. Sociobiol.* **49**: 100-110.

Stelzner, J.K. (1988) Thermal effects on movement patterns of yellow baboons. *Primates*, **29**: 91-105.

Stelzner, J.K. & Hausfater, G. (1986) Posture, microclimate, and thermoregulation in yellow baboons. *Primates*, **27**: 449-463.

Stephens, D.W. and Krebs, J.R. (1986) *Foraging theory.* Princeton University Press, Princeton.

Stoltz, L. & Saayman, G.S. (1970) Ecology and behaviour of baboons in the Transvaal. *Ann. Transvaal Mus.*, **26**: 99-143.

Struhsaker, T.T. (1967) Ecology of vervet monkeys (Ceropithecus aethiops) in the Masai-Amboseli Game reserve, Kenya. *Ecology.* **48**: 891-904.

Struhsaker, T.T. & Leland, L. (1979) Socioecology of five sympatric monkey species in Kibale Forest, Uganda. *Adv. Stud. Behav.*, **9**: 159-228.

Teaford, M.F. (1993) Dental microwear and diet in extant and extinct Theropithecus: preliminary analyses. In: Jablonski, N.G. (ed) *Theropithecus: The rise and fall of a primate genus.* Cambridge University Press, Cambridge.

Terborgh, J. (1990) Mixed species flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. *Am. J. Primatol.* **21**: 81-100.

Terborgh, J. & Janson, C.H. (1986) The socioecology of primate groups. *Ann. Rev. Ecol. Syst.*, **17**: 111-135.

Terborgh, J. (1983) *Five New World primates.* Princeton University Press, Princeton.

Thouless, C. (1990) Feeding competition between grazing red deer hinds. *Anim. Beh.* **40**: 105-111.

de Waal, F.B.M. (1977) The organisation of agonistic relations within two captive groups of Java monkeys (*Macaca fascicularis*). *Z. Tierpsychol.*, **44**: 225-282.

de Waal, F.B.M. (1987) Dynamics of social relationships. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wranham, R.W. & Struhsaker, T.T. (eds.) *Primate societies.* pp. 421-431. University of Chicago Press, Chicago.

Walters, J. (1980) Interactions and the development of dominance relationships in female baboons. *Folia Primatol.*, **34**: 61-89.

Waser, P.M. & Floody, O. (1974) Ranging patterns of the mangabey, *Cercocebus albigena*, in the Kibale Forest, Uganda. *Z. Tierpsychol.*, **35**: 85-101.

Waser, P.M. (1976) Monthly variation in feeding and activity patterns of the mangabey *Cercocebus albigena. E. Afr. Wildl. J.*, **13**: 249-264.

Waser, P.M. (1977) Feeding, ranging and group size in the mangabey. *Cercocebus albigena.* In: Clutton-Brock, T.E. (eds) *Primate ecology.* pp. 183-222. Academic. London. .

Waterman, P.G. (1984) Food acquisition and processing as a function of plant chemistry. In: Chivers, D.J. & Wood, B.A. (eds) *Food acquisition and Processing in Primates.* Plenum Press, London.

Webster, A.J.F. (1971) Prediction of heat losses from cattle exposed to cold outdoor environments. *J. Appl. Physiol.*, **30**: 684-690.

Whiten, A., Byrne, R.W. & Henzi, S.P. (1987) The behavioural ecology of mountain baboons. *Int. J. Primatol.*, **8**: 367-387.

Whiten, A., Byrne, R.W., Barton, R.A., Waterman, P.G. & Henzi, S.P. (1991) Dietary and foraging strategies of baboons. *Phil. Trans. R. Soc. Lond. B.*, **334**: 187-197.

Whiten, A., Byrne, R.W., Barton, R.A., Waterman, P.G. & Henzi, S.P. (1992) Dietary and foraging strategies of baboons. In: Whiten, A. & Widdowson E.M. (eds.) *Foraging strategies and natural diet of monkeys, apes and humans*. pp 187-197. Clarendon Press, Oxford.

Whiten, A., Byrne, R.W., Waterman, P.G., Henzi, S.P. & McCullough, F.M. (1990) Specifying the rules underlying selective foraging in wild mountain baboons, *P. ursinus*. In: De Mello, M.T., Whiten, A. & Byrne, R.W. (eds.) *Baboons: behaviour and ecology, use and care*. pp. 5-22. University of Brasilia Press, Braslia.

Whitten, P. L. (1983) Diet and dominance among female vervet monkeys (*Ceropithecus aethiops*). *Am. J. Primatol.*, **5**: 139-159.

Wittenberger, J. F. (1981) *Animal Social Behaviour*. Duxbury Press: Boston.

Wrangham, R. (1976) Aspects of feeding and social behaviour in gelada baboons. *A report to the science research council.*

Wrangham, R.W. & Rubenstein, D.I. (1986) Social evolution in birds and mammals. In: Rubenstein, D.I. & Wrangham, R.W. (eds.) *Ecological aspects of socialevolution*. pp. 452-470. Princeton University Press, Princeton.

Wrangham, R.W. (1979) On the evolution of ape social systems. *Soc. Sci. Info.*, **18**: 335-368.

Wrangham, R.W. (1980) An ecological model of female-bonded primate groups. *Behaviour*, **75**: 262-300.

Wrangham, R.W. (1983) Ultimate factors determining social structure. In: Hinde, R.A. (ed.) *Primate social relationships*. pp. 255-261. Blackwell Scientific Publications, Oxford.

Wrangham, R.W. (1987) Evolution of social structure. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wranham, R.W. & Struhsaker, T.T. (eds.) *Primate societies*. pp. 282-296. University of Chicago Press, Chicago.

Wrangham, R.W., Conklin, N.L., Chapman, C.A. & Hunt, K.D. (1991) The significance of fibrous foods for Kibale forest chimpanzees. *Phil. Trans. Roy. Soc. B.*, **334**: 171-178.

Wrangham, R.W., Gittleman, J.L. and Chapman, C.A. (1993) Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behav. Ecol. Sociobiol.* **32**: 199-209.

Zahavi, A. (1971) The social behaviour of the white wagtail (*Motacilla alba alba*) wintering in Israel. *Ibis*, **113**: 203-211.