Individual Time Budgets of Yellow Baboons in Mikumi National Park, Tanzania: Group size and environment

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by Dawn May Hawkins

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I dedicate this thesis to
Guy, my parents & Margaret,
and to all our memories of Nat.

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ABSTRACT

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Multiple regression has been used to generate functional equations describing variation in individual time budgets of baboons in relation to climate and group size. These equations deal with a broad scale of variation i.e., annual cycles between study sites. A fine scale study of individual time budgets of adult yellow baboons was undertaken (1299 hours of individual follows from July 1993 to August 1995 inclusive) in Mikumi National Park, central Tanzania, in order to assess: (1) the implications of finer scale variation for assumptions implicit in the functional equation approach; (2) the ability of these equations to predict annual variation within a population over three decades. The latter was made possible by the existence of data from previous studies at this long-term site. In addition, ecological monitoring (32 one hectare plots monitored quarterly from December 1993 to August 1995 inclusive) was conducted in order to assess potential causal mechanisms underlying relationships between climate and behaviour.

Variation within days and years was found to be significant and considerable. Researchers are generally aware of such temporal variation and its implications when making comparison between groups. In contrast, variation generated by interindividual differences is often overlooked. Significant interindividual variation, at a level potentially sufficient to confound comparison at a broader scale, was found in relation to sex (females socialized more and fed less) and age (feeding decreased and resting increased with age) but, not reproductive status or rank. The conservative approach, of only making comparisons between groups where data have been collected using compatible sampling decisions, is recommended.

Within year variation was found in the amount of time spent in different activities and in the scheduling of these activities throughout the day. Based on the pattern of this variation in relation to climate and ecological factors, it was hypothesized that feeding time is kept to a minimum in order to minimize costs associated with heat stress and poor visibility.

The data and procedures used to generate functional equations have certain constraints and assumptions. Nevertheless, they do an adequate job of predicting values at independent sites according to criteria set by previous authors and, at present, represent the most statistically and biologically acceptable way of relating time budgets, group size and climate at a broad scale. However, these criteria are lenient and it is premature to embed them in more complex models at this stage.

Values generated by the functional equations provided an adequate qualitative, but a poor quantitative, prediction of observed patterns over three decades. This may be due to an unrecognized influence of cyclic or extreme weather and/or the importance of factors extraneous to climate, in shaping the Mikumi ecosystem (e.g., fire, patterns of fruiting). It could also result from short comings of the functional equations. Although the equations do not work for Mikumi, the case for other sites, has still to be adequately tested.

Halfway through this study the two study groups fused. This provided an opportunity to investigate the effects of a sudden doubling of group size on individual time budgets. Time spent feeding decreased while resting time increased; indicators of intra-group aggression remained unchanged. A variety of ecological factors created a situation in which individuals could gain foraging benefits from the fusion without incurring costs of increased intragroup competition. This coincided with demographic events which facilitated the two troops joining. Anti-predation benefits may also have played a role in both the fusion and the subsequent range change.

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CHAPTER 1. INTRODUCTION

Time budgets represent the way in which an animal distributes its time between different categories of behaviour, for example feeding, moving, resting and socializing (section 2.2). This thesis deals with individual time budgets in primates, specifically the yellow baboons (*Papio cynocephalus)* of Mikumi National Park in Tanzania. The inspiration for this work came from two main sources: theoretical studies of Robin Dunbar and a long-term research project on baboons in Mikumi.

In 1992, Robin Dunbar published a paper entitled "Time: a hidden constraint on the behavioural ecology of baboons" (Dunbar 1992a). In this paper, Dunbar developed a model[1] of maximum ecological group size, using time budget data from a 18 different studies across Africa. Embedded in this model, were analyses relating time budgets to environment and group size; a set of multiple regression equations, models in themselves, that used climatic variables (total rainfall, rainfall diversity, temperature) and group size to describe the percentage of time baboons spent in different activities. These "functional equations", as Dunbar termed them, were a continuation of previous work (e.g., Dunbar & Sharman 1984; Dunbar 1988; Dunbar 1990). Given the complex patterns of variation in time budgets observed in primates (section 2.5) the possibility of being to be able to predict time budgets from group size and a few easy to measure climatic variables is appealing. Such an approach to predicting behaviour has been aptly described by Bronikowski & Altmann (1996) as "from the sky down".

Dunbar's (1992a) paper raised a number of questions such as: What are the causal relationships between climate and behaviour (Chapters 4 and 6)? To what extent does from whom data are collected from (e.g., males versus females) and the time frame over which these data are collected (e.g., wet season versus dry season) affect variation within sites, and what are the implications of this for interpopulation comparisons (Chapters 5 & 6)? Dramatic changes in group size had occurred in the Mikumi baboons (section 3.3.1) over the last three decades. Could the equations, based largely on interpopulation data, adequately predict any accompanying changes in time budgets (Chapter 9)? The situation in Mikumi was ideally suited to collecting data to investigate some of these questions and

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[1] A model is a "simplified representation, which is designed to faciliate prediction and calculation, and which can be expressed in symbolic or mathematical form" (Brown & Rothery 1993:1).

comparable data from previous studies in Mikumi existed which would enable exploration of yet others.

This was the foundation on which this thesis is built. However, along the way two other issues arose. Firstly, midway through the period of data collection of this study, the two main study troops in Mikumi fused. This is a rare event in primate demography and the opportunity to explore the short-term consequences of a sudden doubling of group size was irresistible, as was the temptation to think a little as to its causes (Chapter 7). Secondly, as more work was produced on the functional equation approach to predicting time budgets (Bronikowski & Altmann 1996; Dunbar 1996; Williamson 1997) certain problems regarding procedures being used to generate and test the functional equations emerged and it became apparent that a thorough critical review was required (Chapter 8).

The structure of this thesis is as follows. After this brief introduction, Chapter 2 provides a review of work done on time budgets in primates and the factors potentially influencing them. This is followed by a general methods chapter (Chapter 3) with details of the study site, study animals and other broadly applicable methodological information. Chapters 4 to 9 inclusive, are the six main results chapters tackling the issues outlined above. Finally, Chapter 10 provides a concluding, overall discussion.

CHAPTER 2. INDIVIDUAL TIME BUDGETS

2.1 INTRODUCTION

This chapter provides a review of the study of individual time budgets in the Primate order. The next section (2.2) defines the main features of individual time budgets. This is followed by a consideration of the methodology used to record data on individual time budgets (section 2.3). The scales over which time budgets can vary are outlined in section 2.4, while section 2.5 reviews the patterns and possible factors underlying this variation. The potential use of multivariate analyses to generate functional equations to help describe and understand gross scales of variation is considered in section 2.6. The chapter ends with a summary (section 2.7).

2.2 WHAT ARE TIME BUDGETS?

Time budgets (also known as activity budgets e.g., Sharman 1981) are a fundamental descriptor of an animal's behaviour. This thesis is concerned with individual time budgets rather than group time budgets. Individual time budgets refer to amount of time individual animals spend in different behavioural activities. Group time budgets, on the other hand, refer to the amount of time a group of animals spend in different behavioural activities, usually based only on the predominant activity of the group. In this thesis, "time budget" will mean "individual time budget" unless otherwise stated.

Martin & Bateson (1986) summarize the four basic measurable features of behaviour as latency, frequency, duration and intensity. Time budgets are concerned with **duration** and are usually expressed as the mean percentage of a day that an animal is recorded performing defined behaviours.

As a number of authors have pointed out (e.g., Altmann 1974; Lehner 1996; Martin & Bateson 1986), it is useful to distinguish states, on-going behaviours of measurable duration, from events, instantaneous behaviours of minimal duration. In fact, behaviours fall along a continuum between these two extremes and therefore the terms "state-like" (meaning towards the state end of the spectrum) and "event-like" (meaning towards the event end of the spectrum) may be more fitting. The position of a behaviour along this continuum is a product of both the structure of the behaviour and the criteria by which the behaviour is defined. Rhine & Linville (1980) for example, discuss the implications of definition in relation to behaviour involving the consumption of food. Within this state-event conceptual framework it is only appropriate to consider time budget data for **state-like** behaviours. The concept can not usefully be applied to event-like behaviours which, by definition, approach instantaneous occurrence.

Many authors define behavioural states used to collect time budget data so that they are **mutually exclusive** (e.g., Dunbar 1992a). An alternative approach is illustrated by Leger (1977) who listed the behaviours of the chimpanzees he studied in a hierarchy and followed the rule "that if a focal animal engaged in more than one category simultaneously, only the higher ranking category would be noted" (Leger 1977: 389). Event-like behaviours tend not to be mutually exclusive with state-like ones e.g., moving (state) and vocalizing (event).

Common time budget categories are **feeding**, **moving**, **socializing** and **resting** (Dunbar 1988). A fifth category, **other**, generally accounting for less than 2% of the budget (Dunbar 1988) is used as a catch all for any states not included in these main categories. 'Other' may include, for example, drinking, copulating and self grooming. The relevance of these categories will obviously vary between species but all are applicable and commonly used for primates (Dunbar 1992a, 1988). Where states are defined as mutually exclusive or recorded so that only one is registered at any one time, the percentage time spent in these different time budget categories should total 100%.

A time budget represent the way in which an animal distributes its time between different activities and thus represents underlying decisions on the use of time (Dunbar 1992a). Time budget data can be used in a wide variety of studies e.g., to assess the welfare status of captive animals (e.g., Fowler & Pankhurst in prep) and in biological modelling (Caraco 1979a&b; Dunbar 1992a).

Table 2.1 Methods used to measure time budgets in baboons studies. Last column indicates whether individuals animals were identified.

STUDY	RECORDING METHOD	IDS
Sharman 1981	(1) Individual activity records of all visible individuals every twenty minutes during periods of social activity; (2) At other times, every time an individual was observed its activity was recorded.	no
Dunbar & Dunbar 1974	Individual activity records of all visible individual every 10 minutes.	no
Nagel 1973	Individual activity records of all visible animals at between 10 and 30 minutes.	no
Barton 1989	Thirty minute individual follows with continuous sampling.	yes
Eley et al. 1989	Individual activity records of all individuals every half hour.	yes
Post 1978	(1) Twenty minute individual follows with instantaneous sampling (sample interval = 1 minute); (2) 15 minute individual follows with continuous recording.	yes
Rasmussen 1978	Three or 1.5 hour individual follows with instantaneous sampling plus one-zero sampling of grooming (sample interval = 5 minutes).	yes
Aldrich-Blake et al. 1971	Individual activity records of all visible animals every quarter hour.	no
Harding 1976	Individual follows of varying length (until focal lost) with principle activity of the subject during the previous recorded at 1 minute intervals.	yes
D.M. Hawkins (this study)	One and a half or three quarter hour follows with one-zero and instantaneous sampling (sample interval = 5 minutes).	yes
G.W. Norton (unpublished protocol)	One and a half hour follows with one-zero and instantaneous sampling (sample interval = 5 minutes).	yes
Cowlishaw 1993	One hour individual follows with instantaneous sampling (sample interval = 5 minutes).	yes
Kenyatta 1995	Thirty minute individual follows with continuous recording of eg., grooming plus instantaneous sampling of all activities (sample interval = 1 minute).	yes
Dunbar & Dunbar 1988	Thirty minute individual follows with instantaneous sampling (sampling interval = 30 seconds).	yes

2.3 MEASURING TIME BUDGETS

Table 2.1 summarizes the recording methods used in a range of baboon studies collecting data on individual time budgets. There are essentially two basic methods chosen - individual activity records and/or individual follows.

Individual activity records are taken on the behaviour of all (Eley et al. 1989) or all visible (Aldrich-Blake et al. 1971; Dunbar & Dunbar 1974; Nagel 1973; Sharman 1981) animals at set intervals. The potential for collecting biased data if the behaviour of only visible animals is recorded, is considerable. Conspicuous behaviours, for example, are likely to be registered disproportionately more often than more docile behaviours. Microhabitat variations in visibility will tend to interact with this effect to produce further biasing. For example, Sharman (1981) used the individual activity records only during periods where the predominant group activity was social behaviour because the visibility at other times was so poor. At times outside periods of social activity he recorded the behaviour of every animal he saw and the time at which the observation was made.

Individual follows involve recording the behaviour of an identified individual for a specified amount of time. During a follow, duration data can be recorded either by continuous recording (Barton 1989; Kenyatta 1995; Post 1978) or time sampling (Cowlishaw 1993; Dunbar & Dunbar 1988; Hawkins this study; Kenyatta 1995; G.W.Norton unpublished data; Post 1978; Rasmussen 1978; Whiten et al. 1987).

Continuous recording involves making a real time record of all behaviours under consideration. Time sampling involves dividing the follow into equal sampling intervals e.g., 2 minute intervals in a 20 minute follow. Intervals are separated by sampling instants. There are two basic time sampling options: one-zero and instantaneous (Lehner 1996; Martin & Bateson 1986). For one-zero sampling, behaviours are recorded if they occur at least once during the sampling interval. For instantaneous sampling, only the behaviour occurring on the sampling instant is noted.

A number of authors have unreservedly condemned the use of one-zero as a measure of behaviour (Altmann 1974; Dunbar 1976; Kraemer 1979); whereas others have asserted the usefulness of this technique (Bernstein 1991; Leger 1977; Lehner 1996; Martin & Bateson 1986; Rhine & Ender 1983; Rhine & Flanigan 1978; Rhine & Linville 1980; Rhine et al. 1985). Nevertheless there does appear to be a consensus that instantaneous data collection should be the time sampling method of preference when measures of duration only are required. One-zero measures reflect both frequency and duration, the relative duration, the relative contribution of which depends on the structure of the behaviour under consideration and the sample interval employed (Kraemer 1979; Rhine & Linville 1980; Rhine & Ender 1983; Martin & Bateson 1986). One-zero measures are most highly correlated with duration when sample intervals are short. Instantaneous sampling reflects only duration and is only correlated to frequency to the extent that the duration and frequency are intercorrelated (Kraemer 1979). However, since the two techniques are easy to combine there is often no need to choose between them. Collecting one-zero data in addition to instantaneous data has many advantages including enabling the relative scores for each behaviour to be compared. This can reveal information about the structure of the behaviour which instantaneous data on its own can not. One-zero data are also particularly useful in two other circumstances. Firstly, for recording event-like behaviours in situations where taking actual frequency is not practical. Secondly, for looking at temporal association of behaviours.

2.4 SCALES OF VARIATION

Studies of time budgets have investigated variation in relation to who is being considered (interspecific and intraspecific variation) and when they are being considered (temporal variation) i.e., they have looked at variation at different scales. This section aims to review these types of comparison and the studies which have considered them. No attempt is made either to discuss patterns of variation in detail or to discuss potential factors underlying these observed patterns; that is left to section 2.5.

2.4.1 Interspecific & Intraspecific Variation

2.4.1.1 Interspecific

Clutton-Brock and Harvey (1977) present estimates of ecological and behavioural variables, including time budgets, from 56 primate species representing 8 different families. Although the authors caution that "individual estimates shown in this table may be unrealistic and that they should not be used for reference" (Clutton-Brock & Harvey 1977:583), the data do indicate considerable differences between species e.g., time spent feeding ranges from 11% for black-handed spider monkeys to 54% for siamangs.

2.4.1.2 Intraspecific

Bernstein (1976) suggested that activity budgets were largely species specific. However, since this time primatologists have become increasingly aware of the flexibility of behaviour within species, both within and between populations. Within populations variation exists between groups and even between individuals within a group.

Dunbar (1992a) investigated variation between 18 populations from the genus *Papio* including *P.papio, P.hamadryas, P.anubis, P.cynocephalus* and *P.ursinus*. Based on previous taxonomic debate and blood protein analyses he argued that "these are better considered as subspecies" (Dunbar 1992a:38) and thus we can take his study as documenting intraspecific variation between populations.

In a companion paper to Clutton-Brock and Harvey's (1977) interspecific review, Clutton-Brock (1977a) considered intraspecific variation. His review of time budget data concentrated mainly at the within populations level, primarily on temporal variation (section 2.4.3) within groups. Differences between groups (Bronikowski & Altmann 1996) and between individuals within groups (e.g., Barton 1989; Kenyatta 1995) are further levels of intraspecific variation.

2.4.2 Temporal Variation

Temporal variation includes variation between years, within years and within days. Although temporal variation complicates all types of comparison, it has only been studied specifically within populations.

Studies of time budgets across multiple years are rare (but see Bronikowski & Altmann 1996). In some cases, data across years are lumped and inter-year variability ignored (e.g., Agetsuma 1995a; Mitani1989). Within year variation has been identified in a wide range of primate species (*baboons* Altmann & Altmann 1970; Barton 1989; Dunbar 1977; Iwamoto & Dunbar 1983; Kamal et al. 1995; Nagel 1973; Post 1981; Sharman 1981; *capuchins* Robinson 1986; *colobus* Clutton-Brock 1974; Dasilva 1992; *macaques* Agetsuma 1995a; *mangabeys* Barrett 1995; *orangutans* Mitani 1989; *primates* Clutton-Brock 1977b; *siamangs* Chivers 1977; *vervets* Baldellou & Adan 1997; Harrison 1983; Isbell & Young 1993; *woolly monkeys* Defler 1995). Studies finding no significant variation in time budgets within years are few (*gorillas* Watts 1988; *mangabeys* Waser 1975) and are associated with non-seasonal habitats.

Within each 24 hour period the majority of primates are active during daylight hours. During these hours variation in time budgets has been found (*baboons* Aldrich-Blake et al.1971; Altmann & Altmann 1970; Dunbar 1977; Harding 1976; Kenyatta 1995; Post 1978, 1981; Sharman 1981; *capuchins* Robinson 1984; *colobus* Clutton-Brock 1974; *howler monkeys* Coelho et al. 1979; Richard 1970; *macaques* Bernstein 1976; *mangabeys* Barrett 1995; *primates* Clutton-Brock 1977b; *siamangs* Chivers 1977; *spider monkeys* Coelho et al. 1979; Richard 1970; *squirrel monkeys* Hawkins 1992; *woolly monkeys* Strier 1987). The peaks and lulls in different activities may or may not be associated with certain times of day, although the extremes of the alert period are characteristically spent in less energetic pursuits i.e., resting and/or socializing. Seasonal variation in daily patterns of time use within years has been found in those studies which have looked at their data in this way (Barrett 1995; Clutton-Brock 1974; Post 1978, 1981; Robinson 1984; Sharman 1981; Strier 1987).

2.5 PATTERNS & CAUSES OF VARIATION

Factors affecting feeding time have been given the most attention, while changes in other time budget components have mostly been related to time spent feeding. Increased feeding time is likely to lead to reduced resting time and ultimately reduced social time (e.g., Altmann 1980; Dunbar 1988; Dunbar & Sharman 1984; Iwamoto & Dunbar 1983; Kenyatta 1995; Lee 1986). In this section, only factors affecting time budget components not mediated by other components are considered.

2.5.1 Individual Differences

Characteristics of an individual, such as their body size, sex, reproductive status, rank, age, internal state and health, can potentially influence their allocation of time to different activities. Consequently even individuals of the same species living in the same group can differ in their time budgets .

2.5.1.1 Body size

Interspecific variation in time spent feeding with body weight has been clearly documented by Clutton-Brock and Harvey (1977): The heavier the species the more time it spends feeding but, as as body weight gets heavier, the increase in feeding time becomes progressively smaller. The relationship is positive because larger animals have to ingest more nutrients in order to sustain a greater mass, and allometric because metabolism becomes more efficient with increasing body size in endotherms (Peters 1983; Schmidt-Neilsen 1990).

Body size can also vary considerably intraspecifically. For example, in a consideration of variation of body weight in baboons across 19 populations, Dunbar (1990) documented a range of 16.2 to 34.4kg for males and 9.7 to 15.9kg for females with adult male generally weighting about twice as much as adult females (mean across populations of 24.5kg versus 13.3kg). Such body size differences can generate variation in time budgets between individuals within species just as they can between species. Intraspecific variation has been mostly considered in relation to sexual dimorphism (section 2.5.1.2) but may also contribute to patterns related to age (2.5.1.5) and dominance status (2.5.1.4).

2.5.1.2 Sex

Sex differences in feeding time amongst adults have been found less often than predicted on the basis of body size differences. Only for the most extremely dimorphic of primates, the gorilla and the orang-utan, are there suggestions that males may feed for longer than females (Fossey & Harcourt 1977; Harcourt & Stewart 1984; Rodman 1977; Watts 1988). Where males and females are closer in size, no significant differences between the sexes have been found (*baboons* Barton 1989; Dunbar 1977; Post 1981; Post et al. 1980; *woolly monkeys* Defler 1995; *chimpanzees* Doran 1997; *guereza* Oates 1977; *vervets out of mating season* Baldellou in litt.; *in wet season* Isbell & Young 1993; Harrison 1983) or females have been found to feed for longer (*mangabeys* Waser 1977; *vervets in mating season* Baldellou in litt. but note reverse found by Harrison 1993 *in dry season*). For species where males and females are of similar size, females generally feed for longer (*siamangs* Chivers 1977; *indris* Pollock 1977; *howler monkeys* Smith 1977).

Several authors have considered explanations to account for longer feeding time per unit body mass by females (Barton 1989; Clutton-Brock 1977a; Harcourt & Stewart 1984; Rhine & Westlund 1978). The two most popular explanations concern diet quality and reproductive costs. Males may obtain a higher quality diet either as a consequence of priority of access through their social status or, because greater physical strength to process food packages. Females may have relatively greater nutritional needs in order to cover the costs of reproduction. Other explanations include faster feeding rates by males and differential thermoregulatory constraints.

If priority of access to food by males is a mechanism by which the larger bodied male sex manages to fulfill its nutritional requirements in the same time as smaller bodied females, then conditions of high quality clumped food could produce sex differences in feeding time (Harrison 1983). If high quality food can be monopolized by males, and the alternatives for females are poor, then males might actually be expected to feed for less time than females when they would ordinarily feed for similar times. This explanation has been evoked to explain rank differences detected when high quality food is clumped (see section 2.5.1.4).

No differences between the sexes in overall social time have been found (*baboons* Post 1981; *woolly monkeys* Defler 1995; *chimpanzees* Doran 1997). However, sex differences between time spent in affiliative versus agonistic social behaviours have been detected; females spend more time in affiliative social interactions (*vervets* Baldellou in litt.; Isbell & Young 1993) and less time in agonistic interactions (*baboons* G.W. Norton unpublished data) than males. Such differences are to be expected as a consequence of the female bonded structure of vervet and savannah baboon societies (Wrangham 1980).

Sex differences in time spent moving (*baboons* Barton 1989; *woolly monkeys* Defler 1995; *chimpanzees* Doran 1997) and time spent resting (*woolly monkeys* Defler 1995; *chimpanzees* Doran 1997) have not been found to date.

2.5.1.3 Reproductive status

The costs of reproduction borne by females can not only affect sex differences in time budgets but may also lead to differences between adult females in different reproductive states. Cycling, pregnancy and lactation all place different constraints upon use of time by females (e.g., Altmann 1980; Kenyatta 1995).

Changes in the energetic demands of reproduction would be expected to result in differences in feeding time. Energetic demands increase as pregnancy progresses and are highest during lactation. Early lactation, when the infant is solely dependent on its mother and growing most rapidly, is particularly demanding (Lee 1987). The prediction of elevated feeding times during pregnancy and lactation has been supported by several studies on baboons (*olives* Barton 1989; Silk 1986; *yellow* Altmann 1980; *gelada* Dunbar & Dunbar 1988). However, studies by Kenyatta (1995 *olive baboons*) and Post et al. (1980 *yellow baboons*) suggest that elevation of feeding times during lactation may be suppressed under drought conditions. This supports Barton's (1989) suggestion that the energetic costs of reproduction may be borne by females in all stages, if cycling females have to gain weight lost during more directly demanding phases.

Potentially important constraints may be placed on locomotion by increased body bulk during pregnancy and by having to carry infants after birth (Altmann & Samuels 1992). The later stages of pregnancy and early post natal stages are likely to be most restrictive especially to movement in trees. These costs are mostly borne by the female although in callitrichids, where twin births are normal, males do help to transport infants after birth (Kleiman 1977). Restrictions imposed can slow movement and this could be compensated for by an increase in time spent moving.

2.5.1.4 Rank

Higher ranking individuals, generally by definition, can supplant lower ranking individuals from food items (Drews 1993). Higher ranking individuals therefore have greater dietary choice (Barton 1989; Gautier-Hion 1980) and should be able to fulfill their dietary needs in less time. However this differential may only operate when high quality resources are highly clumped and easily monopolized. If resources are dispersed, or patches are large relative to group size, supplanted individuals can readily obtain good alternatives; an argument that could also apply to priority of access mediated sex differences (section 2.5.1.2). Data are consistent with this prediction. Studies of wild baboons have found no association between rank and feeding time (*olives* Barton 1989, *yellows* Post et al. 1980) except where garbage pit raiding occurs and high quality and clumping of food resources are extreme (Altmann & Muruthi 1988). Similar observations have been made on vervets (Isbell & Young 1993; Whitten 1983).

If subordinates are being supplanted more often, this could be detected as an increase in moving time. Isbell & Young (1993) found that lower ranking females moved more than higher ranking females but found a reverse trend in males. This could be related to more agonistic interactions occurring between males (section 2.5.1.2).

2.5.1.5 Age

Body size accounts for some differences in feeding time between age classes ie., smaller bodied younger animals spend less time feeding (*vervets* Harrison 1984; *yellow baboons* Post et al. 1980). However, the most obvious difference between adult and pre-adult age classes is manifested in their social time. In common with other young mammals, pre-adult primates devote up to 10% of their time to play, either social or non social (Bekoff & Byers 1992). Since play is not a common feature of adult behaviour, this alone is a noticeable difference between individuals in different age classes. Social play can account for higher social time in infants and juveniles compared to adults as, for example, found for woolly monkeys by Defler (1995). When environment conditions are harsh, play behaviour is reduced in order to allow more time for higher priority activities (Barrett et al. 1992; Lee 1984; Sommer & Mendoza-Granados 1995) and consequently time budgets of young and old become more equitable.

Time budgets also vary within age classes. Changes associated with early development and weaning, e.g., increasing exploratory behaviour, have been found (*tufted capuchins* Byrne & Suomi 1995; *yellow baboons* Wasser & Wasser 1995). Few data are available on behaviour changes that accompany ageing in adults (but see Davis & Leathers 1985). Within the adult class, differences related to the ageing process would be expected to manifest themselves in time budgets. For example, if teeth wear down, this may make feeding less efficient and lead to longer feeding times.

2.5.1.6 Disease

Although the effects of disease on time budgets can be easily hypothesized (e.g., a high parasite load could increase nutritional needs and result in greater feeding time) they have not been directly tested. Alternatively, natural selection may have favoured animals whose disease condition is not reflected in their time budgets. The advantages of this include not looking or being vulnerable to predators. This topic awaits detailed investigation.

2.5.1.7 Internal state

Decisions about how to spend time are affected by internal state (Alcock 1996). For example, if an animal is hungry, it will be motivated to spend time moving to and consuming food. This in turn could underlie peaks of early morning feeding after the night time fast. Although internal state can undoubtedly act as a proximate causation of some types of variation in time budgets, the link between the two remains unexplored for free-ranging primates.

2.5.2 Social Environment

An animal's social environment is provided by the other members of its group. Two important features of this environment are how many group members there are (i.e., group size) and who these group members are in terms of age-sex and relatedness (i.e., group composition).

2.5.2.1 Group size

Three main approaches have been taken to assess the effect of group size (cf. foraging party size, Chapman 1988b; McFarland-Symington 1988a&b; Sakura 1991) on time budgets. Firstly, comparisons can be made between coexisting groups of different sizes (*chacma baboons* Cowlishaw 1993; Whiten et al. 1987; *capuchins* de Ruiter 1986; *vervets* Isbell & Young 1993; *gelada* Iwamoto & Dunbar 1983; *yellow baboons* Stacey 1986, *spider monkeys* Strier 1987; *macaques* van Schaik et al. 1983; *mangabeys* Waser 1977; *gorillas* Watts 1988). Secondly, if group sizes change over time, within group comparisons can be made (*mangabeys* Barrett 1995; *yellow baboons* Bronikowski & Altmann 1996; *vervets* Isbell & Young 1993; *gorillas* Watts 1988; *tamarins* Garber 1988). Thirdly, groups from different populations during the same or at different times can be compared (*baboons* Dunbar 1992a).

Comparisons of time spent feeding between groups have demonstrated most possible pattern: smaller groups feeding for more time (*capuchin* de Ruiter 1985, *woolly spider monkeys* Strier 1987), smaller groups feeding for less time (*baboons* Cowlishaw 1993, Stacey 1986; *managbeys* Waser 1977) and no significant relationship between feeding time and group size (*vervets* Isbell & Young 1993, *long-tailed macaques* van Schaik et al. 1987[1]; *chacma baboons* Whiten et al. 1987). The overall picture is similarly inconclusive for within group data, although there has been no demonstration of feeding time decreasing with increasing group size. Barrett (1995 *mangabeys*) and Watts (1985 *gorillas*) have both found within group variation in group size to be positively correlated with feeding time. However, Watts concluded that variation associated with group size was " very small and less than that associated with variation among vegetation zones" (Watts 1985: 206). Studies on baboons and vervets in Amboseli indicate no statistically significant association between group size and feeding time (Bronikowski & Altmann 1996[2]; Isbell & Young 1993). Garber (1988) found no association between group size and feeding time in mixed troops of tamarins.

Very few studies have considered other time budget components but the pattern of inconsistency does appear to be repeated in the limited data available. Individuals in larger groups have been found to spend more time moving (*vervets between* groups Isbell & Young 1993; *mangabeys* Waser 1977), less time moving (*woolly spider monkeys* Strier 1987) and similar time moving (*capuchins* de Ruiter 1986; *vervets within groups* Isbell & Young 1993; *baboons* Stacey 1986; Whiten et al. 1987); more time resting (*vervets within groups* Isbell & Young 1993) and similar time resting (*capuchuns* de Ruiter 1986; *vervets between groups* Isbell & Young 1993; *yellow baboons* Stacey 1986); more time socializing (*vervets within groups* Isbell &Young 1993) and similar time socializing (*baboons* Stacey 1986; Whiten et al. 1987).

Cases where no relationship between group size and time budgets are detected may also be explained if group size effects only manifest themselves above a threshold level. Waser (1977) pointed out that in a heterogeneous environment, patches may contain sufficient resources to support additional individuals at no extra energetic cost. He estimated that this threshold group size was 12 to 15 for mangabeys in Kibale Forest.

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[1] This paper states that feeding time increases with increasing group size. However, this conclusion is actually restricted to feeding on dispersed items. When feeding times on clumped and dispersed food items are combined there is no significant relationship between group size and feeding time (Kendall rank correlation n=5, T=-0.60, p=0.14; group sizes from their table 1, feeding times estimated from their figure 3 for group activity - text reports similar pattern for individual data.)

[2] Kendall Rank correlations on data in their table 2: Alto's group n=9, T=0.03, p=0.92; Hook's group n=9, T=-0.11, p=0.67.

Thus it appears that no consistent relationship between group size and time budget components has been found. However, although not normally a main time budget component because of its event-like characteristics, vigilance does appear to show a consistent pattern. Studies of individual vigilance behaviour in relation to group size show a common trend. Individuals in larger groups spend less time scanning their environment than individuals in smaller groups (*chacma baboons* Cowlishaw 1993; *capuchins* de Ruiter 1986; *vervets* Isbell & Young 1993; but see critical review in Elgar 1989).

Both Isbell & Young (1993: 383) and van Schaik et al. (1983: 174) give comprehensive lists of factors potentially confounding their within and between group comparisons. These include population decline, rate of predation, quality of home range, group fusion, temporal variation and observer differences.

2.5.2.2 Group composition

The composition of a group in terms of age-sex and relatedness of its members may influence time budgets and other aspects of behaviour in two ways. As Dunbar (1988:96) puts it: "First, it imposes constraints on the choice of social partners open to them. Secondly, it may influence the level of competition for access to specific resources, thereby increasing the costs of obtaining that resource or limiting the animal's access to them."

Studies have concentrated on relating specific aspects of social behaviour to demographic descriptors such as sex ratio (e.g., de Waal as reported in Dunbar 1988:101) and number of play partners (e.g., Lee 1986). These relationships, while important in determining detailed patterns of socialization, probably have little consequence on how much time is spent socializing overall.

2.5.3 Ecological Environment

An animal's ecological environment comprises its abiotic and biotic surroundings with the exception of other group members which make up its social environment as discussed in the previous section. The ecological environment provides resources, such as food, water and refuges. It also presents hazards, such as predators, other troops and climatic extremes.

2.5.3.1 Resources

Although food is by far the most often investigated resource (e.g., Clutton-Brock 1977a; Post 1978), resources also include water and refugia. The defining features of any resource are its quantity, quality and distribution. All of these can vary in both time and space and each is potentially a major determinant of intraspecific variation in time budgets. Temporal variation of resources mostly occurs on within year and between year scales. For example, vegetable food resources generally vary from one season to the next and from one year to the next, rather than from hour to hour. Although, some resources, such as insect food and dew, can vary within days.

The quality of a resource refers to its content and determines the benefit gained. The quality of food is also defined by the immediate costs of its acquisition. If food resources are good, less feeding time will be needed in order to fulfil the animal's requirements. Thus food quality depends not just on its calorific value but on the specific nutrients it provides e.g., proteins, vitamins, (Johnson 1989; Clutton-Brock 1977a) and its ease of harvesting, handling, processing and digestion.

The distribution of resources describes their spacing and determines the costs of locating the resource, both in terms of energetic expenditure and risk. The distribution of food items ranges from clumped in small, discrete and widely spaced patches (i.e., highly patchy) to evenly dispersed over large areas (i.e., non patchy or very large patches) (Barton 1989; G.W.Norton unpublished data.). Time spent moving to find food depends on the size and spacing of patches as well as the distribution of food items within patches.

Resources are often described as better or worse in certain places or at certain times of year. Although this grossly simplifies a complex classification based on the three characteristics of quantity, quality and distribution, it can still be useful to a limited extent. At their best, resources are high in quantity and quality with a closely spaced distribution. At their worst, they are low in quantity and quality with a widely spaced distribution.

The distribution of food is much harder to measure than its quality or, especially, quantity (Barton 1989). However, any direct assessment of resources accompanying behavioural observations requires additional equipment and effort. For this reason, within year variation has traditionally been described in relation to climate, with time budgets at wet times of year being compared to time budgets at dry times. This is based on the mostly untested assumption (Barton 1989; Clutton-Brock 1977a) that rainfall can be used as an indirect measure of resources (section 2.5.3.2). In most, but not all, cases food resources have been assumed to be better in wet rather than dry months (Clutton-Brock 1977a). There is a trend in more recent studies to carry out vegetation monitoring independent of behavioural observations (Barton 1989; Barrett 1995; Cowlishaw 1993; Kenyatta 1995; Norton et al. 1992; Robinson 1986) so that the assumption is tested at least for vegetable food resources. In those study sites where climate shows clear seasonality (i.e., all those cited except Barrett 1995), the general conclusion has been that wetter times of year are better times for food, although the relationship may be lagged (Barton 1989).

Whilst it seems clear that food resources can influence how primates spend their time, the exact responses of different species, and even different populations of the same species, varies. Clutton-Brock (1977a:552) posits that when food availability declines, non-migratory animals might be expected either to:
(1) increase search time (accepting increased energetic costs of food-finding);
(2) reduce selectivity (accepting decreased benefit per capita from reduced food quality).
These strategies cannot be distinguished on the bases of changes in time spend feeding in relation to food availability. In both cases, feeding time would have to increase to compensate for increased cost or reduced benefit. However, search time (which would be reflected in time spent moving) would be predicted to increase for the first strategy but not the second.

The optimal strategy will be that which allows the animal to maintain the most favourable cost: benefit ratio. This, in turn, will depend both on intrinsic and extrinsic (ecological) factors. As an example of the former, the use of cheek pouches by cercopithecine monkeys probably helps them to reduce the increased energetic costs of food-finding in strategy (1) (Gutierrez-Diego et al. 1998; G.W.Norton & D.M.Hawkins unpublished data); whereas, the digestive system of colobine monkeys helps them to reduce the decrease in benefits gained from feeding on lower quality food in strategy (2).

A complication to these predictions relating feeding time to food availability, is that an animal's feeding time may be constrained by other time budget components e.g., time for socializing to maintain group cohesion (Dunbar 1988) or for resting time in order to digest food or for thermoregulatory reasons (Knight 1998).

The discussion so far assumes that an *energy maximizing* strategy is being adopted i.e., that net energy gain is translated into increased reproductive success (Schoener 1971). However, it must be considered that an animal can reach a threshold above which further net energy gain is not translated into increased reproductive success. At this point a *time minimizing* strategy becomes optimal. If food availability decreases, an animal that is above this threshold would be expected to employ neither strategy (1) or (2) but to accept a loss in mass. In general, the closer the animal is to this threshold the smaller the increase in feeding time accompanying reduce food availability would be need to be; a decrease in feeding time may even be favourable.

In short, a complex array of factors underlie the relationship between time budgets and resources. Moreover, methodological problems make even preliminary interpretation of existing data (e.g. Agetsuma 1995a; Altmann & Altmann 1970; Barton 1989; Barrett 1995; Clutton-Brock 1977a; DaSilva 1992; Isbell & Young 1993; Iwamoto & Dunbar 1983; Mitani 1989; Post 1982, 1978; Robinson 1986; Sharman 1981; Silk 1986; Waser 1975; Watts 1988) in relation to the predictions outlined above problematic. For example, time budget data may not be comparable between studies due to differences in sampling and definition (Clutton-Brock 1977a; Dunbar 1988:90-91; Post 1978:15-17). Another very important consideration is whether assessment of food resources is based on assumption or data and what characteristics are being considered.

An illustration of how difficult it is to interpret even the most consistent and clear findings comes from studies of garbage and crop raiding primate groups. Raiders feed for significantly less time than their wild feeding counterparts (Altmann & Muruthi 1988; Eley et al. 1989; Muruthi et al. 1991). However, is this because they are adopting a time minimizing strategy or, is it because humans frequently chase them from their food?

2.5.3.2 Climate

Climate can affect time budgets directly and indirectly. Indirect effects are mediated by other aspects of the animal's ecological environment, particularly those provided by vegetation (see previous section). The indirect effects of climate on resources are the most important focus for answering many questions in behavioural ecology. However, it is useful to understand the full climate-vegetation-behaviour relationship in the context of modelling behaviour using climatic parameters.

Regular midday rest periods of mangabeys in Kibale during the wet months may be a consequence of rain storms which occur at this time of day (Barrett 1995). In this example rainfall is acting directly on behaviour. However, its indirect effects are generally assumed to predominate (Dunbar 1992a). Resource characteristics (section 2.5.3.1) are affected by both the amount and pattern of rainfall. Rainfall has a potent effect on biomass and other features of vegetation (e.g., Walter 1973; Woodward 1987) as well as the availability of drinking water. This effect is not likely to be immediate and are more probably lagged as Barton (1989) has shown. Seasonal patterns of rainfall, time budgets and resources were discussed in the previous section.

Temperature may also have an indirect effect on time budgets via growth and condition of vegetation (Dunbar 1992b). The availability of insect foods can also be highly dependent on temperature e.g., The amount of time Yakushima Macaques spend feeding on insects is positively correlated to temperature, probably reflecting increased availability of this food type (Agetsuma 1995a).

Temperature has a strong direct effect on thermoregulation. Thermoregulatory mechanisms buffer body temperature against extremes of ambient temperature. These mechanisms can be either physiological (e.g., sweat when hot, shiver when cold) or behavioural (e.g., rest more when hot and less when cold) (Schmidt-Nielsen 1990). Both physiological and behaviour mechanisms have consequences for time budgets. Physiological mechanisms increase an individual's demand for food for metabolic energy and hence more feeding would be predicted in extreme conditions. Such demands will be constrained by the availability of food and water in the environment. In general, behavioural mechanisms should manifest themselves in increased resting in hotter times of the year and, more specifically, at hotter times of the day. Resting in shade increases the effectiveness of behavioural thermoregulation. This strategy will therefore be constrained by the availability of shade.

Primates which dwell in temperate regions or at high altitudes (e.g., *Japanese macaques on Yakushima Island* Agetsuma 1995a&b; *gelada baboons on the Ethiopian Highlands* Iwamoto & Dunbar 1983) have to cope with overcooling as a major problem rather than overheating. The majority of primates are tropical species that do not live at extreme altitude (Smuts et al. 1987) and have to cope with extreme heat but may also experience low temperatures overnight.

Some indication of the specific temperatures at which problems are experienced comes from work by Muller et al. (1983). These researchers studied two adult male colobus and two adult male Skyes monkeys. They found that low temperatures had little effect but that normal body temperature could not be maintained above 33.5-35.5 degrees Celsius. The thermoneutral zone extended from approximately 5 to 28 degrees Celsius in both species.

The effects of temperature and rainfall may interact. Stelzner (1988) observed that opportunistic behavioural thermoregulation in the Amboseli baboons increased with availability of shade (provided by vegetation and indirectly affected by rainfall) and ambient temperature. The baboons moved more slowly and rested more often when they encountered shade and temperatures were high. Pochron (1999) has shown that heat load reducing behaviours by baboons in Ruaha National Park are constrained in the dry season by the need to meet nutritional requirements. Rainfall and temperature may also interact via humidity. More rainfall leads to higher humidity and this can impair an animals ability to cool evaporatively.

The demands of physiological and behavioural thermoregulatory mechanisms on time budgets are potentially in conflict e.g., increasing feeding time to serve physiological mechanisms reduces time available for resting. Resolution of this conflict will depend on the availability of constraining resources and absolute value of the ambient temperature.

2.5.3.3 Predators & competing groups

It is easy to postulate how strategies to avoid predation could influence time budgets. For example, in order to avoid predation baboons may choose to travel longer, but less risky, routes to food trees. This risk may be actual or perceived; it may be associated with the likelihood of encountering predators, or the ability to detect them (e.g., poorer visibility in denser vegetation leads to reduced ability to detect predators). The consequent effect on time budgets would be more time spent moving. However, because the effects of predation are highly linked to habitat and group size (Cowlishaw 1993), they are most often studied and considered in relation to these two factors (sections 2.5.3 and 2.5.2.1).

Other groups may affect access to resources and patterns of movement, and consequently time budgets, in a similar way to predation. Inter-group competition is largely determined by relative group sizes and patterning of resources (Wrangham 1980). Thus, as with predation, its effects are closely linked to habitat and group size.

2.6 FUNCTIONAL EQUATIONS

An obvious conclusion from the previous section (2.5) is that consistent patterns of variation in time use by primates in relation to specific individual, social or ecological features are rare. This is particularly the case for broader scales of comparison, for example, interpopulation as opposed to interindividual differences. Even though interpopulation comparisons are more vulnerable to problems consequent of methodological differences, underlying causal factors also become more complex.

The approach primarily developed by Dunbar (1988, 1992a, 1996; Chapter 1) uses stepwise multiple regression to describe variation in time budgets of baboons, at a gross scale, in relation to a few simple-to-measure meteorological variables and group size. In this way, the apparently bewildering patterns of variation observed are reduced to relatively simple mathematical equations. These equations can be seen as models of time budgets or, to use Dunbar's terminology "functional equations". Although cause and effect cannot be directly inferred from these functional equations, they facilitate the hypothesis and investigation of causal relationships.

As already stated, the functional equations focus on a broad scale of variation. In terms of interspecific and intraspecific variation (section 2.4.1) they operate on the intraspecific, inter-population/study level. On a temporal scale, the time budget data used are figures averaged across one or more years. The functional equation approach assumes that, by averaging out a lot of detail, large scale patterns will be revealed. However, this assumption remains to be tested and other scales of variation should not necessarily be ignored in the assessment and application of the functional equations. For example both interindividual (Chapter 5) and different time scales (Chapter 6) should be assessed in relation to the sampling regimes used to collect data used to generate the equations.

2.7 SUMMARY

An (individual) time budget refers to the duration an animal spends in its primary state-like behaviours; for primates these are generally regarded as feeding, moving, resting and socializing and account for more than 98% of its day. The two main methods used to collect data on time budgets are individual activity records and individual follows. Of these, the latter is less vulnerable to bias and should be the favoured technique. Within individual follows, continuous or instantaneous sampling is the best method for estimating duration but, the merits of using one-zero sampling to explore features of behaviour other than duration should not be neglected.

Comparison between individual time budgets can be made on different scales ranging from interspecific to intraindividual and from annual to within day cycles. Patterns of variation in time budgets in relation to individual, social and ecological factors are complex, as are the potential underlying causes of this variation. Understanding scales of variation and comparing only studies using compatible methodology can reduce this complexity.

Multivariate stepwise regression has been used to describe broad scale intraspecific variation. This technique generates functional equations which model time budgets using climate and group size as predictors. Whilst not directly inferring causality, they do act as a helpful descriptive and investigative tool. However, narrower scales of variation must be understood and taken into account if the power of this approach is to be maximized.

CHAPTER 3. GENERAL METHODS

3.1 INTRODUCTION

This research was conducted in Mikumi National Park in association with the long-term baboon project established in 1974 (Norton & Hawkins 1996; Rhine 1986). Pilot work for this study took place in July & August 1992 during which time preliminary observations of baboon behaviours were made and vegetation plots were set up. Collection of data on baboon behaviour for this study began in July 1993 and ended, 26 months later, in August 1995. Data from vegetation monitoring used for this thesis come from a 21 month period from December 1993 to August 1995.

This chapter describes the study site (section 3.2) and provides details of the collection of raw data on the baboons (section 3.3), vegetation (section 3.4) and climate (section 3.5). Data management for the baboon (section 3.3.4), vegetation (section 3.4.3) and climate (section 3.5.3) data is outlined and an overview of statistical analyses given (section 3.6). Further details on data processing and analyses can be found in the appropriate results chapters.

3.2 STUDY SITE

3.2.1 Location & General Features

Mikumi National Park covers an area of 3,300km^2 in central Tanzania, 300km west of Dar es Salaam (Fig 3.1; inset) and is contiguous with the Selous Game Reserve to the south. The north of the park is centred on the seasonally flooded Mkata floodplain. To the east, west and south the land rises into wooded hills. In the transition zone between the floodplain and the hills there is a complex mosaic of different vegetation types. Drainage systems create watercourses called "korongos". These flow from the hills to the floodplain where they join the central Mkata drainage system and river.

3.2.2 Climate & Fire

Mikumi National Park experiences a unimodal pattern of annual rainfall. The dry season lasts from June to November, the remainder of the year is the wet season. Based on an array of ecological criteria, Norton (1994b) suggests further division of the annual cycle into quarters as summarized in Table 3.1.

Figure 3.1 Mikumi National Park and its location within Tanzania (inset).

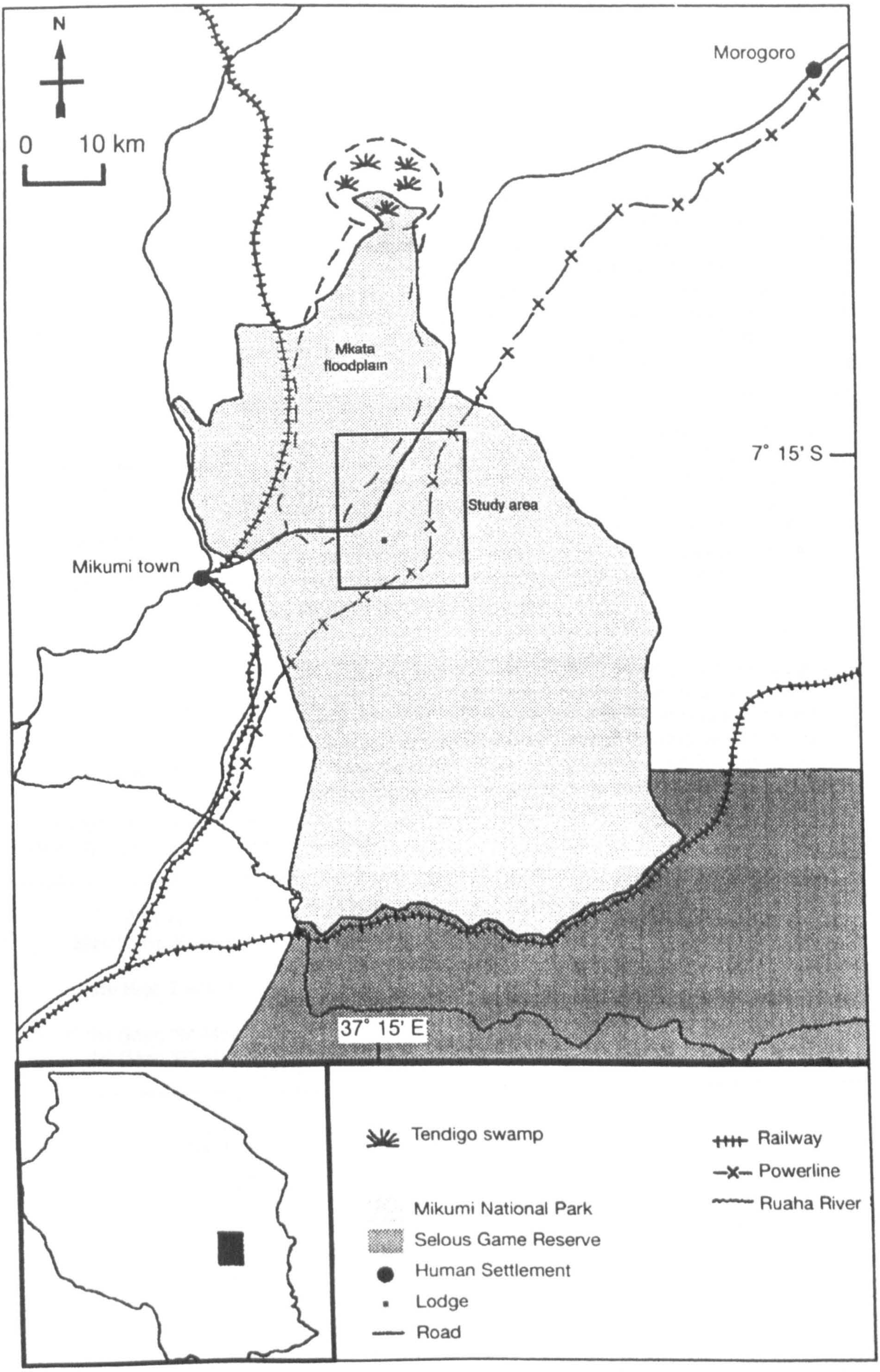


Table 3.1 Definition of seasonal quarters (after Norton 1994b).
The first column includes the term used to identify the quarter in the text, the months falling in that quarter, the alternative name (in italics) and the specific quarters falling within the main data collection period of this study.

QUARTER	**DESCRIPTION** (modified from Norton 1994b)
DRY 1: **June, July, August** ***Early Dry Season*** Dry1 '93 (June-Aug. '93) Dry1 '94 (June-Aug. '94) Dry1 '95 (June-Aug. '95)	Little or no rain falls and temperatures are relatively cool. Cover density declines as natural falling of grasses is expedited by foraging of large ungulates and fire. Fires which occur are relatively cool early burns may occur late in the quarter, but are usually localized and leave considerable unburned or partly burned cover. Free standing water is abundant for most of quarter in permanent water holes, watercourses, depressions and buffalo wallows.
DRY 2: **September, October, November** ***Late Dry Season*** Dry2 '93 (Sep.-Nov. '93) Dry2 '94 (Sep.-Nov. '94)	Conditions are dry and dusty except for possible rain in late November. Temperatures increase as the quarter progresses. Electric storms are common in latter part of quarter, usually at night. Fires in this quarter tend to be hot late burns which remove most of the remaining perennial and annual cover, most of which has gone to seed. There is a gradual decline in freestanding water and increasing faunal dependence on permanent waterholes.
WET 1: **December, January, February** ***Early Wet Season*** Wet1 '94 (Dec. '93-Feb. '94) Wet1 '95 (Dec. '94-Feb. '95)	Rain falls regularly in this quarter. Temperatures are hot and humidity is high. Grass flushes occur especially in burned areas. There is rapid growth of herbaceous species. Grass height and density increases through the quarter, replacing herbaceous cover. Water is commonly available, however, early in the quarter the pattern and amount of rains may result the intermittent availability of rain pools, and other water sources.
WET 2: **March, April, May** ***Late Wet Season*** Wet2 '94 (Mar. '94-May '94) Wet2 '95 (Mar. '95-May '95)	Rain falls in short showers on most days, with occasional days of heavy rain. Rains decline in frequency and intensity at the end of the quarter. Temperatures decrease as the quarter progresses. In many areas the cover is dense and high, especially from grasses. Freestanding water is ubiquitous.

Norton (1994b) also reviews three ways of grouping seasonal quarters into annual cycles: calendar year, ecological year and seasonal year. Data in this thesis are presented by ecological or seasonal year. An ecological year in Mikumi is defined as December-November. An ecological year therefore starts with the wet season, which in turn determines the food and water in the subsequent dry season. The disadvantage of this definition is that the onset of rains is highly variable. Contrastingly, the start of the dry season in June is highly consistent. Thus a seasonal year, which is defined as June-May, reliably contains all the rain from one wet season and one dry season.

Fires are an annual occurrence in Mikumi National Park and a potent force in the ecology of the system. Cooler "early burns" tend to occur in July and August, hotter "late burns" in September and October (Norton et al. 1997; Stronach 1988a&b).

3.2.3 Topography & Vegetation

The vegetation types found in Mikumi National Park are described in detail elsewhere (Lovett & Norton 1989; Hawkins et al. 1996; Norton 1993; Norton et al. 1987; Norton et al. 1992) and are summarized in Table 3.2. As the land rises from the floodplain to the hills it forms a "catena" (Milne 1947). The complex mosaic of vegetation types interwoven with one another found in the transitional zone is characteristic of such topographical forms. It is produced by the interaction of slope and soil with patterns of rainfall and fire. Korongos are lined with thick riverine vegetation except on the floodplain.

Table 3.2 Summary of habitat types found in Mikumi National Park. This classification follows that proposed by Norton et al. (1987).

HABITAT TYPE	NOTES
WOODLAND	*Brachystegia* (miombo) woodland is found on hill tops and upper slopes of catena. On lower footslopes, miombo intermixes with woodland predominated by *Combretum spp.* and *Terminalia spp.* with other habitat types in the transition zone between hills and trees. Over 30 trees per hectare.
OPEN WOODLAND	Occurs in complex mosaic of vegetation types in transitional zone on lower footslopes of slopes. Between 11 and 30 trees per hectare.
WOODED GRASSLAND	Occurs in complex mosaic of vegetation types in transitional zone on lower footslopes of slopes. Between 2 and 10 trees per hectare.
FLOODPLAIN	Seasonally flooded grassland found on Mkata Floodplain. Only 1 or two trees per hectare.
RIVERINE	Riverine vegetation is dense forest or thicket vegetation lining seasonal watercourses called "korongos". Since riverine vegetation generally occurs in narrow strips, the one hectare plots used in this study containing riverine vegetation also includes adjacent vegetation types and are therefore better described as riverine edge.
AFROMONTANE FOREST	An isolated patch of montane rainforest occurs on top of Malundwe Mountain (1,255m) - outside the study area at the centre of Mikumi National Park.

3.2.4 The Study Area

The study area of Mikumi's long term baboon project, and hence of this study, is located near the centre of the northern half of the park (Fig 3.1) The western edge of the study area lies on the eastern side of Mikumi's floodplain (altitude approx. 430m-540m). It then extends eastwards through the transitional zone of the catena into the wooded hills with peaks of over 700m .

The study area contains all vegetation types found within the park except afromontane forest (Table 3.2). A detailed vegetation map of the study area can be found in Norton et al. (1987) and is summarized, along with other features of the study area, in Figure 3.2. The five drainage systems, which run east to west within the study area, are: *Kikoboga, Visada, Viramba, Morogoro* and *Mgoda*. The *Baboon Hills* are a distinctive ridge of hills (altitude approx. 760m) in the core of the Viramba baboons range which are orientated approximately north-south. The *Small Knoll* is separate peak (approximately 720m) south of the Baboon Hills. The *Dell* is a permanent waterhole in the valley between the *Baboon Hills* and the *Small Knoll*. Other permanent waterholes are the *Large Waterhole*, the *Small Waterhole* and the *Pot Hole*. There is also a permanent waterhole just south of the *Pot Hole*.

An imaginary grid is used by the long-term project to record locations within the study area to within 180m. The grid is composed of large and small squares. Large squares are 720m by 720m (approx. area 0.5km^2). Each large square is divided into 16 small squares, 180m by 180m each. These are identified using the co-ordinates 1 to 4 north-south (1 = most southerly) and east-west (1 = most easterly). The full coordinates of a single small square follow the following format: First north-south axis (large square number followed by small square number); then east-west axis: (large square number followed by small square number) (Fig. 3.2).

Figure 3.2 Map of study area (next page with key below). This map is based on personal observations of this author and G.W. Norton, Norton et al. (1987) and Tanzania Ordnance Survey maps 1:50,000 series Y742 (D.O.S. 422) sheets 200/1 ("Doma" Edition 2 D.O.S. 1971) and 200/3 ("Kikoboga" Edition 2 D.O.S. 1970). As an example of how locations are identified using grid locations, as described in the text: the Viramba River crosses the TANZAM Highway at location 022 064.

Vegetation Zones

☐ floodplain

☐ mosaic of grassland, woodland and riverine forest

🟩 wooded hills (Miombo)

═ main road (Tanzam Highway)

┈ road to Tourist Lodge

◆ Mikumi Tourist Lodge

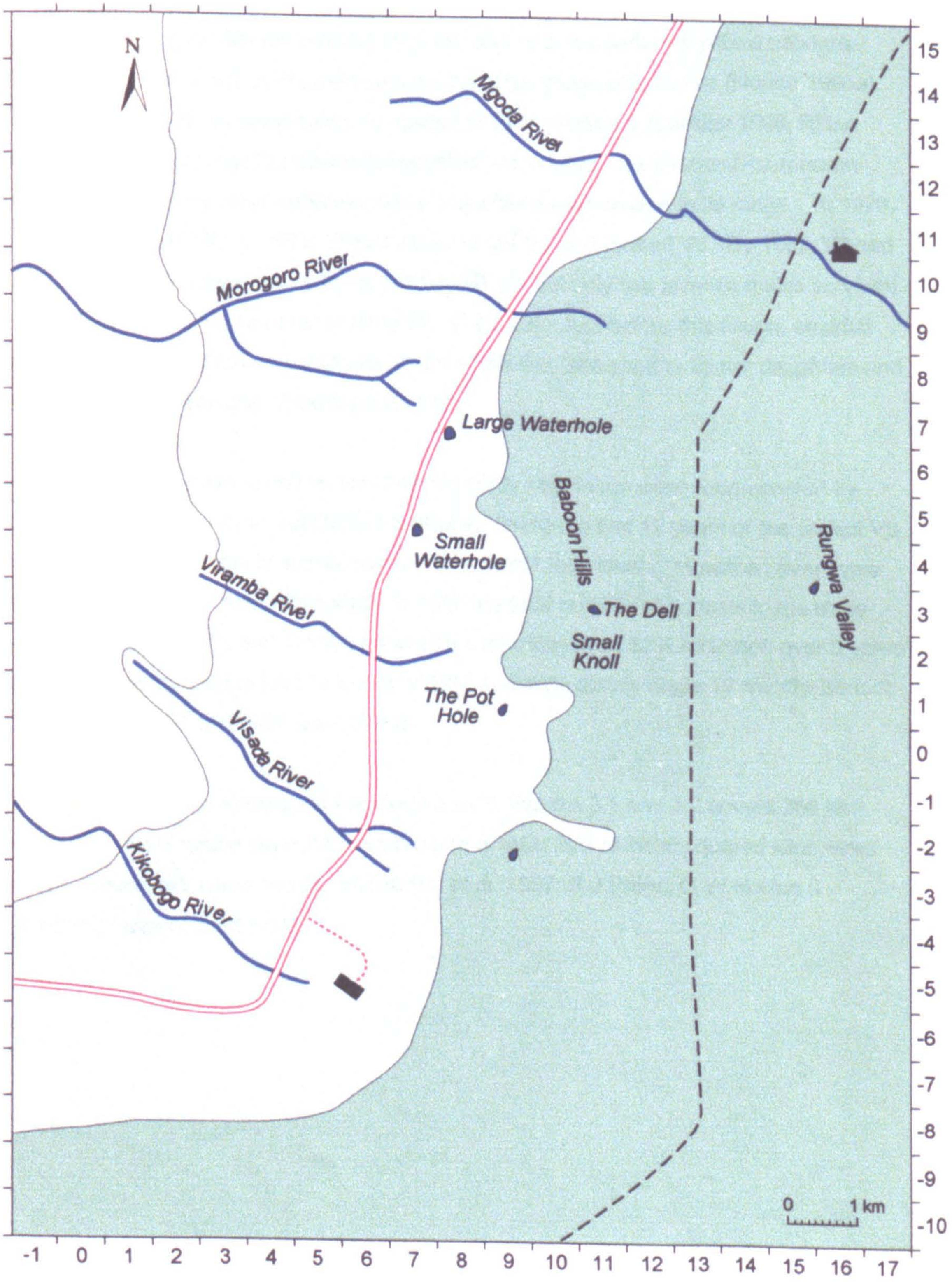
⌂ Mgoda Ranger Post

~ main river channels ("Korongos")

- - - - powerline (approximate location)

● permanent waterhole

Figure 3.2


N
Mgoda River
Morogoro River
Large Waterhole
Baboon Hills
Small Waterhole
Viramba River
The Dell
Small Knoll
Rungwa Valley
The Pot Hole
Visada River
Kikobogo River
0 1 km
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
-1
-2
-3
-4
-5
-6
-7
-8
-9
-10
-1 0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17

3.3 BABOONS

3.3.1 Study Animals

3.3.1.1 History

The baboons found in Mikumi National Park are part of a population of yellow baboons (*Papio cynocephalus*) which is continuous over a large geographical area (Norton 1994a). A long-term study of the these baboons started in 1974 (Norton & Hawkins 1996; Rhine 1986). A single troop was habituated for detailed behavioural observation (Rasmussen 1978) and named "Viramba" (abbreviated to V0) after a watercourse in its range. In 1978, V0 spilt into V1 and V2. In 1979, fifteen baboons left V1 and formed V3. By 1989, V3 had only 8 members and they attempted to merge with V2 but only two juvenile males survived. In July 1994, V1 and V2 reunited to form V4. (Fig. 3.3). Just before this fusion, an adult female (later named Kuvimba) and two juvenile females (assumed to be her daughters and later named Kuongeza and Kicheko) joined V1.

These fission and fusion events in the Viramba study population were accompanied by dramatic changes in overall numbers of animals. During the first 12 years of the project V0 remained relatively stable in size between 115 and 161 individuals. However, every year between 1987 and the end of this study in 1995 the total number of animals in the study population declined (Fig 3.4). This chronic effect resulting in an 82% reduction over 8 years was punctuated by extreme acute losses of 32% and 45% during single 12 months periods ending in July 1990 and 1994 respectively.

The rectangular area indicated as the study area in Figures 3.1 and 3.2 covers 256 km^2. Since 1974, the Viramba baboons have been in at least 200 of these squared kilometres and have made extensive use of 144 (Norton et al. 1987; R.J.Rhine, G.W.Norton & S.K.Wasser unpublished data).

Figure 3.3 Fission and fusion events occurring in the Viramba study population.

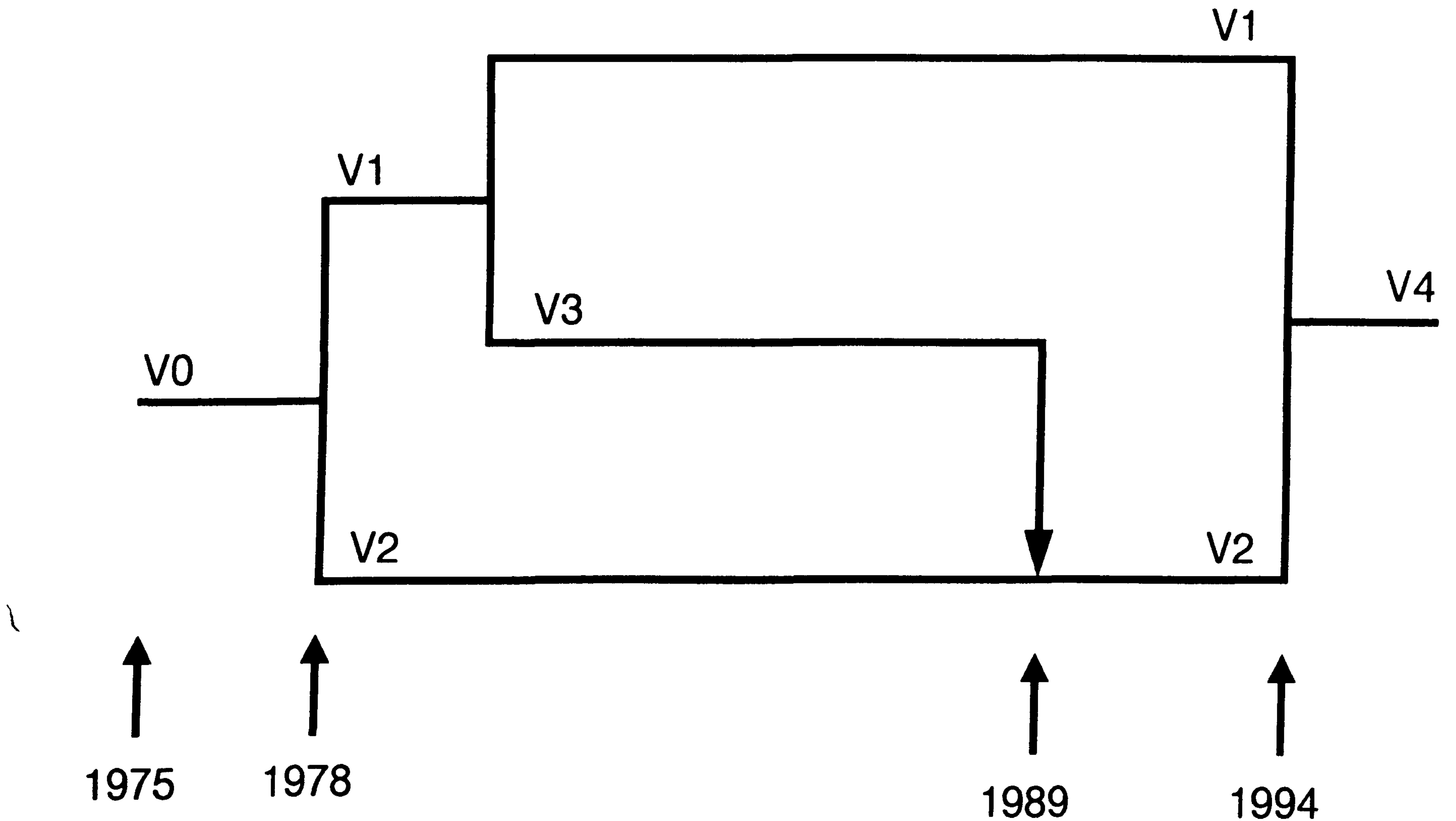
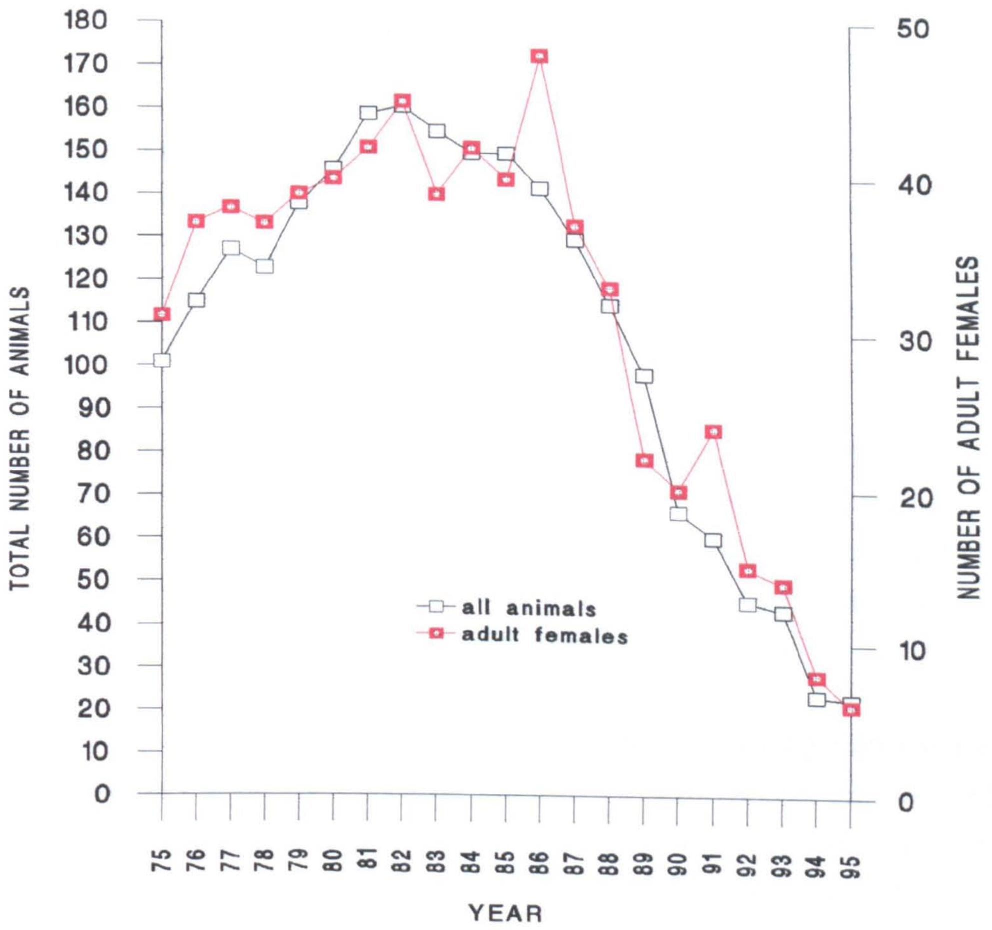


Figure 3.4 Size of the Viramba study population 1974-1997.



3.3.1.2 Population decline: potential causes

The population decline in the Viramba study animals was part of a parkwide phenomenon. Baboons numbers declined by at least 60% and mean troop size declined from 65-70 individuals per troop in 1984 to 30-35 in 1993. There has been a decline in the overall number of troops as well (Norton 1994a).

Population dynamics are a product of the interaction of deterministic & stochastic components driven by life history variables and environmental factors. The resultant changes in population size over time may exhibit any of a wide range of patterns including cyclic or chaotic forms (Begon et al. 1996; Godfray & Grenfell 1993; May 1981; Southwick 1980). Consequently "the reasons why populations decline to small values are many and varied and often ill understood" (May 1994:368). Hence, it is not remarkable that the reason, or more probably reasons, for the rapid park wide population decline in the Mikumi baboons are not immediately apparent (Norton 1994a).

Preliminary analyses of demographic data indicate that the decline in the Mikumi baboon population is not purely a consequence of demographic stochastity (G.W. Norton pers. comm.). The main environmental factors which could be responsible are predation and vegetation change (Norton 1994a). A potential minor factor, especially since 1991, could be road deaths. Observer effects and disease seem unlikely causes.

An increase in leopard sightings, as well as confirmed and suspected predation of the baboons, indicate that increased predation has played a role. However, the size and extent of the decline suggests other factors must also have operated. Vegetation change in riverine patches or on a broader scale within the herb layer could have affected both predation risk and food resources. This could be an interactive problem related to changes in cover, refugia and food foraging requirements as well as limitations on energy. The animals do not appear malnourished but this does not mean that they are not at the survival limit of their energy budgets ("Mitch", Chief Vet. Smithsonian Zoo., pers. comm.). Energetic and other stresses may be making individuals more vulnerable to a host of mortality risks.

The TANZAM highway runs through Mikumi National Park for 50km. Animal casualties on the highway, including baboons, have increased since refurbishment was completed 1991 (Drews 1991; Hawkins 1994). Such events may account for a few of the observed deaths in the study troops but, many of losses occurred before road repairs were completed and from troops which do not include highway areas in their range.

There has been no obvious epidemic disease. Internal parasite loads (monitored by R.Ashford, University of Liverpool) appear to be within tolerable 'healthy' animal limits (Norton 1994a). Observer effects on either baboon or predator behavior (Isbell & Young 1993) can almost certainly be ruled out in Mikumi because decline occurred in both habituated and unhabituated troops.

What triggered the decline is not necessarily its continued propagator, nor is the cause of acute decline necessarily the same as the cause of chronic decline. For example for what ever reasons there are now small troops, they may be more vulnerable to successful predation because of their smallness. Alternatively changes in food resources, mediated by vegetation change, may not only have caused the decline directly but may also have led to increased foraging in areas of high risk from other factors.

3.3.1.3 Composition of troop

The composition of the study population at the start of the data collection period for this study is given in Table 3.3. The age-sex (Table 3.4) and reproductive status of adult females (Table 3.5) were categorized by this study following definitions established by the long-term project and associated shorter term studies.

Behavioural data for this study were only collected on adults and subadults.

Table 3.3a Composition of V1 on 1st July 1993.

Age is given to nearest year for adults and subadults and nearest month for juveniles and infants (y=year(s) and m=month(s)).

NAME (ID Number)	AGE	D.O.B	MOTHER	NOTE
ADULT FEMALES				
Tai (24)	14 y	01/May/79	Subiri	Gave birth Dry 1 '93 Went missing Wet 2 '94
Swali (32)	12 y	17/Feb/81	Shida	Gave birth Dry 1 '94
Kikubwa (38)	11 y	08/May/82	Kadogo	Gave birth Wet 1 '94 & Dry 1 '95
Tanganyka (41)	10 y	14/Apr/83	Mchina	Gave birth Dry 2 '93 Went missing Dry 1 '94
Siafu (56)	7 y	01/Jan/86	Estha	Gave birth Dry 1 '93 & Dry 2 '94
Simu (58)	7 y	19/Aug/86	Gunia	Gave birth Wet 2 '94 Went missing Wet 2 '94
Konda (62)	6 y	01/Jan/87	Mwembambe	Went missing Wet 2 '94
ADULT MALES				
Mvua (238)	?	?	?	
Choma (239)	?	?	?	
SUBADULT MALES				
Mwitalia (134)	8 y	03/Jun/85	Mzungu	
Kiwiko (136)	8 y	01/Aug/85	Mgongo	
Hondohondo (149)	5 y	10/Mar/88	Tai	
JUVENILE FEMALES				
-small				
Kitovu (79)	2 y 9 m.	15/Apr/91	Ubavu	
JUVENILE MALES				
-large				
Gundi (156)	3 y	22/Jun/90	Bahasha	
Volcano (158)	3 y 4 m	10/Nov/90	Dunia	
INFANT FEMALES				
Pemba (85)	1 m	30/May/93	Tanganyika	
INFANT MALES				
Unko (162)	11 m	03/Jun/92	Simu	
Chu chu (164)	5 m	20/Jan/93	Konda	
Panzi (165)	14 days	20/Jun/93	Siafu	

Table 3.3b Composition of V2 on 1st July 1993.
Age is given to nearest year for adults and subadults and nearest month for juveniles and infants (y=year(s) and m=month(s)).

NAME (ID Number)	AGE	D.O.B.	MOTHER	NOTES
Adult Females				
Mtumishi (26)	14 y	04/Jul/79	Asha	Gave birth Dry 1 '95
Kiuno (27)	13 y	21/Feb/80	Mwajuma	Gave birth Dry 1 '93 Went missing Wet 2 '94
Rahisi (29)	12 y	04/Feb/81	Fedha	Went missing Dry 1 '94
Uhai (39)	9 y	07/Mar/84	Mto	Went missing Dry 2 '93
Chukua (50)	8 y	01/Jan/85	Mzigo	Went missing Dry 2 '93
Heshima (54)	7 y	21/Jan/86	Haki	Gave birth Dry 1 '95
Ruaha (55)	7 y	13/Apr/86	Mto	
Adult Males				
Hunzuni (240)	?	?	?	
Subadult Males				
Nyigu (139)	7 y	09/Jul/86	Asali	
Sharubu (142)	7 y	01/Aug/86	Mui	
Bruce (143)	7 y	01/Jan/86	Branga	Transferred out Aug'93
Nidhamu (146)	6 y	24/May/87	Haki	
Tarishi (148)	5 y	16/Jan/88	Mtumishi	
Digi digi (150)	5 y	05/Jul/88	Kidiri	
Msomi (151)	5 y	24/Jul/88	Asha	
Juvenile Females				
-large				
Mjinga (75)	2 y 9 m	01/Apr/90	Jangiri	
Mphishi (76)	2 y11 m	28/May/90	Mtumishi	
Juvenile Males				
-large				
Dalali (160)	3 y 2 m	19/Aug/90	Rahisi	
-small				
Karani (166)	2 y 4 m	14/Nov/91	Mtumishi	
Simba (168)	1 y 1 m	06/Jun/92	Chukua	
Infant Females				
Jamhuri (80)	6 m	08/Jan/93	Uhai	
Hayupo (81)	5 m	12/Feb/93	Rahisi	
Mfanya (82)	3 m	11/Apr/93	Mtumishi	
Tirrika (83)	2 m	27/Apr/93	Ruaha	
Infant Males				
Mungwana (169)	9 days	93176	Heshima	

Table 3.4 Age-sex classes used for Viramba baboons.
Number code given is that used for data collection and data input to computer.

AGE CLASS (number code)	DEFINITION	NOTE
Black Infant (14) -Female (15) -Male (16)	0 to 6 months	Infant changes from black to brown during this time and is predominantly brown by 6 months.
Brown Infant (11) -Female (12) -Male (13)	6 months to 1 year.	
Small Juveniles (8) -Female (9) -Male (10)	1 to 2.5 years	
Large Juveniles (5) -Females (6) -Males (7)	 2.5 years to menarche 2.5 to 5 years	
Subadults (4)	5 years to consort/transfer	Applies to males only.
Adult (1) -Females (2) -Males (3)	 From menarche After consort/transfer	

Table 3.5 The reproductive statuses of females.
Number code used for data collection and data input to computer.

CODE		STATUS	NOTE
Number	**Letter**		
12	M	Menstruating	
11	F1	Flat - post menstruation	
21	E1	Swelling - going up	
22	E2	Full swell	
23	E3	Swelling - going down	
10	FU	Flat - unknown	
31	NVP	Non visibly pregnant	Usually a guess
32	VP	Pregnant	
41	L1	Lactating- first sixth months	With black infant
42	L2	Lactating - second six months	With brown infant
43	L3	Lactating - longer than 12 months	
40	LF	Flat - infant lost	In post partem amenorrhoea

3.3.1.4 Sleeping sites, water & human interference

The baboons in Mikumi National Park sleep in groves of tall trees (Norton et al. 1987). Currently over 100 sleeping sites have been identified and their locations recorded.

Free standing water accumulates throughout the wet season and by the start of the dry season is widely available. As the dry season progresses the baboons become increasingly dependent on permanent waterholes; at least six of these last throughout the annual cycle, even in very dry years. In addition, water usually remains in parts of the Mgoda and Visada water courses (Fig 3.2) all year round. The most important waterhole for the baboons during their late dry season ranging is *The Dell* (Fig 3.2).

The study animals range well within the boundaries of Mikumi National Park and thus do not have the opportunity to raid crops. The Mikumi Tourist Lodge is at the extreme, rarely used, southern limit of their range and they do not raid the hotel's trash pit (although Lodge Troop, whose range overlaps that of Viramba, does). The Viramba range is away from the Park Headquarters and rangers village.

The main human interference of the Viramba animals is via the TANZAM highway. These effects can be direct (e.g., death from being hit by a vehicle, feeding of animals by tourists and other road users) or indirect, through the roads impact on the ecosystem in general. However, the road occupies only a small portion of the study area and the Viramba baboons spend relatively little time in its vicinity (G. W. Norton & S. K. Wasser unpublished data).

3.3.2 Data Collection on Individuals

3.3.2.1 Follow & interval length

Behavioural data were collected during "individual follows"; periods of observation and data collection from a single individual referred to as the "focal" animal (Martin & Bateson 1986). All data were recorded, by hand, on to checksheets. A sampling interval of five minutes was used. Previous studies (e.g., Rasmussen 1978, G.W.Norton unpublished protocol) have found this length to be the most practical under the conditions in Mikumi, which require monitoring of the environment for hazards (e.g., buffalo, lion or elephant). The time taken to do this as a proportion of a five minute interval is small and instantaneous observations are not disrupted.

During the first year, follows of 90 minute length were used, following the protocol of Norton (unpublished). However, observers found that continued concentration for one and a half hours was very demanding. While this long follow length was important for questions being investigated by Norton, there was no *a priori* reason to believe that reducing the length of follows would cause a biasing in time budget data. In addition, pairwise statistical comparisons of percent of follows spent in different time budget components based on 90mins compared to the first 45 minutes of the same follow revealed no more significant results[1] than would be expected by chance using a significance level of < 0.05. Therefore, in August 1994 follow length was reduced, by half, to 45 minutes.

3.3.2.2 Data collected

At the start of each follow the information below was recorded at the top of the checksheet:

- troop (V1, V2 or V4);
- focal name & ID number (Tables 3.3), age-sex (Table 3.4) and reproductive status (Table 3.5);
- date, start time, sampling period (Table 3.6);
- observers name.

---

[1] Wilcoxon Matched-Pairs Test: V1, early dry: n=53, feed Z=-0.42, P=0.67, move z=-1.73, P= 0.08, rest z=-0.60, p=0.55, social z=-1.44, P=0.15;V1, late dry: n=9, feed Z=-0.10, P=0.92, move z=-1.15, P= 0.25, rest z=-0.42, p=0.67, social z=-1.44, P=0.65;V1, early wet: n=50, feed Z=-0.79, P=0.43, move z=-1.17, P= 0.24, rest z=-1.21, p=0.23, social z=-0.04, P=0.97;V1, late wet n=80, feed Z=-0.70, P=0.48, move z=-0.44, P= 0.66, rest z=-0.02, p=0.99, social z=-1.50, P=0.13;V2, early dry: n=33, feed Z=-1.97, P=0.05, move z=-0.59, P= 0.55, rest z=-1.33, p=0.18, social z=-1.88, P=0.06;V2, late dry: n=11, feed Z=-1.84, P=0.07, move z=-1.18, P= 0.27, rest z=-0.98, p=0.33, social z=-1.35, P=0.18;V2, early wet: n=26, feed Z=-0.32, P=0.75, move z=-1.31, P= 0.19, rest z=-0.31, p=0.76, social z=-0.95, P=0.34;V2, late wet n=73, **feed Z=-3.11, P=0.002**, move z=-0.59, P= 0.56, rest z=-1.29, p=0.20, social z=-1.72, P=0.09.

Table 3.6 Time periods used for sampling.

PERIOD	TIME (24 hr clock)
1	07:00-09:30
2	09:30-12:00
3	12:00-14:30
4	14:30-17:00

The occurrence of behaviours (as defined in Table 3.7) were recorded using one-zero and instantaneous sampling (section 2.3). Instantaneous data were used for analysis of state-like behaviours, while one-zero data were used for analysis of event-like behaviours. In addition one-zero data were used to detect temporal association of behaviours within intervals.

Occasionally, the focal was out of sight on the instant and this was noted. In addition, the amount of time, if any, a focal was out of sight during a follow was estimated to the nearest minute and recorded on the instant at the end of that interval.

Table 3.8 indicates how behavioural categories recorded on the checksheets were combined into the main time budget components used for the majority of analyses in this thesis. These main time budget components were chosen to correspond with definitions in Dunbar (1992a).

Table 3.7 Behavioural categories recorded on checksheets and their definitions.
Time focal was out of sight, to nearest minute, during each interval was recorded on the instant. It was also recorded if the focal was out of sight on the instant.

CHECK SHEET CATEGORY	**DEFINITION**
FEED	Focal acquiring food (including searching, digging, harvesting, ingesting but not chewing or swallowing).
CHEEK	Focal chewing or swallowing food from cheek pouches.
MOVE	Focal changing location by more than 5 metres.
SOCG	"Social behavior: affiliative, give". Focal giving affiliative social behaviour (mostly grooming but also eg., lip smack) to conspecific(s) in group.
SOCR	"Social behavior: affiliative, receive". Focal receiving affiliative social behaviour (mostly grooming but also eg., lip smack) from conspecific(s).
AGG	"Social behavior: agonistic, give". Focal giving agonistic social behaviour (eg., supplant) to conspecific(s).
AGR	"Social behavior: agonistic, receive". Focal receiving agonistic social behaviour (eg., supplant) from conspecific(s).
SELF GROOM	Focal scratching or grooming itself.
ORIENT	Focal showing directional vigilance - looking or glancing in one direction with our without moving in short spurts in that direction.
ATTEND	Focal scanning troop and/or looking at conspecific(s).
SENTRY	Focal scanning environment from a raised position (eg., tree, termite mound, rock).
DRINK	Focal drinking free standing water.
INACTIVE	Focal apparently doing nothing.

Table 3.8 Main time budget components used in analyses and corresponding checksheet categories.

MAIN TIME BUDGET COMPONENTS	**CORRESPONDING CHECKSHEET CATEGORIES**
FEED	Feed
MOVE	Move
REST	Inactive, Cheek, Attend, Orient, Self groom, Sentry
SOCIAL	Soc:af+, Soc:af-
OTHER	Soc:ag+, Soc:ag-, Drink

3.3.2.3 Sampling regime

Baboons were followed from the time they were found in the morning (generally in or near a sleeping site) until they were at, near or heading towards a sleeping site for the following night. Follows were conducted between 07:00 and 17:00. This "observation day" was divided into four 2.5 hour time periods (Table 3.6).

Up to two 90 minute or four 45 minute follows were carried out by an observer during each period. The choice of focal for each follow was made according to a "sampling order sheet" compiled by generating a random list of the names of all study individuals. If the next baboon on the list could not be located after a reasonable search then the name after that was selected; the missed individual being returned as the subsequent choice. The choice of focal was also moderated by the requirement to sample each individual as evenly as possible across different periods.

One thousand two hundred and ninety nine (1299) hours of focal follows were conducted during the 26 months of behavioural data collection from July 1993 to August 1995 (inclusive). A summary of focal observation by troop, year and seasonal quarter are presented in Table 3.9.

3.3.2.4 Replication of methods & inter-observer reliability

The methods used for this study follow those of Norton (published protocol). Reliability crosschecks between all observers collecting data for this study and Norton were carried out in the field. Inter-observer reliability within this study was maintained by regular crosschecks and by comparing a sample of follows done by different observers on the same focal at the same time. No inconsistencies were found between observers for the behavioural categories used for the analyses in this thesis.

Table 3.9 Summary of individual follow data.
Number (#) of follows and hours of observation are given by troop and follow length (eg., V1@90mins = 90 minute follows conducted on members of V1). Table also indicates number of days on which follow data were collected from different troops.

YEAR	1				2				3	
QUARTER	**Dry 1**	**Dry 2**	**Wet 1**	**Wet 2**	**Dry 1**	**Dry 2**	**Wet 1**	**Wet 2**	**Dry 1**	**TOTAL**
# FOLLOWS										
V1@90mins	53	6	51	82	63					407
V2@90mins	33	11	26	75	7					
V1@45mins					60					918
V2@45mins					34					
V4@45mins					163	176	185	207	93	
TOTAL	**86**	**17**	**77**	**157**	**327**	**176**	**185**	**207**	**93**	**1325**
# HOURS										
V1@90mins	79.5	9	76.6	123	94.5					
V2@90mins	49.5	16.5	39	112.5	10.5					
V1@45mins					45					
V2@45mins					25.5					
V4@45mins					122.25	132	138.75	155.25	69.75	
TOTAL	**129**	**25.5**	**115.5**	**235.5**	**297.75**	**132**	**138.75**	**155.25**	**69.75**	**1299**
# DAYS OBS.										
V1 only	16	4	18	15	18					71
V2 only	9	7	10	15	4					45
V1 & V2		1	2	12	9					24
V4					22	26	19	30	16	113
TOTAL	**25**	**12**	**30**	**42**	**53**	**26**	**19**	**30**	**16**	**253**

3.3.3 Data Collection on Groups

In addition to data on individual animals, behaviour relating to the group was recorded on the instant inbetween each 5 minute individual follow. This included data on the majority group behaviour used for some analyses in Chapter 6 of this thesis. The following categories were used:

Inactive: Animals appear to be doing nothing

Feed: Animals are involved in the acquisition of food including searching, digging, putting food in mouth.

Social: Animals are interacting with one another.

Orient: Animals are looking in one direction, moving in short spurts in that direction or glancing periodically in that direction

Move: Animals are changing position.

Run: Animals are running.

Drink: The troop is at water and at least 3 animals have drunk.

If animals were more or less evenly engaged in two of these categories, both were recorded. If conditions on an instant were such that an assessment of group activity could not be made, e.g., too few animals in view, this was recorded.

3.3.4 Data Management

Data on checksheets were entered directly into SPSS for Windows 6.0 (SPSS 1993). Two main data files were created. Information at the top of each sheet (date, time, focal name e.t.c.) was input into a file called FOLLOW.SAV; this file contained one line of data per follow. One-zero and instantaneous records were input into a file called DATA.SAV; this file contained 19 (for 90 minute follows) or 10 (for 45 minute follows) lines per follow. A reference number was assigned to each follow and used to identify data in the two files belonging to the same follow.

Data in DATA.SAV were aggregated by follow for percent of non-missed instances on which each behaviour was recorded (instantaneous data) or the percent of intervals during which each behaviour occurred (one-zero data; intervals during which the focal was out of sight for more than one minute were excluded). These aggregated files were merged with FOLLOW.SAV to produce the primary working files for subsequent analyses as described in Chapters 5 to 8 and 9.

3.4 VEGETATION

The vegetation data used in this study were collected as part of a long-term vegetation monitoring programme initiated in July 1992 by this author in collaboration with Herbert V. Lyaruu, Guy W. Norton and Sam K. Wasser (Norton et al. 1992). Collection of basic habitat data and vegetation mapping had been carried out prior to this (e.g., Norton et al. 1987) but, collection of data on important vegetation data had not been formalized into a regular on-going project. The vegetation programme is more extensive than reported; only collection of data used for analyses in this thesis are described.

3.4.1 Plots

The main data for the vegetation monitoring programme comes from permanent plots whose centres' are marked by 4 foot galvanized metal pipes. At each site data are collected from two different plot types: variable radius (based on 11 trees nearest to the plot centre; Hall 1991) and fixed radius (1 hectare). There are currently 52 such plot sites in the study area (Fig. 3.5).

Data used to calculate grass height as well as food, shade and visibility indexes (Chapter 4) were taken from a subset of 32 plots (Fig 3.5) monitored quarterly from wet1 94 to dry 1 95 inclusive. All plots monitored in dry 1 and dry 2 of 1992, 1993 and 1994 were used to calculate percentage of plots fully or partially burned (Chapter 4) in these years (sample sizes were variable and are given in Fig. 4.10).

Figure 3.5 Location of vegetation plots (next page with key below).

Vegetation Zones

□ floodplain

□ mosaic of grassland, woodland and riverine forest

▨ wooded hills (Miombo)

═ main road (Tanzam Highway)

┈ road to Tourist Lodge

◆ Mikumi Tourist Lodge

⌂ Mgoda Ranger Post

∼ main river channels ("Korongos")

---- powerline (approximate location)

● permanent waterhole

Numbers indicate locations of plots used to calculate vegetation indexes and grass height (Table 4.1).

P signs indicate locations of other plots.

3.4.2 Data Collection

3.4.2.1 Tree layer

Data on trees in the variable radius plots only were used in this study. These plots were defined by the 11 trees nearest to the plot centre. When each plot was established its radius was calculated as the mean distance of the two outermost trees from the centre of the plot. The plot radius therefore indicates the size of the plot containing 10 trees (rad_{10}) and is smaller at sites where tree density is higher. Data collected on each tree at the time each plot was set up included its circumference breast height (CBH).

Phenological data were collected both when plots were set up and during quarterly monitoring. Initially only presence or absence data were recorded. In December 1993 (i.e., at the start of wet 1 94), a new protocol was introduced whereby the percent of the maximum possible present was recorded for leaves (lf), flowers (fw) and fruits (fr). Although maximum capacity had to be imagined, consistency between observers was reasonable (same category choosen >90% of the times during crosschecks).

3.4.2.2 Understory

Data on the herb layer were collected during quarterly monitoring from four 100m transects within each fixed radius plots orientated north-south at 20 and 40 metres east and west of the central pole. Data were taken every 10 metres (estimated by taking 10 strides) along each transect generating a total of 44 point samples. Data collected at each point included the identity of any grass, herb or shrub touching the tip of the researcher's shoe and the nearest herb or shrub within 1 metre if grass or bare ground occurred at the toe. These data could then be used in conjunction with the food list published in Norton et al. (1987), to find the number of points out of 44 (p), where a baboon food occurred within 1 metre.

During each monitoring, data on grass height, visibility and fire were also assessed. Grass height was measured at 5 and 10 metres from the centre of the plot in each main compass direction (north, east, south, west). Mean height at 5 metres (H_5) and 10 metres (H_{10}) could then be calculated. Two people were needed to measure visibility. The first would stand at the plot centre and the second 5m or 10m from the plot centre with a 2 metre rule. Starting with their index finger at the top of the ruler this second person lowered their finger it was no longer visible to the person watching them from the plot centre. The height of the finger from the ground at this point was recorded; the lower the visibility the higher the height recorded. This procedure was repeated for 5 and 10 metres in each main compass direction (north, east, south, west). Mean visibility at 5 metres (V_5) and 10 metres (V_{10})

could then be calculated. The percent of each quadrant of each fixed radius plot which had been burned was estimated and recorded.

3.4.3 Data Management

Data on tree circumferences, tree phenology, grass height, visibility and fire were entered directly into SSPS for Windows 6.0 (SPSS 1993). The number of point samples with a baboon food within 1 metre (p) were counted from the raw data and subsequently entered into SPSS.

3.5 CLIMATE METHODS

Climate data used in this thesis comes from park records and from the long-term research project and were made available for this study by Mikumi National Park staff, Ramon J. Rhine, Guy W. Norton and Sam K. Wasser. All temperature data are in degrees Celsius and rainfall in millimetres (converted from inches for earlier records).

3.5.1 Temperature

Daily maximum and minimum shade temperatures were recorded at the baboon project's field station each evening. At the time of writing this thesis these data were available to this author for most months from May 1975 to March 1984 and August 1989.

In addition, as part of the long-term baboon project, air temperatures were measured every half hour when following the Viramba baboons.

3.5.2 Rainfall

Rainfall data have been collected daily at the baboon field station since it was established in 1974. In addition, rainfall data have been collected by park staff from a second rain gauge located at the "Kikobogo Weather Station" since the park was gazetted in 1964. This weather station is located at the park headquarters approximately 100m from the baboon field station. In fact weather data have been collected at the Kikobogo weather station since 1946 (Anon 1984 in Williamson 1997).

The proximity of the two rain gauges monitored by the park and by the baboon research project has proved fortuitous and has enabled baboon researchers and park staff to work in collaboration to maintain a complete and reliable database on rainfall. Analyses of this database for monthly and annual patterns of rainfall from 1964 to 1993 have been reported by Norton (1994b).

3.5.3 Data Management

Most rainfall data were obtained from G.W.Norton already entered into SPSS for Windows 6.0 (SPSS 1993). Additional rainfall and temperature were then added to this data file.

3.6 STATISTICAL ANALYSES

Sample sizes were generally small and data could not be confirmed to be normally distributed. Thus, except for multiple regressions in Chapter 8 and time series analyses in Chapter 9, nonparametric statistics (Siegel & Castellan 1988; Sokal & Rohlf 1981) were used . All statistical analyses, except permutation test, were performed using SPSS for Windows 6.0 (SPSS 1993). Permutation tests were performed by hand. All tests used were two tailed. Null hypotheses were rejected at the 0.05 significance level; the word "significant" in the text indicates the null hypothesis was rejected.

In this thesis, the mean is widely used to indicate the central tendency of data. The use of medians in conjunction with non-parametric statistics was considered because the types of non-parametric tests used in this thesis (all based on ranks) compare medians rather than means. However, means are widely reported in the biological literature even when non-parametric statistics have been used (e.g., Linville et al. 1998; Kotrschal et al. 1998). Most importantly other studies of time budgets, to which data from this study are directly comparable, present means (e.g., Dunbar 1992a). Ideally, all studies using non-parametric statistics should provide both the mean and the median of their data, but this would make reporting cumbersome.

One reason for reporting means rather than medians for behavioural data is that when behaviours are rare the median will be zero and this gives the impression that the behaviours do not occur at all. Moreover, although the mean and the median do not coincide unless data are normally distributed (as stated this was not generally assumed) they are directionally related if the data have similar kurtoses and variances and are skewed in the same direction. Such criteria probably apply to much, if not all, of the data in this thesis. Thus, in terms of illustrating the relationship between samples, the mean suffices whether the data are normal or not, and can provide a useful indication of what animals are actually doing.

For any twenty statistical tests using an alpha of 0.05 and you would expect to find one significant result by chance alone. A way of dealing with this phenomenon for any given set of tests is to use the Dunn-Sidak or the Boneferroni correction method (Table 3.10; Sokal and Rohlf 1995) so that the risk of committing a type I error overall (experimentwise error) does not exceed 0.05. Such corrections for multiple testing are generally not used unless there is some rationale for grouping a set of tests together plus there is some additional reason for being cautious. Where tests are non-orthogonal, there is the additional issue to consider: if the outcome of a single test is significant then the outcome of other tests are more likely to be significant. Sokal and Rohlf (1995) recommend employing the Dunn-Sidak or Boneferroni method (Table 3.10) under such circumstances. While these corrections do not directly deal with the issue of lack of dependence, the use of experimentwise error does make the interpretation of probabilities more conservative. When unplanned comparisons suggested by inspection of the data are made, multiple testing of all possible comparisons is implicit. These tests are typically non-orthogonal and Sokal and Rohlf (1995) again recommend the use of techniques which, like the Boneferroni and Dunn-Sidak methods, are based on generating more conservative experimentwise significance levels.

There are two examples in this thesis where series of tests are non-orthogonal and where correction of the significance levels using the Boneferroni or Dunn-Sidak method (Table 3.10) might be considered appropriate. Firstly, in Chapter 4, results from a series of Spearman rank correlations are reported. However, as these tests were performed only for comparison with similar analyses presented in other studies which did not use these corrections, the corrections were not employed here either. Secondly, for analyses in Chapter 5, data were tested overall, and then broken down into subsets covering different time frames. The need to apply correction factors here is more debatable. Although corrections were not employed,this would be a more cautious approach and reference to Table 3.10 is recommended.

Table 3.10 Effect of applying Boneferroni and Dunn-Sidak methods to a significance level of 0.05. For equations used see Sokal and Rohlf (1995:239-238). Values are given to three decimal places. Sokal and Rohlf (1995: 240) recommend the use of the slightly less conservative Dunn-Sidak method over that of the Boneferroni method. However, the values are very similar and Boneferroni is easier to calculate.

METHOD	NUMBER OF TESTS					
	1	2	3	4	5	6
Boneferroni	0.050	0.025	0.017	0.013	0.010	0.008
Dunn-Sidak	0.050	0.025	0.017	0.013	0.010	0.009

CHAPTER 4: RAINFALL, FOOD & COVER

4.1 INTRODUCTION

4.1.1 Aim

Using data from 18 different baboon populations, Dunbar (1992a) derived functional equations relating time budget components, day journey length and group size to environmental variables (section 2.6). His analyses indicate that rainfall is a key factor underlying interpopulation variation in baboon time budgets. The precise causal mechanism by which rainfall has this effect has not been established. Dunbar's work suggests that indirect effects mediated by plant foods are most important; higher and less seasonal rainfall leading to more and less patchily distributed food and hence lower constraints on time budgets. Dunbar identified the foods in the shrub/herb layer as being generally the most crucial but recognized that this may vary between habitats. Aspects of vegetation other than those providing food may also play an important role in the indirect effect of rainfall on baboon behaviour in some habitats (section 4.1.2). These other aspects need not necessarily follow a "wetter the better" pattern.

This chapter explores the within and between year relationships of rainfall and aspects of vegetation potentially influencing baboon behaviour in Mikumi National Park. Its aim is to provide background ecological information for subsequent chapters. In particular, it will facilitate the interpretation of intrapopulation time budget variation in relation to rainfall (Chapter 6). Associations between rainfall and vegetation identified in this chapter indicate potential vegetation-mediated causal mechanisms for rainfall-time budget relationships. Lack of associations indicate potential explanations for any breakdown of rainfall and time budget relationships in Mikumi National Park.

4.1.2 Relevant Aspects of Vegetation

Vegetation is a provider of two important resources to animals - food and cover (including shade & refugia). In addition, the structure of vegetation is an important determiner of visibility (of conspecifics, food, water and predators) and of ease of movement. Choosing the appropriate parameters to measure in a study of vegetation in relation to animal ecology has to be both species and site specific.

The selection of appropriate **food** measures can be particularly problematic, but in this study was helped considerably by extensive long-term observation of yellow baboons in Mikumi, in particular from a number of comprehensive feeding studies (Norton *et al.* 1987; Rhine & Westlund 1978; Rhine *et al.* 1985; Rhine *et al.* 1986; Rhine *et al.* 1989). The catalogue of plant species from which baboons in Mikumi obtain food from one or more parts (flower, seed, fruit, pod, leaf, root, stalk, exudate, bark, other) numbers over 185 - approximately 30% of species occurring in the study area. Ground (herbs, vines & grasses) and tree layers are more important providers of food to the Mikumi baboons than the intervening shrub layer. Reproductive parts of plants (i.e., pods, seeds, fruits, buds, flowers) are a more important food source than leaves.

The baboons in Mikumi seek and even compete for **shade** cast by vegetation, especially tree canopies, particularly during the hottest times of day (pers. obs.). Shade is therefore a potentially important resource for the Mikumi baboons. As endotherms, baboons use both behavioural and physiological mechanisms to regulate their body temperatures (Schmidt-Neilsen 1990). The behavioural use of shade is energetically less costly than relying solely on physiological processes (providing the costs of finding and obtaining the shade are reasonable). In extreme heat, both behaviour and physiology must be employed to avoid heat stress.

Doing vegetation surveys in Mikumi can be far more nerve racking for a researcher than following baboons because baboons tend not to frequent the extremely tall grass (over 3m not uncommon) in which lion, buffalo and even elephant can "hide" (pers. obs.). Humans can not only miss seeing such hazards in tall grass, they can easily lose sight of their fellow field workers. For a much smaller primate restricted to four legs when moving rapidly, tall grass must be at least equally hazardous and it is likely that baboons avoid it for reasons of reduced **visibility**. Thick grass also provides a physical barrier to movement. Although **ease of movement** was not measured directly and is not considered in this chapter, it is likely that it varies with visibility.

In summary, those aspects of vegetation chosen because of their high potential influence on baboon behaviour in Mikumi and analyzed in this chapter are:-

1. FOOD provided by the following layers:-
    i/ ground (herbs, grass seeds, young grass leaves)
    ii/ tree (leaves, reproductive parts);
2. SHADE provided by the tree canopy;

3. VISIBILITY at ground level.

Refugia, including sleeping sites, are provided by large trees. The quantity and quality of these refugia in aspects independent of food, shade and visibility will generally only change on a longer time scale than considered by this chapter.

4.1.3 Rainfall & Vegetation

Throughout the tropics vegetation is strongly influenced by rainfall. This applies to both spatial variation between sites (Archibold 1995; Coe et al. 1976; Deskmukh 1984; Jackson 1989; Le Houerou & Hoste 1977) and temporal variation within sites (within year: O'Connor & Roux 1995; Prins 1996; between years: Jackson 1989; O'Connor & Roux 1995; Prins 1996). The nature of this influence can account for patterns on a biogeographic scale (Archibold 1995; Walter 1973; Woodward 1987) but descriptions at a more refined level are more problematic. Deshmukh's (1984) final statement is indicative: "...there is no real substitute for detailed measurements of true primary production if savanna ecosystems are to be properly understood".

The potential economic value of being able to predict annual variation of crop yields from meteorological data has stimulated research by agricultural biologists (Biswas & Biswas 1979; Gates 1993; Jackson 1989; MAFF 1976; Thompson 1975; Williams et al. 1975). Their findings illustrate general between year and between site patterns connecting rainfall and crop yields, but fail to produce precise predictions of these relationships based solely on rainfall. This is despite the use of fertilizers and pesticides which decrease variability. Spatial variation in soil type is just one of many potentially complicating factors. As McNaughton (1985:282) puts it: "Local edaphic and other environmental idiosyncrasies, therefore, reduce the predictive power of relationships between productivity and rainfall".

The cost, in time, labour and materials, of surveying vegetation regularly are high. The benefits to animal ecologists of being able to assess habitat quality directly from climatic data are considerable. It is therefore important to pursue research into rainfall-vegetation relationships despite the limitations apparent from previous research. It is highly likely, that for given purposes and scales (temporal and spatial), sufficiently informative relationships can be found.

4.1.4 Complicating Factors in Mikumi

Two factors which may confound rainfall-vegetation patterns in Mikumi National Park are:
1) a mosaic pattern of different habitats related to topography and drainage;
2) fire.

The study area incorporates part of the transitional band between wooded hills and seasonally flooded grassland. This band contains a mixture of habitat types (section 3.2.4). Each of which could respond differently to rainfall. Specific investigation of habitat differences is beyond the scope of this study. The effects of habitat type were controlled in this study methodologically through a repeated measures experimental design (section 4.2).

Fire is an important feature of the Mikumi ecosystem (Hawkins 1989) and is known to affect vegetation (Crawley 1986; Crutzen & Goldammer 1993; McNaughton 1985). However, if fire and climate covary, the predictive powers of climate will not be affected. Thus climate can still potentially act as a surrogate for direct measures of vegetation. Within years, for example, fire and rainfall covary at least to the extent that fires only occur in the dry season.

4.2 METHODS

A comprehensive description of the collection of raw data is given in Chapter 3.This section contains further methodological details pertinent to the analyses performed in this chapter.

Analyses are based on quarters and ecological years (section 3.2.2). Quarters are as defined in section 3.2.2 (Table 3.1; e.g., wet 1 = early wet = December, January & February). The definition of an "ecological year" (section 3.2.2; Norton 1994b) is from December to November inclusive. The ecological year takes the title of the calendar year in which most of its months occur e.g., ecological year 1994 started in December 1993 and ended in November 1994. Similarly, December 1993, January 1994 and February 1994 made up wet 1 of 1994.

4.2.1 Vegetation

A subset of 32 plots (Table 4.1) was used for most analyses in this chapter . This subset was chosen because it contained only plots monitored every quarter from wet 1 1994 to dry 1 1995 (a total of 7 quarters) enabling a repeated measures design controlling for habitat type effects.

Table 4.1 Subset of plots used in analyses for Chapter 4.
For definitions of habitat types and map of location of plots see Chapter 3.

VEGETATION TYPE	PLOTS	NUMBER OF PLOTS
Floodplain	14, 15, 18, 19, 38	5
Wooded Grassland	1, 12, 13, 17, 20, 21, 23, 25, 26, 28, 31, 36	12
Open Woodland	16, 27, 30, 40, 41	5
Woodland	2, 3, 32, 33, 34,	5
Riverine edge	7, 22, 29, 44, 45	5

Although plots were monitored from dry 1 1992, phenology was only scored as present/absent before wet 1 1994. Analysis of these earlier data indicated that such scoring was insufficiently sensitive as a measure of resource presence (D.M. Hawkins, H.V. Lyaruu, G.W. Norton & S.K. Wasser unpublished data). The field protocol was improved in wet 1 1994 to give a better quantitative measure (also bringing this study more in line with food assessment methods carried out by other baboon field studies (e.g., Barton 1989; Cowlishaw 1993; Kenyatta 1995).

Table 4.2 details how variables measuring aspects of vegetation potentially influencing baboon behaviour in Mikumi were calculated. The rationale for selecting these variables is discussed in selection 4.1.2. The analyses in this chapter are based on a total of 224 data points (32 plots repeated for each of 7 monitorings).

Table 4.2 Calculation of variables used in analyses for Chapter 4.
Indices were calculated for each of the 32 plots in each quarter and used as data points in analyses.

VARIABLE (Abbreviation)	**FORMULA**	**A MEASURE OF...**
Total tree food index per plot (TTF)	$\frac{\Sigma\,[cbh(lf^*+fw^*+fr^*)]}{n \times rad_{10}}$	amount of baboons food present in trees moderated by area.
Tree leaf food index per plot (TLF)	$\frac{\Sigma\,[cbh \times lf^*]}{n \times rad_{10}}$	amount of leaves eaten by baboons present moderated by area.
Tree reproductive parts food index per plot (TRPF)	$\frac{\Sigma\,[cbh(fw^*+fr^*)]}{n \times rad_{10}}$	amount of tree flowers and fruits eaten by baboons present moderated by area.
Herb food index per plot (HFI)	p	amount of herbs (incl. corms) eaten by baboons. (NB: Raw data collected by step method over same area in each plot.)
Grass height per plot (GH)	mean of $[H_5 + H_{10}]$	grass height.
Tree shade index per plot (TSI)	$\frac{\Sigma\,[cbh \times lf]}{n \times rad_{10}}$	amount of shade provided by trees moderated by area.
Visibility per plot (V)	mean of $[V_5 + V_{10}]$	visibility; the higher the index the poorer the visibility.

cbh = circumference breast height (m)
lf = % canopy with leaves }
fr = % canopy with fruits } * denotes only included if baboons known to eat
fw = % canopy with flowers }
n = number of trees monitored per plot (i.e., 11)
rad_{10} = radius of variable plot radius (m)
p = number of points, out of 44, where a herb known to be a baboon food was recorded within 1m.
H_5 = mean grass height at 5 metres from plot centre north, east, south & west.
H_{10} = mean grass height at 10 metres from plot centre north, east, south & west.
V_5 = mean visibility index at 5 metres from plot centre north, east, south & west.
V_{10} = mean visibility index at 10 metres from plot centre north, east, south & west.

This study considers only broad scale patterns of vegetation and not the influence of specific habitat types. This would be an interesting topic for future research. For example, riverine vegetation is very important ecologically to the Mikumi baboons (Norton et al. 1987) but was only represented in 5 plots used in the analyses for this chapter and none of these contained solely riverine vegetation.

Other baboon studies have used a more frequent monthly, six weekly or bimonthly, regime to assess habitat (Barton 1989; Cowlishaw 1993; Kenyatta 1995) but this study covered a greater spatial scale over a longer period. Ideally, sampling should be all these things - frequent, covering a large area and long-term - but, in low budget field studies compromises have to be made in order that good quality data can be collected consistently on all required variables. Previous research in Mikumi suggested that quarters would be a reasonable functional ecological time unit for this study (G.W. Norton unpublished data).

Both indices (Cowlishaw 1993; Kenyatta 1995) and biomass (Barton 1989) have been used to quantify food presence in other baboon studies. Indices were used in this study because measurement of biomass takes extra time and biomass may suggest that data are more precise than is actually achieved in practice. However, use of indices limits comparison between different aspects of vegetation (e.g., comparing the amount of food in ground and tree layers) in the same study site and reduces the potential for between site comparisons.

Measures of biomass in general have been assumed to be good measures of food biomass (e.g., Kenyatta 1995 for green-herb layer biomass). Biomass and food biomass are likely to be related but it is probable that for certain plant parts, such as fruits and flowers, the relationship will be lagged. Estimates of food should be based as closely as possible on what the animal actually eats.

4.2.2 Rainfall

Two features of rainfall are important: how much falls (total rainfall) and when it falls (dispersion) (Bronikowski & Webb 1996; Linacre 1992; Williamson 1997). Three measures of annual rainfall variability were used for between year comparisons: Simpson index, Shannon index and number of months with less than 50mm of rain (Bronikowski & Webb 1996). The formulae used for calculating the Simpson and Shannon indices are given in Table 4.3.

Table 4.3 Annual rainfall based on ecological year.
Long-term rainfall averages based on 32 annual cycles from wet 2 1964 to dry 1 1996 inclusive. Values marked with an asterisk (*) are for the same period excluding flood years (>1000mm ie., 1968, 1972, 1979, 1984, 1985; Norton 1994).

Ecological year (start)	**1993 (Dec 92)**	**1994 (Dec 93)**	**1995 (Dec 94)**	**Long-term average +/- standard dev.**
Total rain (mm)	825.30	767.08	809.96	860mm +/- 202.36 787mm +/- 114.79*
# months <50mm	6	6	6	6.26 +/- 1.03 6.46 +/- 0.95*
Simpson index	0.81	0.79	0.81	0.82 +/- 0.03 0.81 +/- 0.03*
Shannon index	0.74	0.74	0.75	0.75 +/- 0.06 0.76 +/- 0.06*

Simpson index = $1 - \Sigma (p_i^2)$

Shannon index = $\frac{\Sigma [p_i \ln(p_i)]}{\ln (12)}$

[NB: since the natural log of zero cannot be calculated a value of 1 was added to every value.]

Where p_i = proportion of annual rain falling in ith month

4.2.3 Fire

Data from all plots monitored in the dry seasons quarters of 1992, 1993 and 1994 were used to assess between year variation in fire. Percent of plots as having burned, whether fully or only partially (at least one quadrant burned, however little), was calculated for each of these quarters.

4.2.4 Statistical Analyses

Non-parametric tests (Siegel & Castellan 1988) were used to assess whether vegetation indices differed significantly between:
- the same quarters in different years;
- different quarters in the same years.

As a repeated measures design was employed, Wilcoxon Matched-Pairs Signed-Ranks Tests were used to tests for differences between two categories and Friedman Two-Way Anovas were used to test for differences between three or more categories. Vegetation indices were treated as dependent variables and quarter or year as independent variables.

4.3 RESULTS

Details of statistical analyses (name of test, sample size/degrees of freedom, value of statistic, probability H_0 is true) are given in the legends of the figures. The word "significant" in the text means statistical significance at the 0.05 level.

Boxplots (SPSS 1993) are used for a number of figures in this section. The box represents the range containing 50% of all data points in the sample i.e., the 25th to the 75th percentile. The thick horizontal black line within the box marks the median value. The "T" shaped "whisker" lines extending above and below the box indicate the range containing all values not outliers (1.5 or more box-lengths from 75th or 25th percentile) or extremes (3 box-lengths or more from 75th or 25th percentile). Outlying values are indicated by small circles (O) and extreme values are indicated by small stars (*). The numbers next to stars and circles are plot numbers, indicating which plots have these extreme or outlying values.

4.3.1 Vegetation

4.3.1.1 Tree layer food

The amount of **tree foods** present varied significantly among quarters in both years. The pattern of variation in both years was also similar, with the amount of food being greater in the wet season than in the dry (Fig. 4.1). In general, the variation between tree food in the same quarter in different years was less than between different quarters in the same year i.e., annual variation less than seasonal variation. However, there was significantly more tree food present in wet 1 and dry 1 of 1994. The outliers and extremes shown on Fig. 4.1 give an indication of the patchiness of food presence. For example, the tree food index for plots 41, 7, 2, 22 and 32 are all much higher than most plots in dry 2 1994. These represent patches of relatively high levels of tree food during a quarter when levels were generally low.

Figures 4.2 and 4.3 show the components of the total tree food index; tree food was clearly dominated by the **leaf food** index (Fig. 4.2). Again, there was a significant seasonal pattern with the presence of tree food being greater in the wet season. Between year comparisons found significantly greater leaf food in wet 2 and dry 1 in 1994.

Figure 4.1 Total tree food index (TFI) by quarter.
There was a significant difference between quarters in both years (Friedman Two-Way Anova for 1994, DF=3, X^2=44.56, **p<0.01**; Friedman Two-Way Anova for 1995, DF=2, X^2=16.22, **p<0.01**). The differences between the same quarters in different years was significant for wet 2 and dry 1 but not wet 1 (Wilcoxon Matched-Pairs Signed-Ranks Test for wet 1, n=32 pairs, z=-1.47, p=0.14; Wilcoxon Matched-Pairs Signed-Ranks Test for wet 2, n=32 pairs, z=-3.82, **p<0.01**; Wilcoxon Matched-Pairs Signed-Ranks Test for dry 1, n=32 pairs, z=-2.95, **p<0.01**). See section 4.3 for information on how to interpret boxplots.

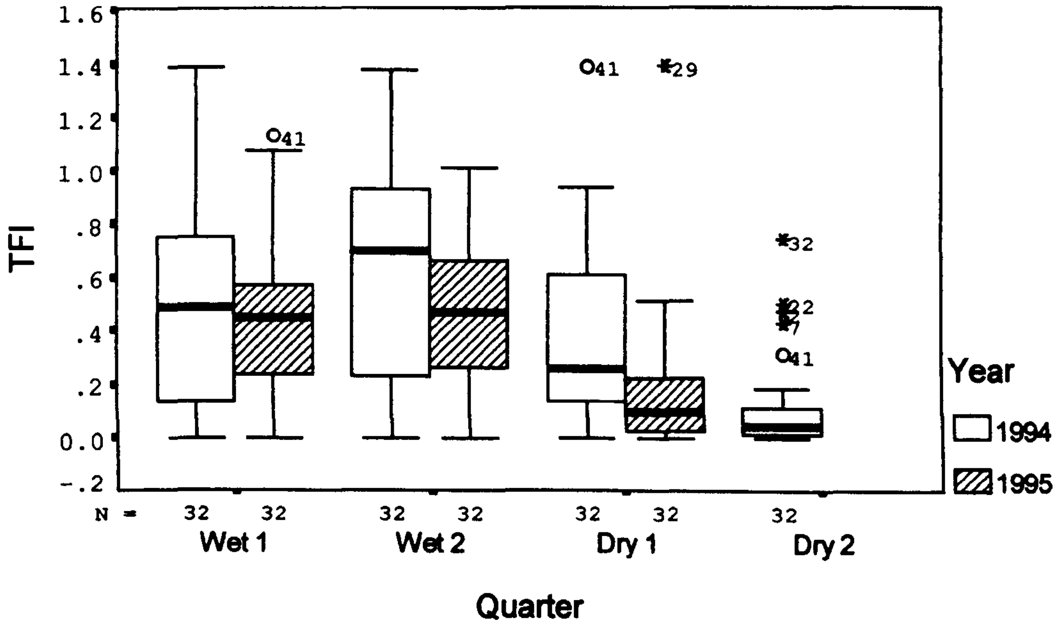
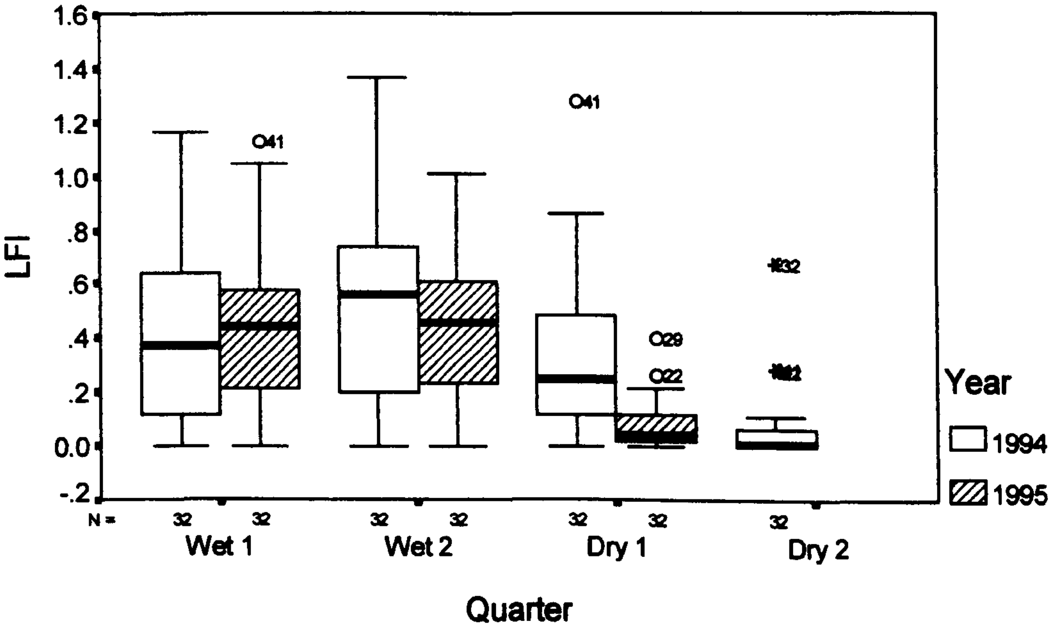


Figure 4.2 Tree leaf food index (LFI) by quarter.
There was a significant difference between quarters in both years (Friedman Two-Way Anova for 1994, DF=3, X^2=60.26, **p<0.01**; Friedman Two-Way Anova for 1995, DF=2, X^2=34.23, **p<0.01**). The differences between the same quarters in different years was significant for wet 2 and dry 1 but not wet 1 (Wilcoxon Matched-Pairs Signed-Ranks Test for wet 1, n=32 pairs, z=-1.49, p=0.14; Wilcoxon Matched-Pairs Signed-Ranks Test for wet 2, n=32 pairs, z =-2.99, **p<0.01**; Wilcoxon Matched-Pairs Signed-Ranks Test for dry 1, n=32 pairs, z=-4.47, **p<0.01**). See section 4.3 for information on how to interpret boxplots.



The presence of food from **reproductive parts** showed no clear pattern (Fig. 4.3). Quarters were not significantly different in 1994, but were in 1995. There was significantly greater food available from the reproductive parts of trees in 1994 for both wet season quarters. There were several extreme and outlying plots in most quarters, and particularly in the dry season, indicating greater patchiness in this resource than for the leaf food. For example, plot 28 had an extreme value in the dry 1 of 1995. Of the eleven trees on this open woodland plot, eight were species whose reproductive parts are eaten by the Mikumi baboons. Moreover, three were large (mean circumference breast height 1.73m) *Sclerocarya caffra* whose fruits are a staple baboon food (Norton et al. 1987). The other five trees comprised three medium *Cassia abbreviata* (mean cbh =0.74m) plus one large and one medium *Xerroderris stuhlmanii* (cbh=0.75m & 1.41m). When these trees fruit the reproductive parts food index for this plot, and consequently its total tree food index, will inevitably be high.

4.3.1.2 Ground layer food

The **herb food** index differed significantly within years but not between (Fig. 4.4). The outstanding feature of 1994 and 1995 was the higher levels in wet 2 compared to all other quarters. However, there were still outliers and extremes representing patches of high food presence in dry 1, dry 2 and wet 1. For example, plot 36 (wooded grassland on the edge of the floodplain), was extreme in wet 1 and dry 1 of 1995 because of high levels of *Blepharus stuhlmannii*, a herb which flourishes in wet areas and is common at buffalo wallows (pers. obs.).

Grass height also differed significantly within years but did not differ significantly between years (Fig. 4.5). Grass provides good baboon food when at its tallest and its shortest. Grass goes to seed at the tallest point of its annual cycle, while at its shortest the leaves are young and nutritious. Baboons rarely eat grass roots in Mikumi (Norton et al. 1987). The data therefore suggest that dry 1 was not a good time for getting food from grass compared to other times of the year.

Figure 4.3 Tree reproductive parts food index (RPFI) by quarter.
There was a significant difference between quarters in 1995 only (Friedman Two-Way Anova for 1994, DF=3, X^2=5.39, P=0.14; Friedman Two-Way Anova for 1995, DF=2, X^2=18.48, **P<0.01**). The difference between the same quarters in different years was significant for wet 1 and wet 2 but not dry 1 (Wilcoxon Matched-Pairs Signed-Ranks Test for wet 1, n=32 pairs, z=-3.08, **p<0.01**; Wilcoxon Matched-Pairs Signed-Ranks Test for wet 2, n=32 pairs, z=-3.80, **p<0.01**; Wilcoxon Matched-Pairs Signed-Ranks Test for dry 1, n=32 pairs, z=-0.11, p=0.91). See section 4.3 for information on how to interpret boxplots.

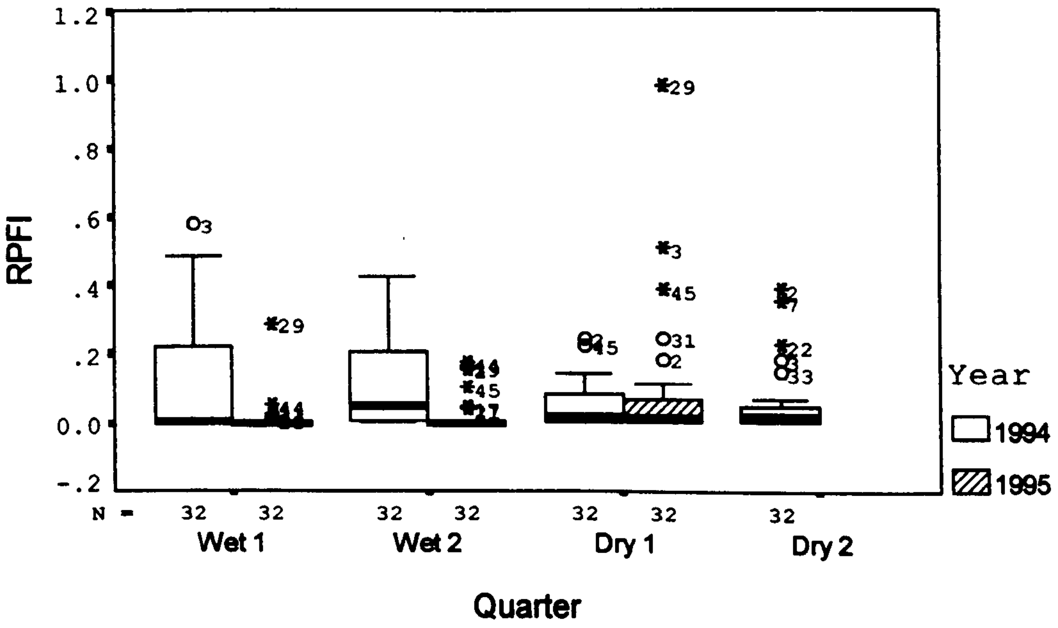


Figure 4.4 Herb food index (HFI) by quarter.
There was a significant difference between quarters for both years only (Friedman Two-Way Anova for 1994, DF=3, X^2=41.18, **$p<0.01$**; Friedman Two-Way Anova for 1995, DF=2, X^2=18.70, **$p<0.01$**). The differences between the same quarters in different years were not significant (Wilcoxon Matched-Pairs Signed-Ranks Test for wet 1, n = 32 pairs, z=-1.54, p=0.12; Wilcoxon Matched-Pairs Signed-Ranks Test for wet 2, n=32 pairs, z=-0.79, p=0.42; Wilcoxon Matched-Pairs Signed-Ranks Test for dry 1, n=32 pairs, z=-0.02, p=0.98). See section 4.3 for information on how to interpret boxplots.

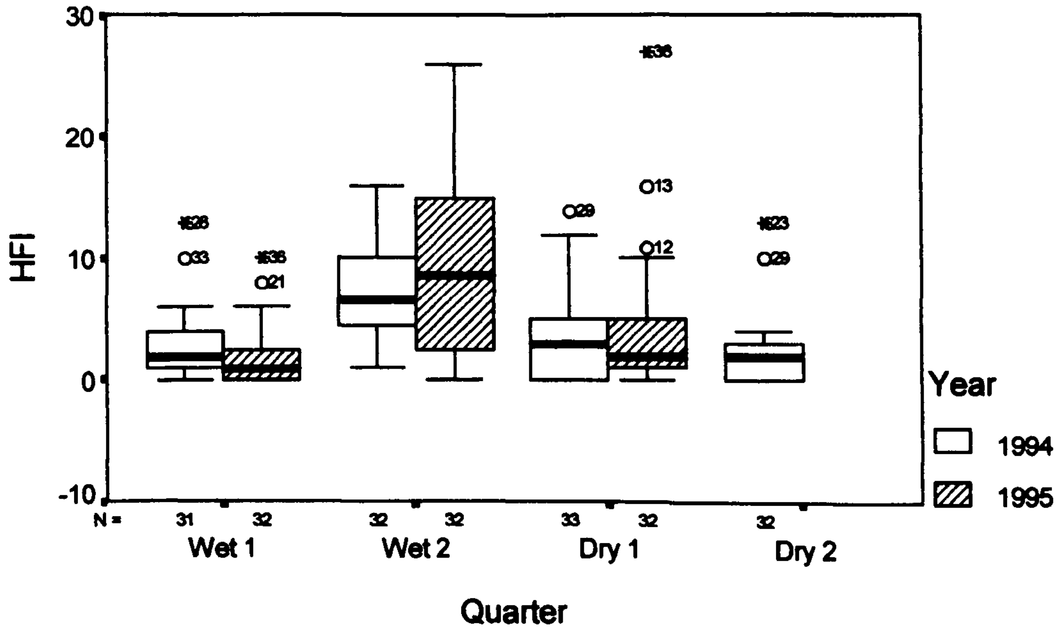
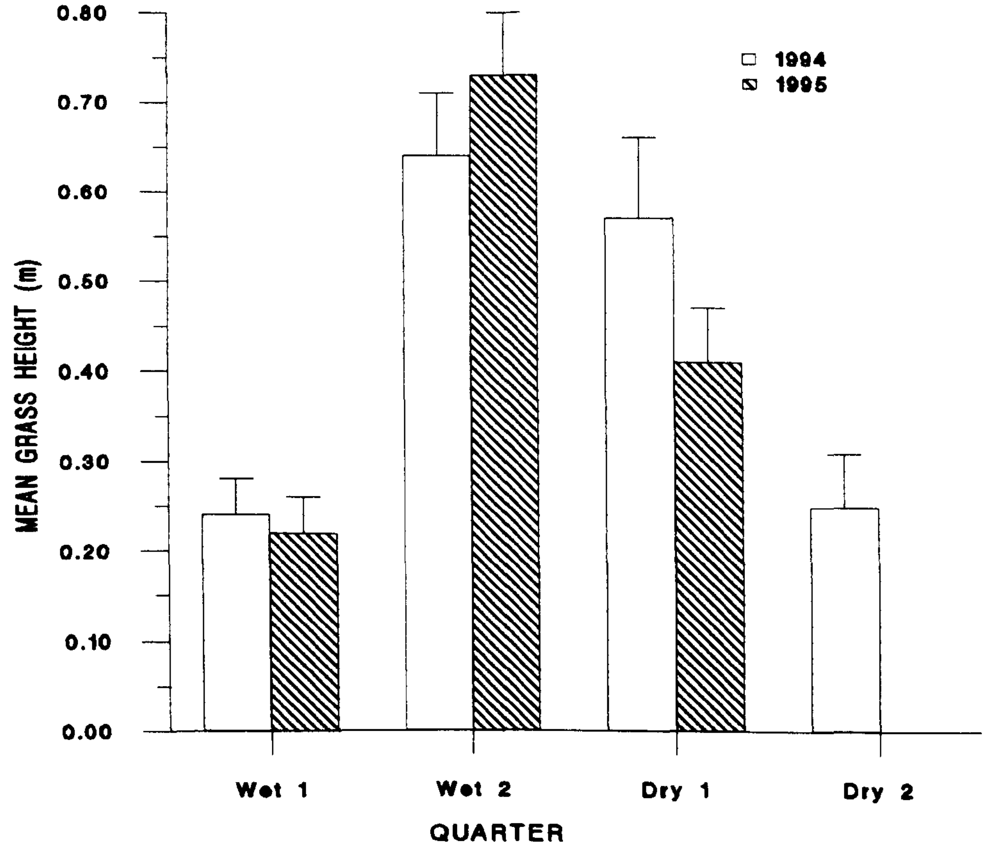


Figure 4.5 Grass height (mean +/- se) by quarter.
There was a significant difference between quarters in both years (Friedman Two-Way Anova for 1994, DF=3, X^2=26.45, **p<0.01**; Friedman Two-Way Anova for 1995, DF=2, X^2=33.81, **p<0.01**). The differences between the same quarters in different years were not significant (Wilcoxon Matched-Pairs Signed-Ranks Test for wet 1, n=32 pairs, z=-0.57, p=0.57; Wilcoxon Matched-Pairs Signed-Ranks Test for wet 2, n=32 pairs, z=-0.80, p=0.42; Wilcoxon Matched-Pairs Signed-Ranks Test for dry 1, n=32 pairs, z=-1.23, p=0.22).



4.3.1.3 Shade & visibility

Although, the absolute values of the **shade** index (Fig. 4.6) were higher than for the leaf food index (Fig. 4.2), they followed the same pattern. The shade index was calculated in the same way as the leaf food index except it included all trees in leaf not just species whose leaves are eaten by baboons (section 4.2). Thus, the shade index will always be equal to or higher than the leaf food index. There was a significant difference between quarters in both years with more shade in the wet season. There was also significantly more shade in wet 2 and dry 1 of 1994 compared to the same quarters in 1995.

Differences in **visibility** were significant within years but not between years (Fig. 4.7). Visibility was best in wet 1 and dry 2.

4.3.2 Rainfall & Fire

4.3.2.1 Rainfall

In Figure 4.8, the mean total rainfall by quarter is shown for all years from wet 2 1964 to dry 1 1996 inclusive (32 years) and for the same period excluding 5 flood years (>1000mm; Norton 1994). Not surprisingly, there is a clear dichotomy between wet and dry season quarters. Wet 1 is on average slightly wetter than wet 2, but the distribution of rain within the wet season varies between years resulting in relatively high standard deviations. Dry 1 is generally drier than dry 2. The end of the rains in May is more reliable than their onset in December; early onset of rain in some years accounts for the higher mean and standard deviation of dry 2.

Figure 4.9 shows the quarterly rainfall for the study period. This mirrors the long-term pattern (Fig. 4.8). Rains started early in 1992 and 1994. More rain fell in wet 1 compared to wet 2 in 1993, but the reverse was true in 1994 and 1995.

Annual measures of rainfall, based on the ecological year, are presented in Table 4.3. Values for the years of study were similar to long-term averages, especially those for non-flood years.

Figure 4.6 Tree leaf shade index (TLSI) by quarter.
There was a significant difference between quarters in both years (Friedman Two-Way Anova for 1994, DF=3, $X^2=68.06$, **p<0.01**; Friedman Two-Way Anova for 1995, DF=2, $X^2=42.25$, **p<0.01**). The difference between the same quarters in different years was significant for wet 2 and dry 1 but not wet 1 (Wilcoxon Matched-Pairs Signed-Ranks Test for wet 1, n=32 pairs, z=-1.61, p=0.1078; Wilcoxon Matched-Pairs Signed-Ranks Test for wet 2, n=32 pairs, z=-2.56, **p=0.01**; Wilcoxon Matched-Pairs Signed-Ranks Test for dry 1, n=32 pairs, z=-4.75, **p<0.01**). See section 4.3 for information on how to interpret boxplots.

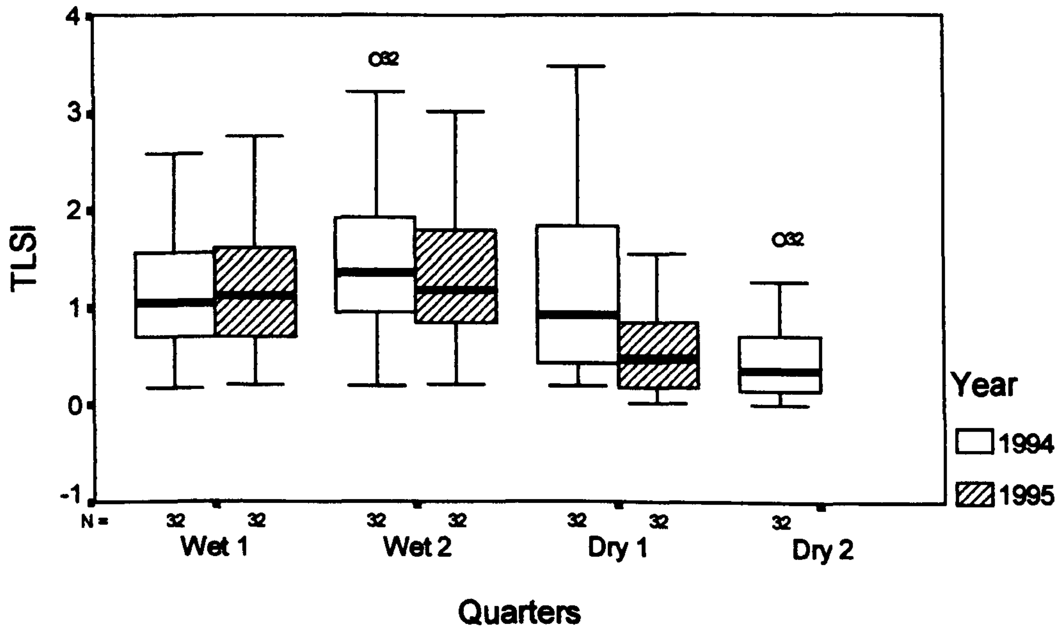


Figure 4.7 Visibility (mean +/- se) by quarter.

There was a significant difference between quarters in both years (Friedman Two-Way Anova for 1994, DF=3, X^2=22.90, **p<0.01**; Friedman Two-Way Anova for 1995, DF=2, X^2=29.31, **p<0.01**). The differences between the same quarters in different years were not significant (Wilcoxon Matched-Pairs Signed-Ranks Test for wet 1, n=32 pairs, z=-0.11, p=0.91; Wilcoxon Matched-Pairs Signed-Ranks Test for wet 2, n=32 pairs, z=-0.88, p=0.38; Wilcoxon Matched-Pairs Signed-Ranks Test for dry 1, n=32 pairs, z=-0.45, p=0.65).

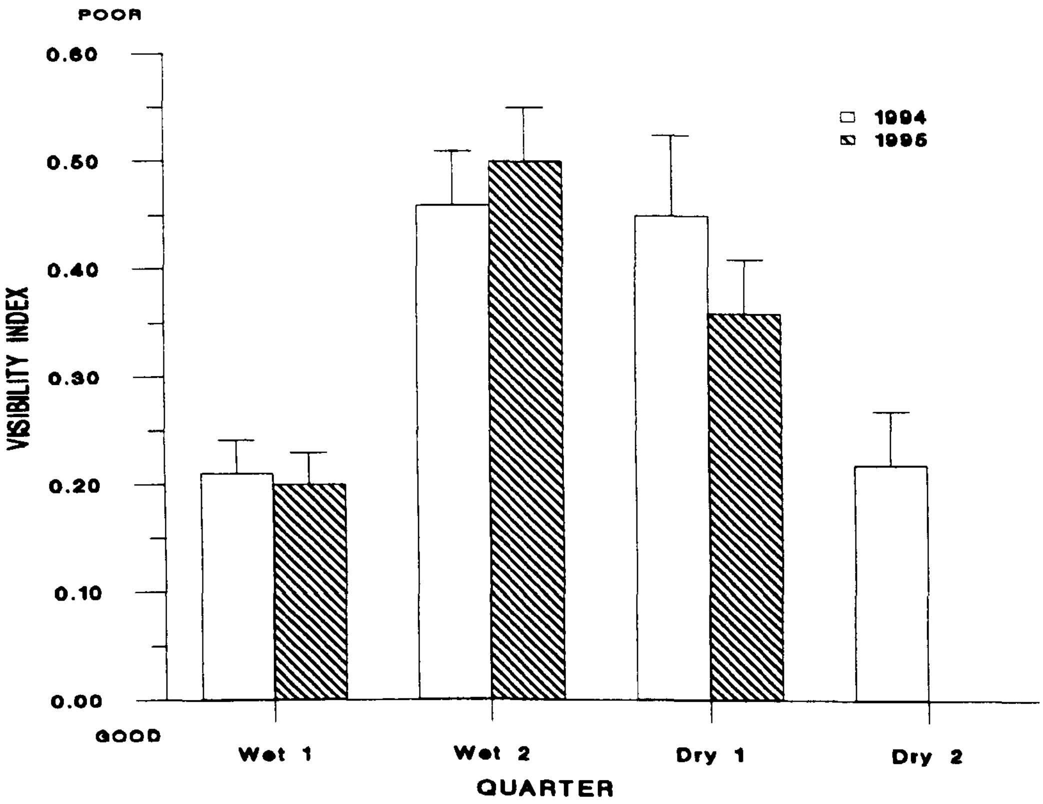


Figure 4.8 Long term mean total rainfall by quarter (wet 2 1964 to dry 1 1996 inclusive). Bars represent mean for all 31 years (plain bars) and the 26 non-flood years during the same period (cross hatched bars). Flood years were those years in which more than 1000m fell during the ecological year (1968, 1972, 1979,1984,1985; Norton 1994b). Lines on bars represent standard deviation.

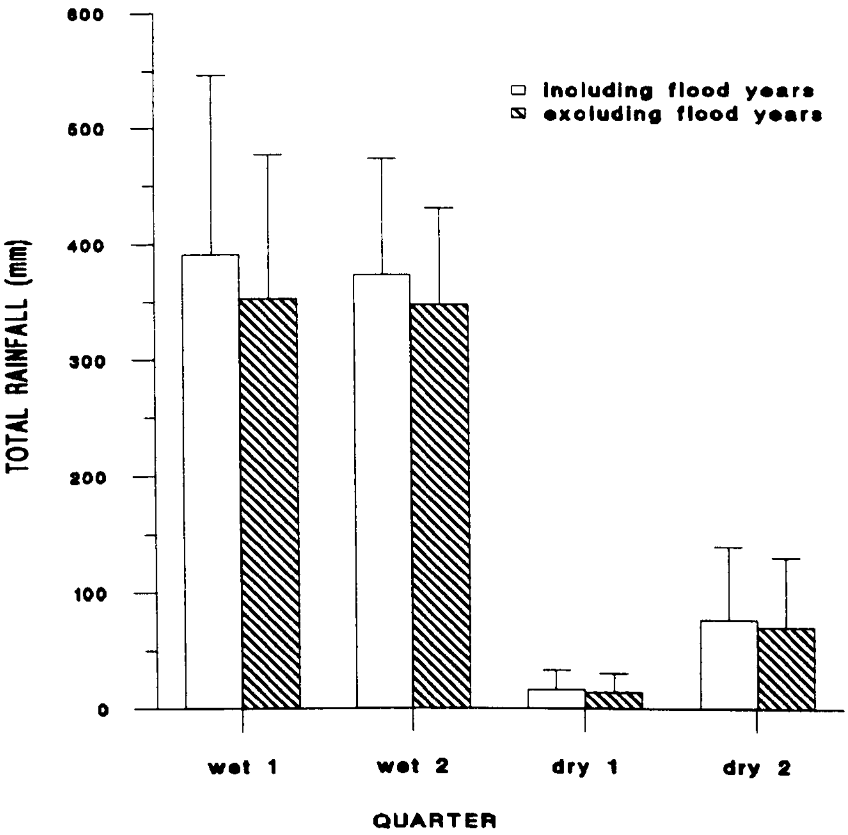
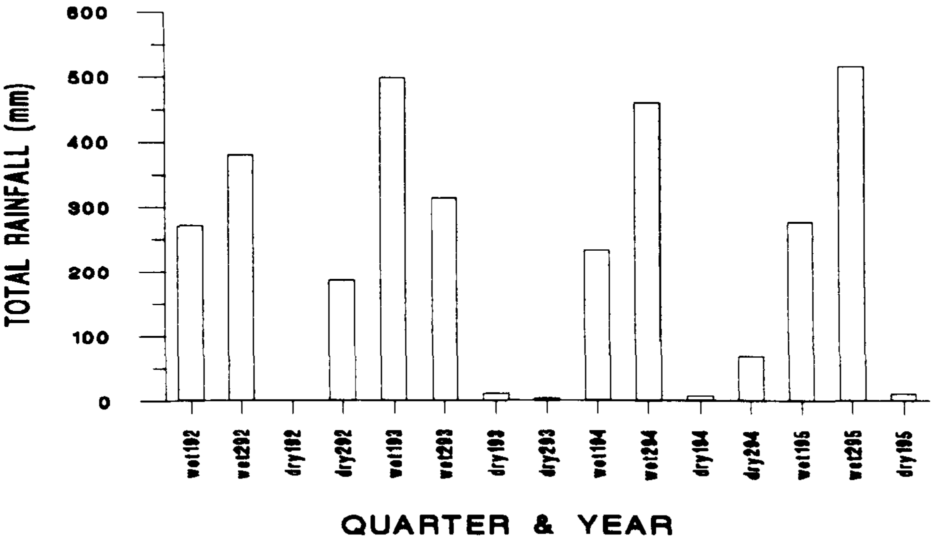


Figure 4.9 Total rainfall by quarter during, or just prior, to study period.



4.3.2.2 Fire

Burning is clearly seasonal; fires are a dry season phenomenon. Fires rarely occur in wet 1 and never in wet 2. Fires occurring in dry 2 tend to be hotter and possibly more damaging to vegetation. The percent of plots recorded as burned in the regular monitoring, which began in Dry 1 1992, is shown in Figure 4.10. Although the sample sizes vary, personal observation (by myself, G.W.Norton, C.Kidung'ho & W.Marwa) and long-term records (G.W.Norton, R.J.Rhine and S.K.Wasser unpublished data) strongly support the suggestion that fires were particularly extensive in 1994.

4.3.3 Patterns of Association

4.3.3.1 Rainfall & vegetation within years

All the vegetation parameters measured by this study, except tree reproductive parts food, were related to either rainfall in that quarter (a current relationship), rainfall in that quarter plus the one before (a cumulative relationship) or the rainfall in the previous quarter (a lagged relationship) as listed below. Spearman rank correlation (R_s) are reported. This statistic has been used in other studies to test for significant associations between food and rainfall (Barton 1989; Cowlishaw 1993; Kenyatta 1995). Cross correlation time series analyses would be more appropriate except that sample sizes are small.

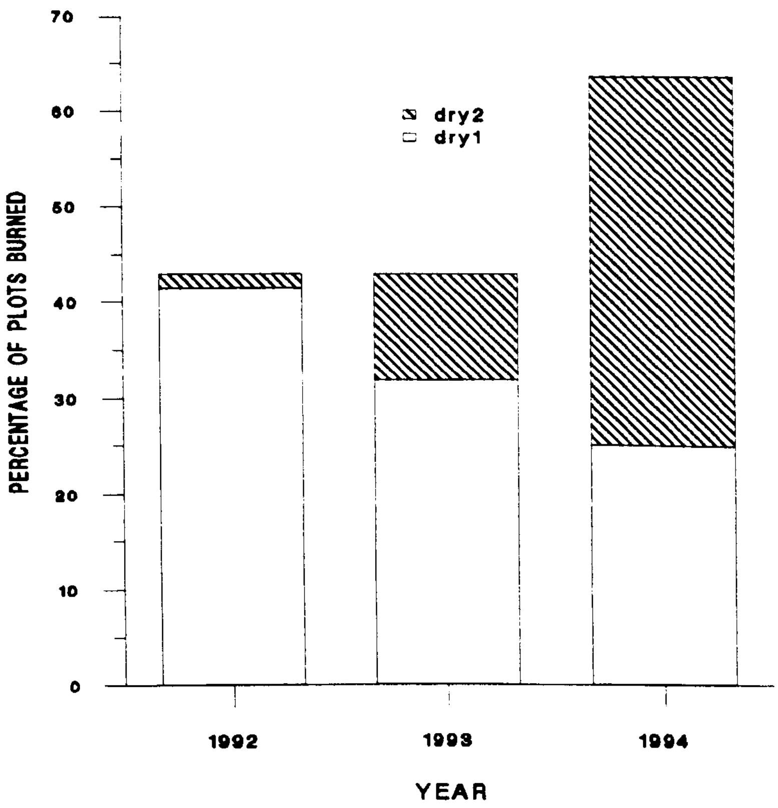
1. Leaf food and shade resources were higher in wet quarters (wet 1 & wet 2) than in drier ones (dry 1 and dry 2). [Rain & leaf food index R_s=0.82; n=7; **p=0.02**; rain & shade index R_s=0.81; n=7; **p=0.03**]

2. The high point for herb food and grass seeds corresponded to when cumulative rain (for the present and previous quarters) was at its highest (i.e.,wet 2). [Cumulative rain & herb food index R_s=0.88; n=7; **p=0.01**; cumulative rain & grass height R_s=0.82; n=7; **p=0.02**]

3. Visibility and food from young leaves were best when the previous month was dry (i.e., dry 2 and wet 1). [Lagged rain & visibility index R_s=0.57; n=7; p=0.18; lagged rain & grass height R_s=0.82; n=7; p=0.18]

The amount and pattern of food provided by the reproductive parts of trees was not simply related to rainfall.

Figure 4.10 Percentage of plots burned in 1992, 1993 and 1994.
Bars represent percent of plots recorded as burned in dry 1 (plain bar) and the percent of plots recorded as burned in dry 2 (plain bar plus cross-hatched bar). Sample sizes vary considerabley [1992 dry 1 n=29 & dry 2 n=7; 1993 n=22 & dry 2 n=14; 1994 dry 1 n=52 & dry 2 n=44] but field notes and personal observation confirm that fires were particularly extensive in 1994.



4.3.3.2 Fire & vegetation within years

Fire has a direct relationship with rainfall since fires are exclusive to dry season quarters, hence the relationship between rainfall and vegetation can be restated in terms of fire as follows:-

1. Leaf food and shade resources were higher in quarters when fire did not occur.
2. The high point for herb food and grass seeds occurred when no fires had happened in the current and previous quarters.
3. Visibility and food from young leaves were best when fires occurred in the previous month.

Again, the amount and pattern of food provided by the reproductive parts of trees appears not to be simply related to fire.

4.3.3.3 Between years

Assessment of associations between years is limited by data only being available for this study from two different years. Moreover, there were no dramatic deviations from the typical pattern of rainfall in either of these years, nor in the preceding one, which might be relevant through cumulative and lag effects. Between year differences found in the tree layer were not associated with differences in rainfall. Burning was particularly extensive in the dry season of 1994, which could be associated with the lower tree layer resources in 1995.

Table 4.4 Summary of quarterly (within year) variation in food measures.
All parameters showed quarterly or seasonal differences except the tree reproductive parts food index. Overall food presence is based on scoring tree leaf food, herb food and grass food as high = 3, medium = 2, low = 1 and then summing the scores (value in brackets) for each quarter. Food patchiness (defined as small (e.g., one or a few fruiting trees), discrete clumps of food) was not measured in detail and is only estimated. Food patchiness is not discussed in any detail in the text.

QTR	**Tree Leaf Food**	**Tree Repro. Parts Food**	**Herb Food**	**Grass Food**	**Overall Food Presence**	**Food Patch - iness**	**Tree Shade**	**Visibility**
Wet 1	high	?	low	high - young leaves	high (10)	low	high	good
Wet 2	high	?	high	high - seeds	high (12)	low	high	poor
Dry 1	medium/ low	?	low	low	low (1)	medium	medium/ low	poor
Dry 2	low	?	low	high - young leaves	low (1)	high	low	good

Table 4.5 Summary of between year differences in vegetation measures.
In general the pattern of variation between years was less than that within years. Resources provided by the tree layer (food & shade) showed some significant differences between years but resources connected with the ground layer (herb food, grass food & visibility) did not. Where no significant difference was found cells have been left blank.

QTR	**Tree Leaf Food**	**Tree Repro. Parts Food**	**Tree Shade**	**Herb Food**	**Grass Food**	**Visibility**
Wet 1		94 > 95				
Wet 2	94>95	94 > 95	94 > 95			
Dry 1	94>95		94 > 95			

4.4 DISCUSSION

4.4.1 Between & Within Year Patterns of Vegetation

There was a strong **within year** pattern for all the aspects of vegetation considered (as summarized in Table 4.4), except tree food reproductive parts (section 4.4.2). Seasonal patterns in aspects of vegetation potentially important to baboons were first quantified by Barton (1989) who concluded "variation in food availability conforms to the common assumption of dry season scarcity and wet season abundance" on the Laikipia plateau in Kenya (Barton 1989:50). This study suggests that there is a similar overall pattern of food presence in Mikumi. However, it would be misleading to make judgements on baboon ecology based on the assumption that *dry times are bad times and wet times are good times* for several reasons. As Barton (1989) points out, lag and cumulative relationships between rainfall and vegetation generate complexity. Differences in the pattern of fruit and flowering within and between years could seriously challenge this assumption for the Mikumi baboons. Evaluation of seasonal patterns in terms of habitat quality in general (rather than based solely of presence of food) must consider other aspects of vegetation (e.g., visibility, shade) and of the environment in general (e.g., drinking water, predation).

Another important issue that must be considered when assessing habitat quality in terms of food is **patchiness**. The quantification of patchiness is problematic (Barton 1989; Bryne et al. 1988; G.W. Norton unpublished data) and hence has been largely dealt with only superficially. This study is no exception, concentrating on the amount of food rather than its distribution. The distribution of food as distinct from its quantity is an important issue for animal ecologists (Oates 1987). For example, where food is plentiful but patchily distributed, the challenge facing the baboons is locating good patches and defending them from other troops (Wrangham 1980). Relatively rare but high value patches can play a key role in sustaining baboons through periods when food in the environment as a whole is scarce, hence Bryne et al. (1988) refer to them as "gold nuggets". These gold nuggets are often dependent on fruiting patterns which this study has shown to be a complex issue (section 4.4.2).

In general, there was little difference in vegetation parameters **between the same quarters in different years** (as summarized in Table 4.5); of course since only two years were compared, the interpretation of this result as a general pattern is limited. Statistical significance was found for tree leaves (tree leaf food & shade) and tree reproductive parts food. Inspection of the raw data shows that differences in leaf percent scores, although consistent across plots in direction, were relatively small (e.g., 80 rather than 90%). In terms of food, slightly fewer leaves is unlikely too be important to the Mikumi baboons since they are not primarily leaf eaters (Norton et al. 1987; Rhine et al. 1989).

Further research should move towards establishing regressional relationships (e.g., Deshmukh 1984; Williams et al. 1975) between climate and baboon resources. While correlational relationships suggest that climate can predict behaviour, more precise regressional relationships should be established to support climate based models of primate behaviour. This would promote better understanding of empirical models (Bronikowski & Webb 1996) and the development of mechanistic models at both the intra and interpopulation level.

4.4.2 Patterns of Fruit & Flowering

Sexual reproductive phase of plant growth and development is controlled by environmental factors in conjunction with endogenous regulating mechanisms (Larcher 1995). For woody vegetation in particular, the process is complex. It is not surprising, therefore, that the relationship between climate and plant reproduction is not a simple one. The phenomenon of masting, for example, is well known but not clearly described in relation to climatic factors (Crawley 1997).

According to Heideman (1989:1059) "in some tropical environments, patterns of flowering and fruiting are clearly correlated with annual variation in temperature or rainfall" and he cites a number of studies to support this statement about within year variation (also see Hall-Martin & Fuller 1975). However, the relationship may be less reliable than for other aspects of vegetation. For example, the relationship between the reproductive parts of *Acacia* sp trees on Laikipia plateau in Kenya and rainfall is less robust than that for herbs (Barton 1989:51*ff*; Kenyatta 1995:54).

Between year patterns are uncertain as studies have generally lacked a long term perspective. Heideman's (1989) limited between year comparison on fruiting and flowering in seasonal tropical rainforest in the Philippines indicated differences between years in the timing and/or magnitude of peaks in tree reproductive parts.

Tropical woodland trees can be highly variable in their fruiting and flowering patterns both within and between populations (Lind & Morrison 1974). Many examples of this can be drawn from research and personal observation in Mikumi National Park; I shall give just two. Firstly, *Dalbergia melanoxylon*, has been the subject of special study in Mikumi since 1992, but no fruits or flowers were observed on regularly monitored trees until July 1995

(Hawkins et al. 1996). Secondly, the crop of tamarind fruits, which is an important staple food for the Mikumi baboons and therefore of particular note to the long-term baboon research, is highly variable from year to year (Norton et al. 1987; R.J. Rhine, G.W. Norton & S.K. Wasser unpublished data; G.W. Norton pers. comm.). Most commonly fruits are on the trees from late May to August but in 1979, for example, fruits lasted from June to January while in 1978 and 1980 crops failed almost completely. Patterns of variability in fruit and flowering appear to be species specific.

4.4.3 Cause & Effect

The patterns of association between rainfall and vegetation within years described in section 4.3.3.1. are likely to have underlying cause and effect relationships through the physiological role of water in plant growth and development (Gates 1993; Jackson 1989; Larcher 1995; Woodward 1987).

The onset of rain stimulates germination and growth. The cumulative relationship of herbs and grass seeds to rainfall reflects a longer response time than that for tree leaves (food & shade). Herbs and grasses must start each year from at, or below, ground level either as seed or vegetative parts. The presence of considerable above ground woody parts throughout the year gives trees a head start in the growing season.

Fire undoubtedly contributes to the lagged relationships of rainfall with visibility and food from young grass leaves. Both these vegetation parameters are poor during dry 1 because ground level vegetation is only removed by the combination processes of burning, trampling and senescence as the quarter progresses. These processes clear the ground; consequently precipitation during dry 2 and wet 1 leads to grass flushes. By wet 2 the ground vegetation has had time to grow tall again, grass leaves are no longer young and visibility is reduced.

The extensive fires in the 1994 dry season may have been the cause of the reduced reproductive food parts in the following wet season through heat damage to flower buds especially by hotter late burns. However, agricultural studies suggest that a longer term data set is needed to assess rainfall-fruit relationships: "Although the impact of drought can be immediate in terms of vegetative growth, it may be 3 years or more before this is reflected in fruit crop yield" (Jackson 1989:209).

The significantly lower leaf levels (shade & food) in wet 2 and dry 1 could be a result of a similar but lagged effect. Why this might be so is not clear. There are other perhaps more plausible explanations. For example there may have been stronger winds in the wet 2 of 1995 with knock on effects into dry 1. The small across plots differences are consistent with this idea but, since wind records are not available, it can not be tested directly. Given the uncertainty of the between year relationships, it would be unwise to make too many suggestions for underlying causal mechanisms of the associations found.

4.4.4 Food Presence & Value

I have been careful to use the word "present" in relation to food as opposed to "accessible" or "palatable". For example a tamarind fruit may be present in the environment but not accessible (e.g., the baboons don't know it's there, the tree has a leopard in it or the tree is surrounded by tall grass). The fruit may be present and accessible but not palatable (e.g., unripe, infected by parasites). The food indices calculated in this study measure presence only; visibility on the other hand could affect accessibility. None of the measures used in this study take in to account palatability. The distinction between present, accessible and palatable merits further consideration in relation to assessment of vegetation mediated effects of rainfall on baboon behaviour.

Bryne et al. (1988) used baboon behaviour to assess "availability" of food in the environment and hence, considered only foods which were present, accessible and palatable. Their measure represents the decisions made by the baboons rather than the ecological context in which these decisions are made. These authors question the value of using "randomized botanical sampling to study the nutrition of an animal like the baboon, which is known to be a highly selective feeder on a catholic range of food types" (Bryne et al. 1988:119). Since botanical surveys, which are independent of the animals' behaviour, provide ecological context, when questions of ecology rather than nutrition are being considered as in this study, such data are important.

Foods that are palatable are not of equal value to a baboon. The absolute value of food depends on its nutritional content and its ease of processing. Its value to a particular baboon will also depend on the physiological state of that baboon. Nutritional content can be evaluated from phytochemical analyses. Such analyses have been carried out in several studies (Barton 1989; Bryne et al. 1988; Cowlishaw 1993; Johnson 1989; Kenyatta 1995), but unfortunately these studies have not dealt with temporal variation in nutritional content which would be expected to occur (Jackson 1989; Larcher 1995). Fewer studies have considered processing costs (but see Bryne et al. 1988) or physiological value other than in relation to lactation (Dunbar & Dunbar 1988; Kenyatta 1995) or disease (Phillips-Conroy 1986).

This study is concerned with the use of rainfall to predict general patterns of food presence and it has been assumed that such broad scale investigation does not require detailed evaluation of food value. As a first stage beyond this work, regular sampling of potential foods for phytochemical analyses would be useful for assessing both the palatability and value of food.

4.5 SUMMARY

Rainfall data are good indicators of quarterly (within year) variation of most vegetation aspects potentially relevant to the behaviour of the Mikumi baboons. The relationships between rainfall and vegetation were current (tree leaf food & shade), cumulative (herb & grass seeds) or lagged (young grass & visibility). These relationships are likely to be causal through the effect of soil water availability on plant growth and development. Fire may also play an influential role but covaries with rainfall and therefore does not confound rainfall-vegetation relationships. The within year relationships found suggest potential indirect mechanisms by which seasonal rainfall patterns could cause time budget variation. If more than one type of mechanism (i.e., current, cumulative or lagged) operates, this would add complexity to rainfall-time budget relationships.

The predictive role of rainfall for between year variation is less clear due to small sample size and few significant between year differences. Fire may play an important role in between year variation in a way not predicted by rainfall. This in turn could offer a potential explanation if rainfall were not found to predict between year variation in baboon time budgets in Mikumi National Park.

The presence of food from the reproductive parts of trees showed no clear relationship to either rain or fire either within or between years. Again, this could offer a potential explanation if rainfall were not found to predict within or between year variation in baboon time budgets in Mikumi National Park.

CHAPTER 5. INTER-INDIVIDUAL DIFFERENCES

5.1 INTRODUCTION

5.1.1 Aim & Rationale

This chapter explores inter-individual differences in time budgets among the adult yellow baboons in Mikumi National Park. Individuals are compared by sex (adult females v. adult males) and by reproductive state, rank and age (adult females only). The level of variation generated by such comparisons is also considered.

Both interpopulation (e.g., Clutton-Brock & Harvey 1977; Dunbar 1992a; Sharman 1981; Dunbar & Sharman 1984) and intrapopulation (e.g., Altmann & Muruthi 1988; Bronikowski & Altmann 1996; Muruthi et al. 1991) comparisons of individual time budgets use mean group figures. In many cases the validity of such comparisons relies on the implicit assumption that variation around the group mean is random. Inter-individual differences (e.g., by sex, reproductive state, social rank and age) could invalidate this assumption (Marsh 1981). Differences in sampling decisions (section 5.1.3) between studies are likely to exacerbate this problem. Considering inter-individual differences is not only important for evaluating existing studies but it is a necessary prerequisite for subsequent chapters of this thesis.

5.1.2 Inter-individual Differences

A full review of inter-individual differences in primate time budgets can be found in section 2.5.1. The main empirical findings and theoretical arguments relevant to this chapter are summarized in Table 5.1. From previous work we might expect to find few statistically significant differences among individuals based on the parameters under investigation in this chapter and, therefore, have little need to worry about non random contributions to group means. However, previous studies have not been exhaustive. They have concentrated on the effects of sex, reproductive state and rank on feeding. Other time budget components and the effect of adult age have been neglected. Moreover they do not test for inter-individual variation under the ecological and demographic environment of this study. It would be unwise to use them to justify the assumption that individuals vary randomly around the group mean.

Table 5.1 Summary of empirical findings and theoretical arguments on inter-individual differences. A full review of factors effecting individual differences in time budgets of primates can be found in section 2.5.1. This table summarizes empirical findings and theoretical arguments especially relevant to this chapter. Thus empirical findings are limited to baboon studies and only sex, reproductive state (= Repro.), rank and age within adult class are considered.

	EMPIRICAL FINDINGS	THEORETICAL ARGUMENTS
	Sex	
Feed	Barton (1989), Dunbar (1977), Post (1981) and Post et al. (1980) all found no difference.	Expected longer feeding time for larger bodied males, assuming rate of nutritional intake equal. That this is not found due to invalid assumption or to females incurring additional costs. Higher rate of nutritional intake in males could be mediated by priority of access and if so could be effected by resource quality and distribution.
Move	Barton (1989) found no difference.	
Rest		Females may take time away from resting in order to devote more to socializing.
Social	Post (1981) found no difference.	Due to female bonded structuring of society, females expected to give greater priority to social behaviour than males.
	Reproductive	**State**
Feed	Elevated feeding times found for pregnant and/or lactating females (Altmann 1980, Dunbar & Dunbar 1988, Muruthi *et al.* 1991) except under drought conditions (Kenyatta 1995, Post et al. 1980).	Harsh environmental conditions may force the costs of reproduction, and thus elavated feeding times, to be spread over entire reproductive cycle leading to no differences. Such constraints could be created by drought and or spatial and temporal heterogeneity of resources.
Move		Differences possible if carrying foetus or infant impedes locomotion of female.
Rest	Dunbar & Dunbar (1988) found time primarily taken away from resting and used to enable increased feeding time during lactation.	Resting time most likely to be reduced to compensate for increased feeding time if necessary during pregnancy or lactation.
Social	Altmann (1980) found time primarily taken away from social time and used to enable increased feeding time during lactation.	
	Rank	
Feed	Altmann & Muruthi (1988) found higher ranking females spent more time feeding on high quality food found in garbage pits. Altmann & Muruthi (1988), Barton (1989) and Post et al. (1980) found no difference in naturally feeding troops.	Differentials only manifested when resources are high quality and extremely clumped enabling monopolization by dominants.
Move		Differences possible if subordinates forced to move more often through supplants.
	Age	
Feed	Muruthi et al. (1991) found that females spent more time feeding when they were nulliparous (ie., younger) than if multiparous (ie., older).	Reduced feeding time would be expected to accompany declining metabolic rate and other physiological changes as animal ages.
Move		Aging processes effecting joints and muscles may restrict time spent moving.
Rest		Aging processes may lead to greater priority given to resting.

5.1.3 Sampling Decisions

Table 5.2 illustrates variation in which individuals are included in the collection of time budget data. There are a variety of logistical and scientific reasons for this variation. Examples of logistical reasons include to enable pooling of data with coworkers (e.g., Rasmussen 1978) and insufficient habituation of certain individuals (e.g., Barton 1989). Scientific reasons relate to the fact that time budget data are often collected as an adjunct to the primary focus of a study (eg., Dunbar & Dunbar 1974). If the assumption that all individuals vary randomly around the group means is invalid, then such sampling decisions could confound the measurement of ecological and demographic effects. For example Harding (1976) sampled only adult males, while Nagel (1973) sampled all individuals. The group mean time feeding time for Harding's study was 47% while for Nagel's it was 30% (Nagel 1973; Harding 1976; Dunbar 1992a). The contribution of females, or more likely young animals, to the group mean in Nagel's study could be responsible for the shorter feeding time.

Table 5.2 Sampling decisions made by studies collecting time budget data on baboons.

STUDY	INDIVIDUALS SAMPLED
Yellow	**Baboons**
Altmann & Muruthi 1988	All adult females.
Bronikowski & Altmann 1996	All adult females.
Hawkins (this study)	All adults.
Muruthi et al. 1991	All adult females.
Norton unpublished data	All adults.
Post 1981 & 1978	Two adult females and two adult males chosen at random from 25 adults.
Post et al. 1980	All individuals except the 6 very youngest.
Rasmussen 1978	3-9 adult males out of 11-16. 7-13 adult female out of 24-31. Choice of females in first half on the study based on those most likely to have offspring in following year and in the second half of the study cycling females chosen
Olive	**Baboons**
Aldrich-Blake et al. 1971	All individuals.
Barton 1989	Nineteen out of 26 adult females. Choice of females based on degree of habituation - unsampled females insufficiently habituated. Plus seven out of sixteen adult males.
Dunbar & Dunbar 1974	All individuals.
Eley et al. 1989	All individuals.
Harding 1976	All adult males.
Nagel 1973	Individuals from all age-sex classes.
Gelada	**Baboons**
Dunbar & Dunbar 1974	All individuals.
Guinea	**Baboons**
Sharman 1981	All individuals.

5.2 METHODS

A comprehensive description of raw data collection is given in Chapter 3 (also refer to Appendix). Chapter 3 also includes definitions of time budget components (Table 3.7) and of (seasonal) quarters (Table 3.1). This section contains only additional methodological information relevant to the analyses performed for this chapter.

5.2.1 Calculation of Daily Time Budgets

This chapter focuses primarily on the main time budget components of feeding, moving, resting and socializing. In addition, time spent giving and receiving social behaviour (i.e., SOCG & SCOR, Table 3.7) and giving and receiving agonistic behaviour (AGG & AGR, Table 3.7) are considered.

The percent of time spent in different activities was calculated for each individual in two stages. First, the mean of follows in each period of the day (Table 3.6) was calculated. Then, the mean of these four periods was determined. Thus each period of the day contributed equally to the final daily time budget value. Individuals not sampled in all periods were excluded from the analyses.

Individual daily time budgets were analyzed for three different time frames:
- the entire study period, all data combined (overall analysis);
- each quarter separately, data for different years combined (analysis by quarter);
- each quarter in each year separately (analysis by year and quarter).

Combining data from different quarters and years could potentially mask effects occurring in particular quarters. Conversely, combining data across years and/or quarters may increase sample sizes and enable otherwise unapparent patterns to be detected.

5.2.2 Statistical Analyses

To test for differences between the sexes, Mann Whitney U tests were performed using time budget components (percent time) as dependent variables with sex (male or female) as the independent variable.

For the overall analyses of main reproductive state (cycling, pregnant, lactating) Kendall rank nonparametric correlations were used to test for an association between time spent in different activities and the number of follows an individual was recorded in a particular reproductive state. For analyses by year and quarter, time budgets were calculated separately for each reproductive state that the female experienced. In general, calculation of a complete budget for only one state in any one quarter was possible. Tests of differences were employed (Mann Whitney U tests for comparing two categories and Kruskal Wallis ANOVAs for comparing three categories) using percent time spent in different activities as dependent variables and reproductive state as the independent variable.

The Kendall rank nonparametric correlation technique was used to test for association of main time budget components with social rank (Table 5.3) and age (Table 5.4). For social rank, only data from dry 2 1994 to dry 1 1995 (inclusive) were used. These data come from the single post fusion troop. Loss of adult females prior to this made similar analyses on the pre-fusion troop problematic and analyses combining data from quarters in different years were not performed.

Sample sizes for all tests are given in the results tables. The possibility of obtaining a significant result at the 0.05 level was checked in all cases. For example a significant result can not be obtained with a Kruskall-Wallis test with sample sizes of 3, 2 and 1. However, with sample sizes of 2, 2 and 2, probabilities of 0.05 can be obtained (Siegel & Catellan 1988). Significance can be obtained for a Mann-Whitney U test with sample sizes as low as 3 and 3 (Siegel & Castellan 1988). For the Kendall rank correlation the minimum sample size is 4 (Siegel & Catellan 1988).

Table 5.3 Ranks used for analysis of association of social status with time budget categories. Ranks based on Mikumi baboon project long-term dataset (R.J.Rhine, G.W.Norton & S.K.Wasser unpublished data, G.W.Norton pers. comm.).

FEMALE'S NAME	SOCIAL RANK	DATE OF BIRTH	AGE RANK
Heshima	7	21st January 1986	2
Kikubwa	4	6th May 1982	3
Kuvimba	3	unknown	
Mtumishi	5	4th July 1979	5
Ruaha	6	13th April 1986	1
Siafu	1	1st January 1979	6
Swali	2	17th February 1981	4

Table 5.4 Ranks used for analysis of association of age with time budget categories. Birth dates from Mikumi baboon project long-term dataset (R.J.Rhine, G.W.Norton & S.K.Wasser unpublished data). Note Kuvimba's was not included as her birth date is not known since she transferred in to the Viramba study population in July 1994 (section 3.3.1).

FEMALE'S NAME	DATE OF BIRTH	AGE RANK
Tai	1st May 1979	12
Mtumishi	4th July 1979	11
Rahisi	4th February 1981	10
Swali	17th February 1981	9
Kikubwa	6th May 1982	8
Tanganyika	14th April 1983	6
Uhai	7th March 1984	7
Siafu	1st January 1986	3
Heshima	21st January 1986	5
Ruaha	13th April 1986	4
Simu	19th August 1986	2
Konda	1st January 1987	1

5.3 RESULTS

5.3.1 Sex

Overall, females socialized significantly more and rested significantly less than males (Fig. 5.1a, Table 5.5a). In particular, females spent significantly more time giving social behaviour than males (Fig 5.1b, Table 5.5a). Males and females did not differ in the amount of time they spent feeding or moving (overall Fig. 5.1, Table 5.5a; by quarter Table 5.5b; by year Table 5.5c). The range between the mean value for males and females is also given in Table 5.5a. The greatest range, of 9.8, was for resting.

This overall pattern was reflected in analyses by quarter (Table 5.5b). Females spent significantly more time giving social behaviour in all quarters and rested significantly less in dry 1 and wet 1 while the result for late dry 2 approached significance.

Again for analyses by year and quarter, significant differences were apparent for resting and socializing (Table 5.5c). Females spent more time in social behaviour than males in all quarters and rested less in most with significant differences found for social behaviour in dry 1 1993, dry 1 1994 and for resting in dry 1 1994 and wet 1 1995 (Table 5.5c). In all quarters females gave more social behaviour than males and received more or similar amounts. This was significant for giving in four quarters (dry 1 1993, dry 1 1994, dry 2 1994 and wet 1 1995) but for receiving only in dry 1 1994 (Table 5.5c).

Figure 5.1 Time spent in different activities by males and females (mean +/-sd). Asterisks (*) indicates significant difference (Table 5.5a). For (b) SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received.

Fig. 5.1a

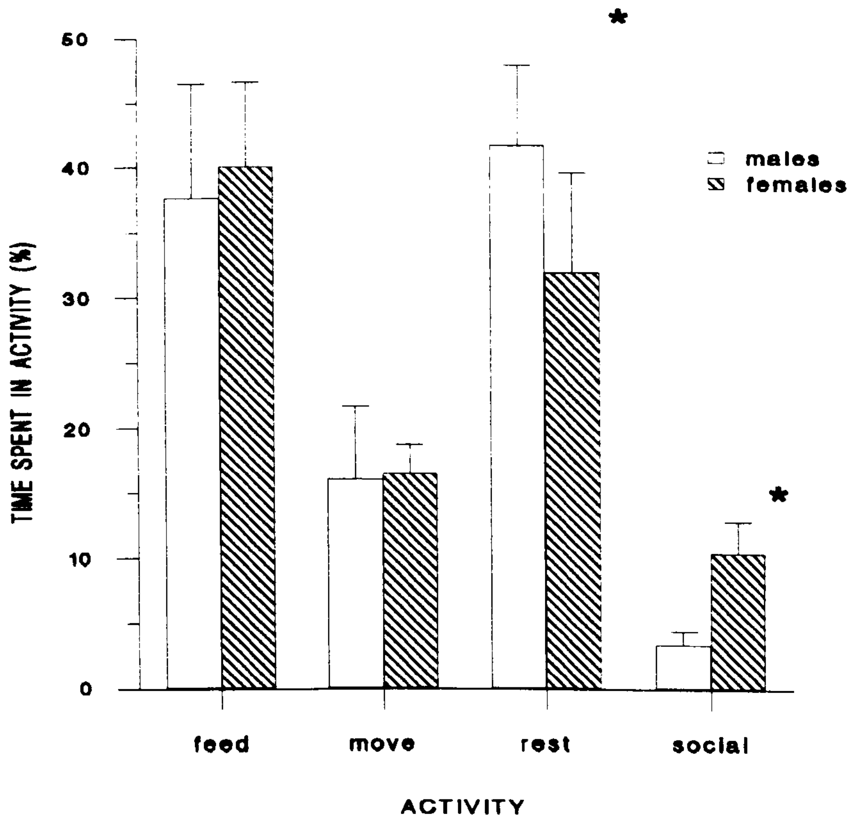
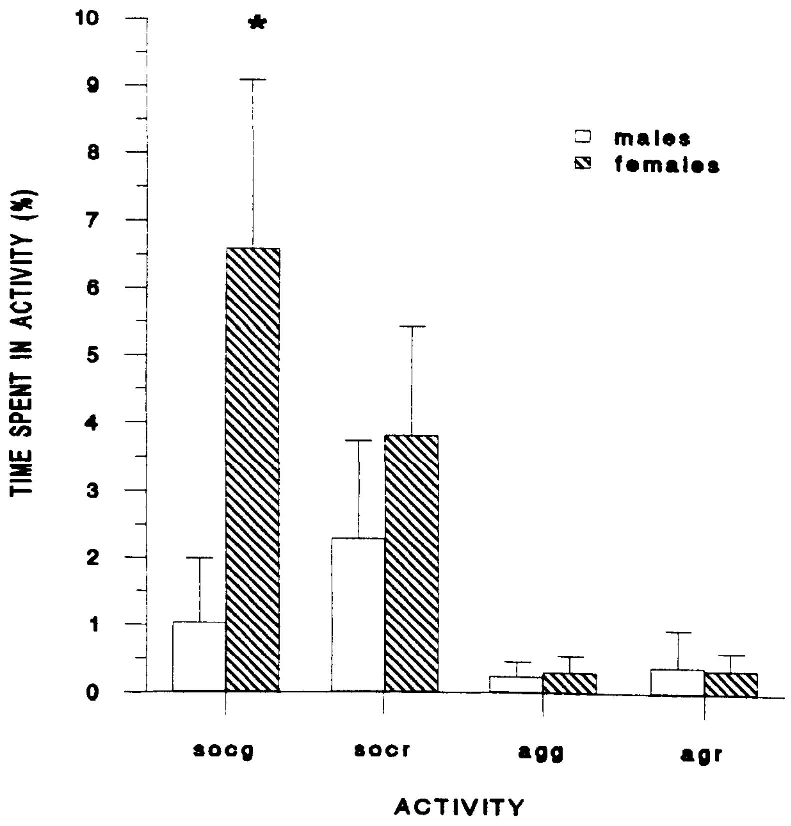


Fig 5.1b



TIME SPENT IN ACTIVITY (%)
10
9
8
7
6
5
4
3
2
1
0
*
□ males
▨ females
socg
socr
agg
agr
ACTIVITY

Table 5.5a Sex differences in time spent in different time budget categories. SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received. The upper row of figures give the results of the statistical analyses and the lower row he range between the mean value for males and females. Samples sizes were: number of adult females = 13; number of adult males = 6). For the statistical results, the U value (top) and probability (bottom) calculated using the Mann-Whitney U test, are given for each behaviour. Values in bold are significant at 0.05 level. See also Fig. 5.1.

	FEED	MOVE	REST	SOC	SOCG	SOCR	AGG	AGR
Stats. U	30.0	32.0	**13.0**	**0.0**	**0.0**	19.0	33.0	34.0
p	0.430	0.539	**0.023**	**0.001**	**0.001**	0.079	0.597	0.658
Range	2.4	0.4	9.8	7.1	5.5	1.5	0.06	0.04

Table 5.5b Sex differences in time spent in different time budget categories by quarter (QTR). The four rows of numbers in each data cell are:

mean/median for females
mean/median for males
U value calculated using the Mann-Whitney U test
probability associated with above U statistic

SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received.Samples sizes are given (nF = number of adult females; nM = number of adult males). Values in bold are significant at 0.05 level.

QTR	nF	nM	FEED	MOVE	REST	SOC	SOCG	SOCR	AGG	AGR
Dry 1	12	6	46.0/45.5 38.2/34.2 20.0 0.134	16.0/17.3 15.6/14.6 30.0 0.574	**26.5/25.8** **43.1/43.4** **3.0** **0.002**	**10.8/10.4** **2.0/2.1** **0.0** **0.001**	**6.0/5.5** **0.8/0.3** **1.0** **0.001**	**4.8/4.4** **1.3/1.1** **3.0** **0.002**	0.2/0.3 0.3/0.1 34.5 0.893	0.2/0.0 0.4/0.1 33.0 0.764
Dry 2	7	3	48.6/49.3 46.7/48.4 10.0 0.909	18.5/18.3 17.3/16.3 8.0 0.569	20.1/20.1 28.8/32.7 3.0 0.088	11.5/7.8 6.7/4.4 5.0 0.210	**7.4/7.9** **1.4/0.8** **0.0** **0.016**	4.0/3.8 5.3/2.3 10.0 0.909	0.3/0.0 0.2/0.0 9.0 0.700	0.4/0.0 0.0/0.0 6.0 0.205
Wet 1	9	2	35.9/35.1 36.0/36.0 8.0 0.814	22.5/21.9 17.1/17.1 2.0 0.099	**33.0/33.4** **44.2/44.2** **0.0** **0.034**	4.8/9.1 2.2/2.2 1.0 0.059	**5.3/5.7** **0.8/0.6** **0.0** **0.034**	2.5/1.4 1.6/1.6 6.5 0.555	0.2/0.0 0.5/0.5 6.5 0.521	0.6/0.5 0.0/0.0 3.0 0.138
Wet 2	11	4	32.0/31.6 36.2/35.0 15.0 0.361	12.9/14.2 8.9/8.9 10.0 0.117	42.8/41.4 48.8/50.3 11.0 0.151	11.4/9.9 5.5/4.5 9.0 0.090	**6.5/5.3** **1.7/0.7** **6.0** **0.037**	4.8/5.3 3.8/3.8 18.0 0.602	0.1/0.0 0.1/0.0 21.0 0.867	0.6/0.4 0.4/0.0 16.0 0.409

Table 5.5c Sex differences in time spent in different time budget categories by year (YR) and seasonal quarter (QTR). The four rows of numbers in each data cell are:

mean/median for females
mean/median for males
U value calculated using the Mann-Whitney U test
probability associated with above U statistic

SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received. The U value (top) and probability (bottom) calculated using the Mann-Whitney U test, are given for each behaviour. Samples sizes are given (nF = number of adult females; nM = number of adult males). Values in bold are significant at 0.05 level.

YR	QTR	nF	nM	FEED	MOVE	REST	SOC	SOCG	SOCR	AGG	AGR
93	Dry 1	10	3	43.1/43.0 39.1/34.4 11.0 0.499	14.1/14.1 15.6/15.8 12.0 0.612	29.9/28.6 40.1/46.1 6.0 0.128	**12.2/12.2 3.2/2.6 3.0 0.043**	**6.6/5.8 0.7/0.7 2.0 0.028**	5.6/5.6 2.5/2.6 7.0 0.176	0.2/0.0 0.8/0.9 7.5 0.086	0.35/0.0 0.5/0.7 12.0 0.582
93	Dry 2	*	*								
94	Wet 1	5	1	**	**	**	**	**	**	**	**
94	Wet 2	10	3	36.1/35.6 38.7/39.0 10.0 0.398	14.8/15.6 9.2/10.0 5.0 0.091	40.1/41.3 46.0/47.7 9.0 0.311	8.0/7.9 5.5/3.8 10.0 0.398	5.3/5.1 2.0/0.7 5.0 0.091	2.7/2.6 3.5/3.1 11.0 0.499	0.2/0.0 0.0/0.0 10.5 0.304	0.5/0.2 0.6/0.0 14.0 0.854
94	Dry 1	8	5	47.0/47.5 39.4/34.9 11.0 0.188	16.7/16.3 15.2/13.0 14.0 0.909	**25.4/26.3 42.6/43.3 2.0 0.008**	**9.9/8.6 2.0/2.0 0.0 0.003**	**4.9/4.9 0.9/0.8 2.0 0.008**	**5.1/3.7 1.1/1.0 3.0 0.013**	0.4/0.4 0.3/0.0 14.0 0.366	0.2/0.1 0.3/0.0 16.0 0.504
94	Dry 2	7	3	48.8/49.3 49.6/48.4 10.0 0.909	18.8/18.5 17.5/16.0 8.0 0.559	19.9/20.1 25.4/27.1 6.0 0.305	10.9/9.5 7.0/4.4 5.0 0.210	**7.0/6.1 1.6/1.3 0.0 0.017**	3.9/3.8 5.5/2.7 10.0 0.909	0.3/0.0 0.8/0.0 9.0 0.700	0.4/0.0 0.0/0.0 6.0 0.205
95	Wet 1	7	2	38.2/37.0 34.9/34.9 5.0 0.558	19.8/20.1 18.4/18.4 5.0 0.558	**32.6/34.7 44.2/44.2 0.0 0.040**	8.9/9.3 2.5/2.5 2.0 0.143	**6.1/6.0 0.0/0.0 0.0 0.040**	2.8/1.5 2.5/2.5 5.0 0.558	0.3/0.4 0.0/0.0 3.0 0.200	0.2/0.0 0.0/0.0 4.0 0.297
95	Wet 2	7	1	**	**	**	**	**	**	**	**
95	Dry 1	6	1	**	**	**	**	**	**	**	**

* insufficient data.

** not possible to obtain significant result with these sample sizes.

5.3.2 Reproductive State

The number of follows that a female was recorded as cycling, pregnant or lactating did not correlate with time spent in different activities, except for pregnancy and lactation with receiving social behaviour (Table 5.6a). In both cases the correlation was positive, showing that pregnant and lactating females received more social behaviour than cycling females.

However, no significant differences were found for time spent in different activities by females in different reproductive states either by quarter (Table 5.6b) or by year and quarter (Table 5.6c). Data from dry 1, pooled across years, provides a typical example of the range between the mean values of individuals in different reproductive states. The greatest range, 5.3, was for social and the mean range for the for main time budget categories was 3.7. The mean range for agonistic and affiliative categories was 1.4.

Table 5.6a Correlations between number of follows females recorded in each reproductive states and time spent in different time budget categories. SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received. The Kendall rank-order correlation coefficient T (top) and probability (bottom) are given for each behaviour. Samples sizes are given (n). Values in bold are significant at 0.05 level.

STATE	n	FEED	MOVE	REST	SOC	SOCG	SOCR	AGG	AGR
Cycling	13	0.25 0.246	0.14 0.501	-0.37 0.076	0.14 0.501	0.04 0.855	0.35 0.099	-0.27 0.198	0.08 0.712
Pregnant	13	-0.11 0.620	-0.05 0.804	-0.13 0.535	0.27 0.215	-0.05 0.804	**0.67** **0.002**	-0.14 0.950	0.00 1.000
Lactating	13	-0.05 0.807	-0.10 0.625	0.03 0.903	0.00 1.000	-0.15 0.464	**0.49** **0.020**	-0.10 0.624	-0.09 0.667

Table 5.6b Differences between individuals in different reproductive states by quarter (QTR.). The five rows of numbers in each data cell are:

mean/median for cycling females
mean/median for pregnant females
mean/median for lactating
chi-squared value from the Kruskall-Wallis test
probability associated with above statistic

SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received. Samples sizes are given (nC = number of cycling females; nP = number of pregnant females; nL = number of lactating females). There were no significant results at the 0.05 level.

QTR	nC	nP	nL	FEED	MOVE	REST	SOC	SOCG	SOCR	AGG	AGR
Dry 1	8	6	11	45.9/45.2 44.5/47.2 46.3/43.5 0.01 0.997	15.4/16.1 19.5/17.4 15.7/17.2 0.55 0.551	28.4/26.1 27.8/28.6 24.6/22.0 0.91 0.636	9.5/7.3 7.5/7.0 12.8/14.5 5.55 0.062	4.8/4.6 4.5/4.8 6.8/5.6 2.25 0.325	4.7/3.4 3.1/2.2 6.0/6.3 3.69 0.158	0.2/0.0 0.3/0.2 0.3/0.0 0.21 0.882	0.3/0.3 0.1/0.0 0.4/0.0 1.38 0.367
Dry 2	5	2	3	49.8/54.9 40.9/40.9 51.9/55.7 2.75 0.253	17.7/18.5 21.0/21.0 21.2/21.8 0.89 0.641	20.3/17.3 21.3/21.3 18.1/16.1 0.72 0.696	10.0/8.3 16.7/16.7 8.1/9.0 0.14 0.932	6.9/6.1 10.5/10.5 4.0/4.8 1.60 0.450	3.1/2.2 5.7/5.7 4.2/4.2 0.36 0.834	0.7/0.5 0.0/0.0 0.0/0.0 2.45 0.156	0.5/0.0 0.0/0.0 0.2/0.0 0.69 0.592
Wet 1	5	2	4	36.8/36.4 42.8/42.8 34.2/33.2 3.16 0.206	22.0/22.0 22.3/22.3 23.9/24.5 0.00 1.000	33.9/33.0 29.8/29.8 30.0/31.6 0.84 0.657	6.9/8.0 4.8/4.8 10.6/12.1 2.00 0.367	5.2/6.3 3.8/3.8 6.6/7.5 1.62 0.445	1.7/1.7 1.1/1.1 4.0/4.6 2.32 0.313	0.2/0.0 0.0/0.0 0.3/0.3 1.09 0.481	0.3/0.0 0.3/0.3 1.0/0.8 2.18 0.276
Wet 2	5	4	10	29.7/28.6 31.0/33.5 37.0/32.8 1.86 0.395	16.8/16.3 11.2/11.0 13.0/13.4 2.22 0.329	42.0/43.9 40.7/39.3 39.4/42.2 0.30 0.860	10.5/7.9 15.9/18.3 9.9/8.8 2.29 0.319	6.8/5.6 9.0/8.5 5.2/4.7 2.09 0.352	3.7/2.3 6.9/6.8 4.6/4.1 0.96 0.618	0.0/0.0 0.1/0.0 0.2/0.0 0.48 0.549	0.9/0.6 0.8/0.8 0.3/0.0 3.23 0.175

Table 5.6c Differences between individuals in different reproductive states by year (YR) and quarter (QTR). The five rows of numbers in each data cell are:

mean/median for cycling females
mean/median for pregnant females
mean/median for lactating females
chi-squared value from the Kruskall-Wallis test or U from a Mann-Whitney U test
probability associated with above statistic

SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received. Samples sizes are given (nC = number of cycling females; nP = number of pregnant females; nL = number of lactating females). There were no significant results at the 0.05 level.

YR	QTR	nC	nP	nL	FEED	MOVE	REST	SOC	SOCG	SOCR	AGG	AGR
93	Dry 1	2	1	7	**	**	**	**	**	**	**	**
93	Dry 2	*	*	*								
94	Wet 1	1		3	**	**	**	**	**	**	**	**
94	Wet 2	3		7	34.4/36.6 - 40.0/38.9 7.0 0.425	20.0/18.7 - 13.7/14.9 5.0 0.210	40.0/41.4 - 36.7/39.1 8.0 0.569	4.7/3.6 - 8.8/8.0 3.0 0.088	0.0/0.0 - 0.2/0.0 5.0 0.210	1.0/0.6 - 0.4/0.0 2.0 0.053	3.7/2.9 - 5.5/5.7 7.5 0.329	1.0/0.7 - 3.2/3.4 7.0 0.395
94	Dry 1	6	2	2	48.3/49.3 50.1/50.1 43.6/43.6 1.74 0.418	17.3/16.5 17.4/17.4 9.2/9.2 3.71 0.157	23.9/23.4 25.5/25.5 33.3/33.3 3.56 0.168	9.8/7.3 5.5/5.5 13.2/13.2 2.25 0.324	0.3/0.2 0.4/0.4 0.7/0.7 1.75 0.418	0.2/0.0 0.14/0.14 0.0/0.0 2.25 0.324	4.5/4.2 3.3/3.3 6.4/6.4 1.38 0.490	5.3/3.4 2.2/2.2 6.8/6.8 0.62 0.626
94	Dry 2	5	2	3	49.8/54.9 40.9/40.9 51.9/55.7 2.75 0.253	17.7/18.5 21.0/21.0 51.9/55.7 0.89 0.642	20.3/17.3 21.3/21.3 21.2/21.8 0.73 0.696	10.0/8.3 16.2/16.2 17.2/16.1 0.14 0.932	0.7/0.5 0.0/0.0 8.2/9.0 1.60 0.450	0.5/0.0 0.0/0.0 0.0/0.0 0.36 0.834	6.9/6.1 10.5/10.5 0.2/0.0 2.45 0.156	3.1/2.2 5.7/5.7 4.0/4.8 0.69 0.592
95	Wet 1	4	2	2	35.9/35.7 42.8/42.8 36.2/36.2 1.79 0.408	21.6/22.0 22.3/22.3 15.0/15.0 4.0 0.135	34.1/35.1 29.8/29.8 33.8/33.8 1.13 0.570	7.7/8.2 4.8/4.8 14.2/14.2 5.13 0.077	0.2/0.2 0.0/0.0 0.6/0.6 3.00 0.223	0.3/0.0 0.3/0.3 0.3/0.3 4.50 0.105	6.1/6.7 3.8/3.8 7.1/7.1 2.67 0.220	1.5/1.5 1.1/1.1 7.2/7.2 0.13 0.921
95	Wet 2	2		3	**	**	**	**	**	**	**	**
95	Dry 1		3	5	- 40.5/42.3 42.3/42.4 7.0 0.882	- 23.4/26.4 17.6/17.2 4.0 0.297	- 26.0/28.8 26.5/26.5 7.0 0.882	- 9.9/12.8 12.8/14.0 5.0 0.456	- 0.3/0.0 0.3/0.0 5.0 0.210	- 0.0/0.0 0.7/0.0 2.0 0.053	- 5.7/7.0 5.9/4.0 7.5 0.329	- 4.2/5.1 6.9/7.8 7.0 0.395

* insufficient data.

** not possible to obtain significant result with these sample sizes.

5.3.3 Social Rank

Time spent in different activities did not correlate with rank (Fig. 5.2, Table 5.7a, Table 5.7b). Figure 5.2b suggests that middle ranking females received and gave more social behaviour than either high or low rankers. The range between the highest and lowest ranking individuals was small in all cases. The greatest range was for moving at 2.7.

In order to assess the possibility that a non-linear association between rank and time budgets exists, additional analyses were performed. Females were assigned to one of three categories (high, medium or low) and differences between these categories tested for using Kruskall Wallis ANOVAs. In all cases the results were not significant.

Figure 5.2 Mean time spent in different activities against social rank for females. There are no significant correlations (Table 5.7a). Rank 1 is most dominant. For (b) SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received.

Fig. 5.2a

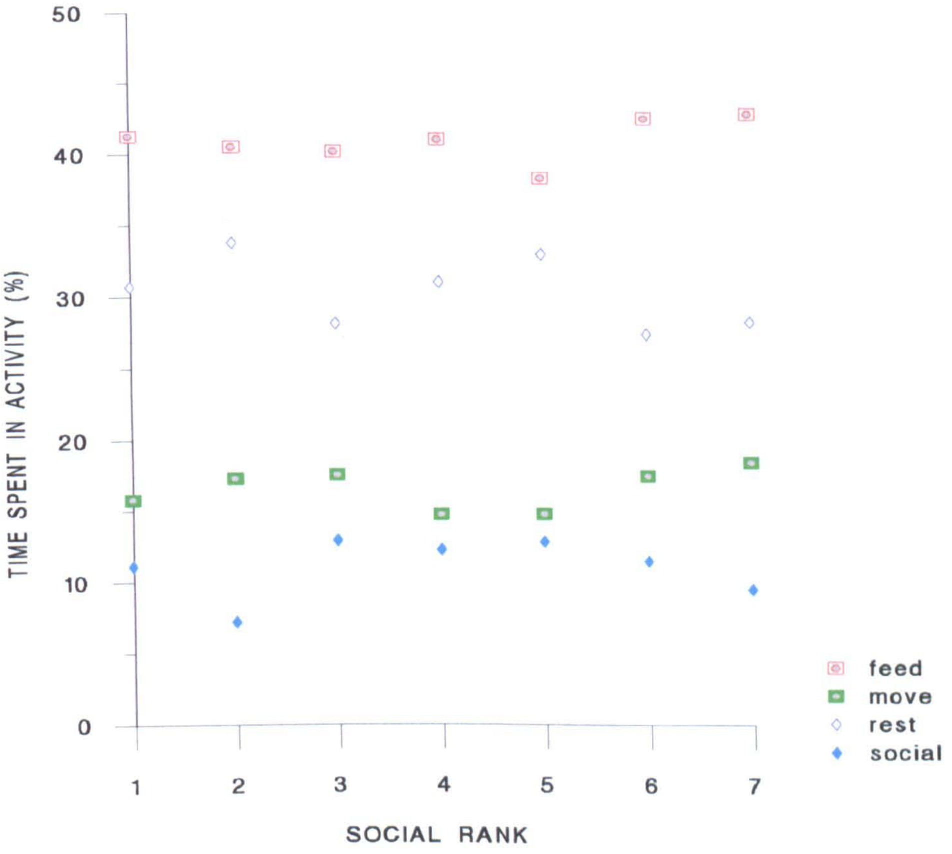
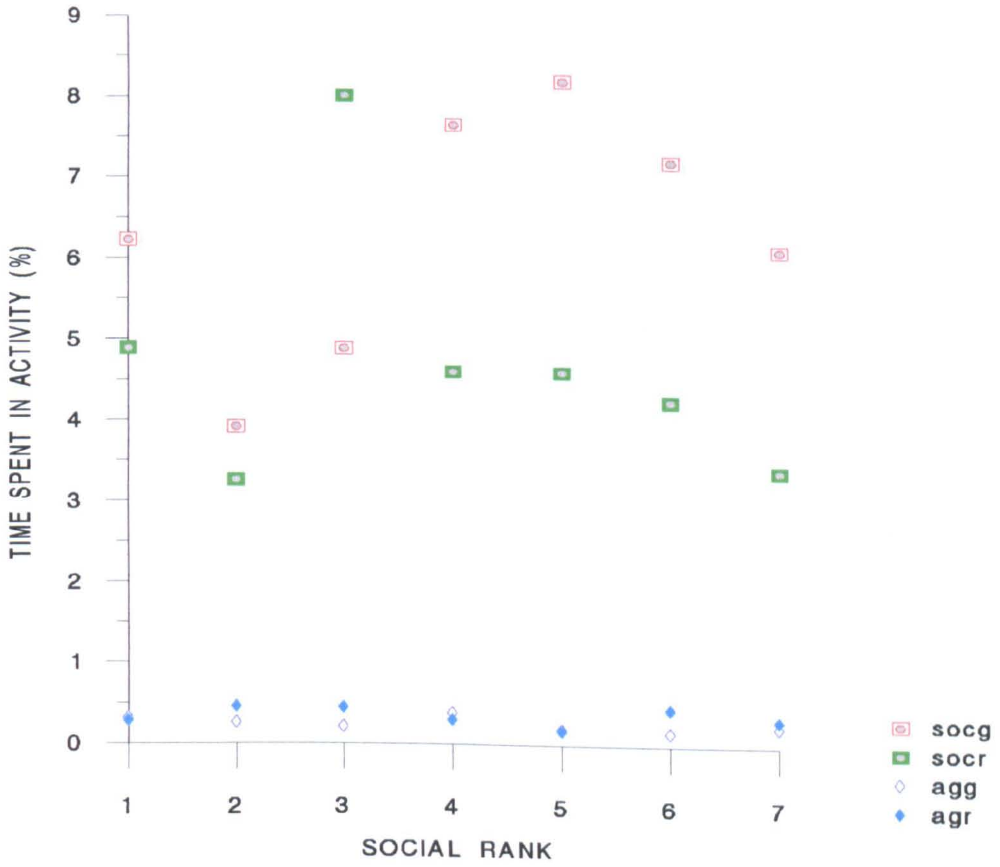


Fig 5.2b



9
8
7
6
5
4
3
2
1
0
TIME SPENT IN ACTIVITY (%)
1
2
3
4
5
6
7
SOCIAL RANK
socg
socr
agg
agr

Table 5.7a Correlations between social rank and time spent in different time budget categories for post fusion troop. SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received. The Kendall rank-order correlation coefficient T (top) and probability (bottom) are given for each behaviour. Sample size is given (n). There were no significant results at the 0.05 level.

n	FEED	MOVE	REST	SOC	SOCG	SOCR	AGG	AGR
7	0.23	0.33	-0.24	-0.05	0.05	-0.43	-0.43	0.24
	0.453	0.293	0.453	0.881	0.881	0.176	0.176	0.453

Table 5.7b Correlations between social rank and time spent in different time budget categories by quarter (QTR) for post fusion troop. SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received. The Kendall rank-order correlation coefficient T (top) and probability (bottom) are given for each behaviour. Samples sizes are given (n). There were no significant results at the 0.05 level.

YR	QTR	n	FEED	MOVE	REST	SOC	SOCG	SOCR	AGG	AGR
94	Dry	7	0.05	-0.05	-0.14	-0.05	0.24	-0.24	0.06	0.12
	2		0.881	0.881	0.881	0.652	0.453	0.753	0.867	0.734
95	Wet	7	0.33	0.54	-0.05	-0.33	0.24	-0.62	-0.41	-0.28
	1		0.293	0.099	0.881	0.293	0.453	0.051	0.210	0.402
95	Wet	7	0.05	0.05	-0.05	0.14	0.24	-0.14	0.00	0.30
	2		0.881	0.881	0.652	0.881	0.453	0.652	1.000	0.362
95	Dry	6	-0.33	0.33	0.33	0.33	-0.07	-0.07	-0.60	-0.35
	1		0.348	0.348	0.348	0.348	0.851	0.851	0.107	0.380

5.3.4 Age

The general pattern across years (Fig 5.3, Table 5.8a) and by quarter (Table 5.8b) was that older animals fed less and rested more than younger animals. For the overall analyses, the results for feeding and resting were significant. The range between the oldest and youngest individuals was considerable for both feeding (26.1) and resting (30.4), otherwise it was less than 8. By quarter, the pattern of feeding less and resting more with increased age was significant for dry 1 and wet 2 only, whereas feeding but not resting showed a significant correlation in early wet.

When broken down by year and quarter the situation was less clear (Table 5.8c). Feeding was negatively correlated with age in all quarters but only significantly in the dry 1 1995. Resting was positively correlated with age in all quarters except the late wet of 1995 (where the correlation approached zero) but again was only significant for dry 1 1995. Moving was negatively correlated with age in wet 2 1994 and receiving agonistic negatively correlated with age in dry 1994 and wet 2 1995. Neither of these were consistent trends, significant or otherwise.

Figure 5.3 Mean time spent in different activities against age rank for females. Line of best fit (using regression) drawn for significant results (Table 5.8a). Rank 1 is youngest. For (b) SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received.

Fig 5.3a

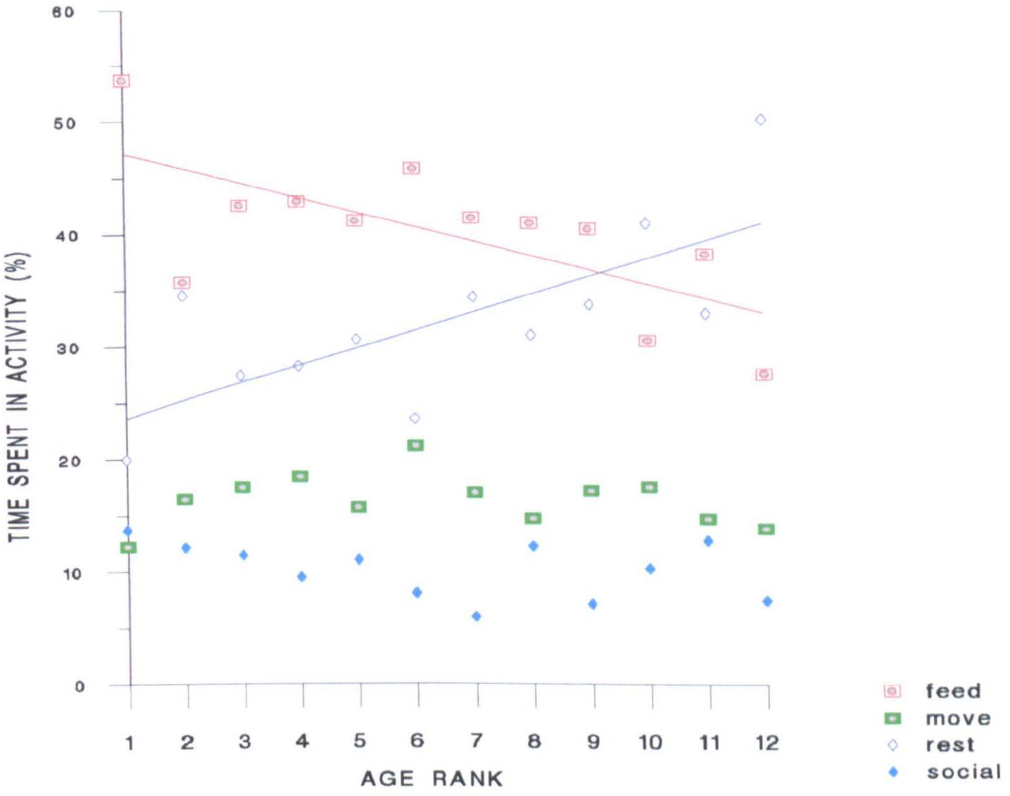


Fig 5.3b

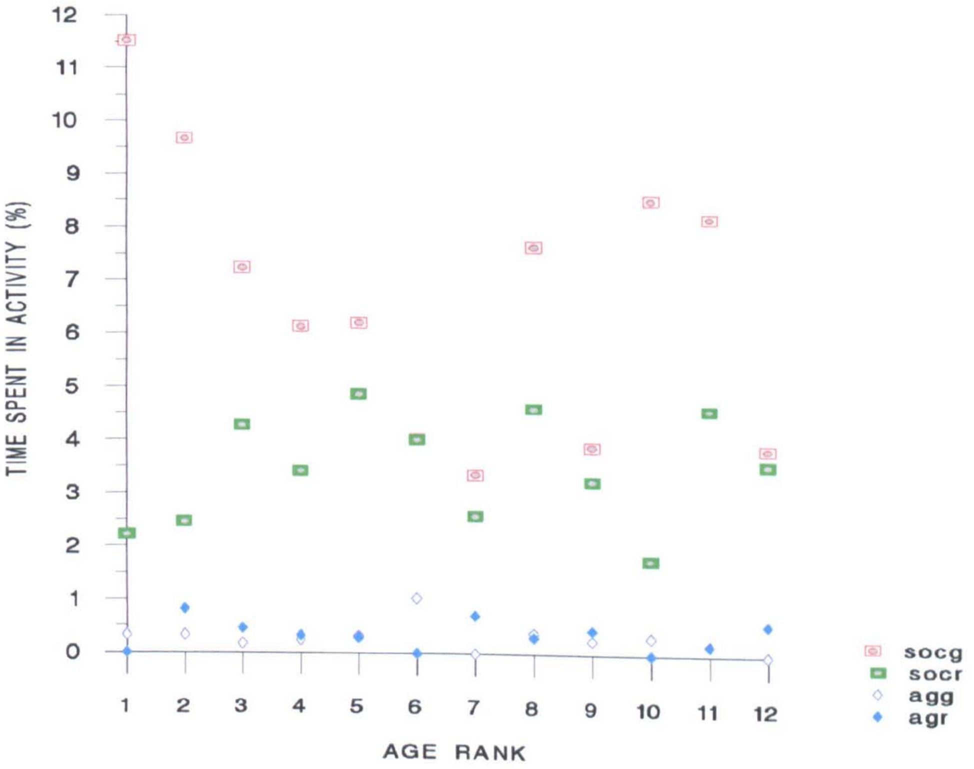

TIME SPENT IN ACTIVITY (%)
12
11
10
9
8
7
6
5
4
3
2
1
0
1
2
3
4
5
6
7
8
9
10
11
12
AGE RANK
socg
socr
agg
agr

Table 5.8a Correlations between age rank and time spent in different time budget categories. SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received. The Kendall rank-order correlation coefficient T (top) and probability (bottom) are given for each behaviour. Sample size is given (n). Values in bold are significant at 0.05 level.

n	FEED	MOVE	REST	SOC	SOCG	SOCR	AGG	AGR
12	**-0.58**	-0.06	**0.52**	-0.30	-0.08	-0.22	0.12	-0.33
	0.009	0.784	**0.020**	0.170	0.729	0.345	0.583	0.13

Table 5.8b Correlations between age rank and time spent in major time budget categories by quarter (QTR). SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received. The Kendall rank-order correlation coefficient T (top) and probability (bottom) are given for each behaviour. Samples sizes are given (n). Values in bold are significant at 0.05 level.

QTR	n	FEED	MOVE	REST	SOC	SOCG	SOCR	AGG	AGR
Dry 1	11	**-0.60**	-0.09	**0.71**	-0.27	-0.38	0.16	-0.22	-0.21
		0.010	0.679	**0.002**	0.243	0.102	0.484	0.366	0.392
Dry 2	6	-0.07	0.07	0.07	0.07	0.47	-0.20	-0.26	0.54
		0.851	0.851	0.851	0.851	0.188	0.573	0.499	0.150
Wet 1	8	**-0.57**	0.21	0.36	-0.28	-0.21	-0.14	0.16	0.04
		0.048	0.458	0.216	0.322	0.458	0.621	0.595	0.899
Wet 2	10	**-0.56**	-0.29	**0.69**	-0.07	0.11	-0.11	0.30	-0.50
		0.025	0.245	**0.006**	0.788	0.655	0.655	0.266	0.052

Table 5.8c Correlations between age rank and time spent in major time budget categories by year (YR) and seasonal quarter (QTR). SOCG = social behaviour given; SOCR = social behaviour received; AGG = agonistic behaviour given; AGR = agonistic behaviour received. The Kendall rank-order correlation coefficient T (top) and probability (bottom) are given for each behaviour. Samples sizes are given (n). Values in bold are significant at 0.05 level.

YR	QTR	n	FEED	MOVE	REST	SOC	SOCG	SOCR	AGG	AGR
93	Dry 1	10	-0.24 0.325	0.11 0.655	0.42 0.089	-0.47 0.060	-0.24 0.325	-0.24 0.325	-0.13 0.602	0.00 1.000
93	Dry 2	*								
94	Wet 1	5	-0.40 0.327	0.60 0.142	0.60 0.142	-0.60 0.142	-0.60 0.142	-0.40 0.327	-0.63 0.157	0.53 0.207
94	Wet 2	10	-0.38 0.128	**-0.51** **0.040**	0.42 0.089	0.11 0.655	0.07 0.788	-0.07 0.788	0.18 0.504	-0.48 0.068
94	Dry 1	7	-0.43 0.176	-0.33 0.293	0.43 0.176	-0.24 0.453	-0.62 0.051	0.05 0.881	0.10 0.761	**-0.73** **0.029**
94	Dry 2	6	0.33 0.348	0.33 0.348	0.07 0.851	-0.50 0.188	0.20 0.573	-0.20 0.573	-0.23 0.499	-0.54 0.150
95	Wet 1	6	-0.07 0.851	0.07 0.851	0.47 0.188	-0.20 0.573	0.07 0.851	0.20 0.573	0.41 0.251	**-0.77** **0.042**
95	Wet 2	6	-0.33 0.348	0.07 0.851	-0.07 0.851	0.07 0.851	0.20 0.573	-0.20 0.573	0.16 0.770	-0.14 0.702
95	Dry 1	5	**-1.0** **0.014**	0.20 0.624	**1.0** **0.014**	0.20 0.624	0.20 0.624	0.00 1.000	-0.60 0.166	0.32 0.480

* insufficient data.

5.4 DISCUSSION

5.4.1 Inter-individual Differences

5.4.1.1 Sex

The lack of sex differences in time spent feeding and moving reported here are consistent with previous studies (section 5.1.2). The reasons for this are also considered in earlier (section 2.5.1.2. as summarized in Table 5.1).

Sex differences in time spent in social behaviour, especially giving, were found. This is consistent with theoretical considerations of the consequences of the female bonded structuring of yellow baboon society (Wrangham 1980) and data from similarly female bonded vervets (Baldellou in litt.; Isbell & Young 1993).

In contrast, Post (1981) found no sex differences in time spent socializing by yellow baboons in Amboseli. Methodology could underlie this apparently contradictory finding. Firstly, Post's sample size was exceedingly small consisting of only two individuals of each sex. Secondly, his definition of social behaviour encompassed all "activity during which an animal's attention and behaviour were clearly directed toward another individual" while the definition used here includes only affiliative interactions, largely grooming. The separation of time spent giving and receiving social behaviour performed by this study indicate that significant differences in giving social behaviour can be masked when it is lumped with receiving such behaviour. Given his broad definition of social behaviour, Post's findings are likely to suffer from a similar masking effect.

The pattern of significant sex differences in giving social behaviour suggests that demographic rather than seasonal factors are important. Significant differences were not found when individuals were in small troops. The significant result in dry 1 1993 occurred before loss of adult females reduced V1 and V2 from medium to small troops. In dry 1 1994 the fusion of V1 and V2 restored group size. This increase in group size, plus possible elevated grooming to cement new relationships, could account for the significant differences found from dry 1 1994 to wet 1 1995. That the differential was not maintained in subsequent quarters may be attributable to the presence of only a single male (i.e., n=1 for males in the analyses), the loss of an adult female (Ruaha) early in dry 1 1995 and/or a decline in the need to cement new relationships.

It has been suggested that grooming behaviour acts as "social glue" (Dunbar 1992a) in baboon societies. Given the central role of females in the female bonded structuring of savannah baboon societies it is not surprising to find females devoting more time to this activity and for this aspect of their behaviour to be more susceptible to demographic events. Demographic effects on individual time budgets are considered further in Chapter 7.

Males rested significantly more than females in dry 1 1994 and wet 1 1995. In both of these quarters females spent significantly more time giving social behaviour than males. This is consistent with the hypothesis that resting time is an important reservoir of unused time which can be coopted for other activities such as socializing (Dunbar & Dunbar 1988; Dunbar 1992a).

5.4.1.2 Reproductive state

The costs of nourishing and carrying infants (Lee & Bowman 1995; Altmann & Samuels 1992) makes pregnancy and, to an even greater extent, lactation, energetically demanding times for females. A number of studies have found feeding time increases accordingly (Altmann 1980; Barton 1989; Dunbar & Dunbar 1988; Muruthi et al. 1991). Differences between females in different reproductive states were thus expected but not found for the main time budget categories. There are two possible explanations for this discrepancy. Firstly, the analyses were coarse grain, with females being classified in broad classes of cycling, pregnancy and lactation. Most studies which have found elevated feeding times during non cycling phases have been more fine grained (eg., Altmann 1980; Barton 1989; Dunbar & Dunbar 1988 but cf. Muruthi et al. 1991). Dunbar & Dunbar (1988), for example, calculated changes in maternal time budgets as lactation progressed from one month to the next. Perhaps with a more fine grained analysis significant differences would have been detected in this study. However this level of variation is unlikely to be important in the context of the main aim of this chapter (section 5.4.1).

A second explanation can be developed from further consideration of Kenyatta (1995) and Post et al. (1980) who found no differences under drought conditions. Although there was no drought in Mikumi during or prior to this study similar constraints may be imposed by the spatially and temporally variable nature of the Mikumi ecosystem. These constraints may interact with birth peaks which have been detected in the early dry season (Wasser & Norton 1993) to force the costs of reproduction to be spread across all stages of the reproductive cycle. Ecological constraints on time budgets will be dealt with further in Chapter 6.

A study of coalition rates amongst females baboons in Mikumi (Wasser 1983) has demonstrated statistically significant differences between observed and expected frequencies of coalition attack and receipt by females in different reproductive states. Coalitions fall into the category of agonistic behaviour. That differences in time spent in the agonistic categories were not detected here may again be attributable to the grain of analyses and level of variation under consideration. Coalitions only account for a proportion of agonistic interactions and even the total amount of time spent in such behaviour is relatively slight. Wasser measured the frequency of coalitions rather than the time they took, which is more appropriate for detailed analysis of behaviours of short duration. Moreover, he performed his analyses using ten subdivisions of the reproductive cycle (eg., pregnancy divided into three trimesters) rather than lumping them into three broad categories as done here.

The overall correlations between number of follows in a particular state and time budget components provide evidence to suggest that pregnant and lactating females attract more social behaviour than cycling females (Table 5.6a). Mikumi females in the first six months of lactation have been found to groom females in the same reproductive state significantly more often than expected by chance alone (Wasser 1983). This could be one proximate explanation for the result obtained for lactation. Wasser (1983) found that a similar grooming pattern for flat females but as this state was considered under the broad category of cycling, any effect on time spent in social behaviour would be unlikely to manifest itself.

5.4.1.3 Social rank

No correlations were found between social rank and time budget components. Previous work on baboons (Altmann & Muruthi 1988) and vervets (Whitten 1983) suggests that resources have to be both of the highest quality and extremely clumped in order for rank differences to manifest themselves in time spent feeding. From Chapter 4 it is clear that both patchiness and the quality of food varied by seasonal quarter in Mikumi during this study. However, levels of clumped quality sufficient to promote rank related differences in feeding time were apparently not reached. Such conditions are likely to be more common for artificially fed primates (e.g., garbage feeders, zoo animals) than for those that feed naturally in the wild.

Wasser's (1983) study of coalitions in the Mikumi baboons found that mid ranking females entered into coalition attacks more frequently than low or high ranking females but that receipt of attacks decreased with increasing social status. Although Figure 5.2 suggested a possible non linear relationship between time spent giving affiliative and rank this was not supported statistically. As discussed above for reproductive state, there are reasons that this study would not expect, nor need, to detect this level of variation. However, further study on possible non-linear relationships between rank and aspects of social behaviour in the Mikumi baboons would be interesting.

5.4.1.4 Age

If physiological changes accompanying aging in baboons are similar to those experienced by humans (Binney 1989) then these could account for the pattern of younger females spending more time feeding and less time resting than older females. Metabolic rate declines in humans, leading to reduced energy requirements. Reduction in the capacity of the body's detoxification system (i.e., liver and kidneys) could also favour reduced food intake. In addition changes in joints and muscles make movement less easy.

The upper end of the age range of female subjects in this study was relatively low. The oldest was Tai who was 16 years old by the end of the study (Table 5.4). This compares to the oldest female subject of the long-term Mikumi baboon project, Asha, who reached at least 22 years (G.W. Norton pers. comm.; R.J.Rhine, G.W.Norton & S.K.Wasser unpublished data). It would be interesting to know if the pattern found for feeding would have held with the inclusion of females older than sixteen. At some point deterioration of dental condition might be expected to reduce feeding efficiency and lead to longer feeding time.

This cross sectional study suggests that effects of age may not be unimportant. Moreover, it indicates that longitudinal studies of aging effects on the behavioural ecology of known individuals over their adult lifetimes are merited. An extensive long term study has described psychological and physiological changes accompanying aging in laboratory rhesus monkeys (Davis & Leathers 1985) but, further investigation into the effects of aging on the behavioural ecology of freeliving primates is needed.

The above discussion relates to the effects of age among adults. Variations in time spent in different activities by individuals from different age classes have not been addressed by the analyses in this chapter but may be considerable. For example, work by Barrett et al. (1992) on gelada baboons has found that play behaviour can occupy up to 8% of a juvenile's time budget. Moreover, they found significant seasonal variation with virtually no time being devoted to play in dry months. Sommer & Mendoza-Granados (1995) found that hourly play rates in pre-adult male langurs were higher than in adults, especially in resource rich habitat. Both the degree and resource dependent nature of age class differences in play are potentially important. Differences in body size are also likely to contribute to differences between age classes.

5.4.1.5 Overview

Time spent feeding was unrelated to sex, reproductive state and rank, but there is evidence that it declined with age. Time spent in social behaviour was unrelated to reproductive state, rank and age, but females tended to spend more time in social behaviour than males. As found in other baboon studies (Bronikowski & Altmann 1996; Dunbar & Dunbar 1988; Kenyatta 1995) time was generally taken from resting when time spent feeding or socializing increased. Time spent moving was most robust and showed no clear relationships with any of the factors investigated. This may be due to constraints imposed by living in a cohesive group.

The patterns described above generally became less consistent as the time frame of analyses was reduced from the full study period, through quarters combined across the study period, to quarters considered separately across the study period. Both biological and mathematical reasons for this must be considered. An example of a biological explanation is the possible influence of demography on the pattern of social behaviour by sex as discussed. However the reduction in sample sizes accompanying smaller time frames could provide a mathematical explanation. This is further suggested by a consistency of trends across quarters (e.g., feeding time always negatively correlated with age) despite the absence of statistical significance within individual quarters.

No seasonal patterns to inter-individual variation were found. The evidence available suggests that demographic factors have a greater influence than ecological factors in this respect. However this could also be a product of sample size reduction effects when data are analyzed separately for each of the nine quarters covered by this study .

5.4.2 Level of Variation

Even if inter-individual differences invalidate the assumption of random contribution to group means of time budget components, the consequences for comparisons between groups may not be important if the level of variation generated is relatively slight. This section compares the level of variation generated by inter-individual differences within populations to that generated by interpopulation comparison of mean group values.

Table 5.9 shows the variation between studies in Dunbar's (1992a; his table 2) dataset of main time budget components. With the exception of age, this is considerably more than that generated by inter-individual differences. The data from this study suggest that comparing, for example, males in one population with females in another does not present problems but, that the age of individuals in different samples should be controlled. However, this study is not exhaustive and sample sizes are relatively small. A conservative approach would be to ensure that sampling decisions are compatible between studies under comparison and that, in particular, the age structure of the populations should be considered when interpreting the results.

Table 5.9 Variation in time use between different populations of baboon. Values calculated from data from 14 population as presented in Dunbar (1992a; his table 2). Example data (see Fig 5.3a) from this study presented in brackets.

	MINIMUM-MAXIMUM (youngest-oldest)	**RANGE (youngest to oldest)**	**STANDARD DEVIATION (of 12 females)**
FEED	20.3-59.3 (27.7-53.7)	39.0 (26.0)	13.05 (6.78)
MOVE	17.6-36.9 (13.9-12.2)	19.3 (1.7)	5.82 (2.36)
REST	5.9-61.4 (50.4-20.0)	55.5 (30.4)	13.36 (7.89)
SOCIAL	4.5-22.7 (7.5-13.7)	18.2 (6.2)	5.25 (2.51)

5.5 SUMMARY

Few significant results were found for the variables tested suggesting that the assumption that all individuals vary randomly around group means may be valid under many circumstances. The main patterns to emerge were sex and age differences. Adult females socialize more and rest less than adult males. Time feeding decreases and time resting increases with age and the range between the oldest and youngest individuals considerable. For these combinations of variables, in particular, caution should be taken when making comparisons between groups in which it is assumed that all individuals vary randomly around group mean. In addition, although not analyzed here, the inclusion of different age classes is also requires caution.

This must be viewed in the context of the level of variation under investigation. Inter-individual variation within populations is generally slight compared to that between groups in different populations. However, a conservative and simple to apply strategy, would be to make only comparisons between groups whose means have between calculated from data collected using compatible sampling decisions. Moreover, differences in the age structure of populations under comparison should be taken in to consideration.

CHAPTER 6. TEMPORAL VARIATION

6.1 INTRODUCTION

6.1.1 Aim & Rationale

The primary aim of this chapter is to investigate associations between temporal variation in time budgets and climate, and to assess possible causal mechanisms for any associations found. This is achieved by exploring temporal variation in the time budgets of adult female yellow baboons in Mikumi National Park and relating this to variation in the Mikumi environment (section 6.1.2; Chapter 4). Three time scales are considered: between years, within years (between quarters and seasons) and within days (between periods). The level of variation generated by temporal variation is also considered.

Temporal variation in time budgets has been well documented (section 2.4.2). It is vital to consider the confounding effects of such variation when making intrapopulation comparisons. For example, comparing data collected in the dry season of one year with the wet of another, or in the morning on one year with afternoon of another, is unlikely to be useful without considering temporal variation. Similarly interpopulation comparisons (e.g., Clutton-Brock 1977a; Dunbar 1992a) must also take in to account temporal variation within populations.

Temporal variation of time budgets has commonly been associated with climate (section 2.5.3.2). This association may be correlational but several cause and effect relationships have been proposed. Greater understanding of these relationships within populations will contribute to our understanding of the climatic factors can cause interpopulation variation in time budgets on a biogeographic scale (Dunbar 1992a).

6.1.2 Climatic Patterns in Mikumi National Park

Climatic data are available from park records and the long-term baboon research project in Mikumi National Park (Norton 1994b; R.J. Rhine, G.W.Norton & S.K.Wasser unpublished data; Mikumi National Park unpublished data). Rainfall data have been collected daily since 1946 at the field station and/or at the nearby Park Headquarters and data were available for analyses from 1964 (section 3.5.2). Min/max temperatures, available for at least 13 years, are collected daily at the field station. In addition, half hourly records of temperature are made in the field when following baboons. Full details of methods used are given in Chapter 3.

6.1.2.1 Within and between years

Within and between year patterns of variation in rainfall in Mikumi National Park were described in Chapter 4 (section 4.3.2.1; Figs. 4.8 & 4.9; Table 4.3). Between year variation is relatively low except for occasional flood years in which total annual rainfall exceeds 1000mm (Norton 1994b). Excluding 5 flood years, total annual rainfall 1964-1996 averaged 787mm. No flood years occurred during or immediately prior to this study and the annual rainfall was typical of nonflood years.

Within years there is a strong seasonal pattern to rainfall. Although this pattern is unimodal (ie., one wet season, one dry season) it is ecologically useful to divide each season into two quarters (Norton 1994b; Norton et al. 1987). A classification of two dry quarters (dry 1 and dry 2) and two wet quarters (wet 1 and wet 2) is therefore used in this study (section 3.2.2). Slightly more rain usually falls in dry 2 than in dry 1 but, almost all rain falls in the wet quarters.

Min/max temperature data for 13 years between 1975 and 1995 indicate that there is little between year variation. Temperatures occurring within the study period are typical of the long-term pattern (Table 6.1).

Table 6.1 Annual minimum and maximum temperatures (mean degrees Celsius +/-sd). Annual means based on mean of monthly values (i.e., n=12). Monthly means used to calculate long-term annual means based on nine or more values.

Ecological Year (start)	**1993 (Dec 92)**	**1994* (Dec 93)**	**1995 (Dec 94)**	**Long-term average**
Mean minimum temperature	18.19 +/-3.19	18.67 +/-3.04	18.38 +/-2.71	18.91 +/-2.39
Mean maximum temperature	30.34 +/-4.47	31.54 +/-1.86	31.48 +/-2.80	31.72 +/-3.20

* Due to technical difficulties no temperature data were collected in July 1994 (in ecological year 1994). Therefore the long-term mean for July (n=13, min=14.69°C+/-1.65) was substituted into the calculations.

Variation in rainfall, like temperature, is far greater within years than between them. The pattern during the study period (Table 6.2) was consistent with longer term data (Fig. 6.1). Minimum temperatures are higher in wet quarters presumably due to cloud cover reducing heat loss; maximum temperatures are highest in wet 1 and dry 2. Considering day time temperatures only, dry 2 is the hottest quarter (Table 6.3).

A summary of conditions of rainfall and temperature by quarter is presented in Table 6.4.

Table 6.2 Minimum and maximum temperatures (mean degrees Celsius +/-sd) by quarter. Quarterly means based on mean of monthly values (i.e., n=3).

YEAR	QUARTER	MEAN MIN. TEMPERATURE	MEAN MAX. TEMPERATURE	MEAN OF MAX. & MIN.
1993	Wet 1	21.33+/-0.69	36.47+/-0.63	28.90
	Wet 2	20.09+/-0.78	29.15+/-3.70	24.62
	Dry 1	14.41+/-1.34	25.56+/-0.76	19.99
	Dry 2	16.94+/-3.02	30.18+/-1.58	23.56
1994	Wet 1	20.40+/-0.29	31.74+/-1.45	26.07
	Wet 2	20.77+/-1.03	30.10+/-1.64	25.43
	Dry 1*	13.92+/-1.57	29.38+/-1.77	21.59
	Dry 2	18.27+/-2.31	33.58+/-1.22	25.92
1995	Wet 1	20.28+/-0.48	33.97+/-0.60	27.13
	Wet 2	19.94+/-0.66	30.87+/-1.64	24.41
	Dry 1	14.45+/-1.67	28.10+/-0.74	21.28
	Dry 2	18.87+/-2.11	32.99+/-3.02	25.93

* Due to technical difficulties no temperature data were collected in July 1994 (in dry 1 1994). Therefore the long-term mean for July (n=13, min=14.69°C+/-1.65) was substituted into the calculations.

Table 6.3 Daytime temperatures (degrees Celsius) from for study period. Overall mean presented based on mean of twenty-two half hourly records taken in field between 07:00 and 17:30.

QUARTER	MEAN	n	ST.DEV.	MINIMUM	MAXIMUM
DRY 1	25.99	22	3.38	19.55	29.71
DRY 2	28.74	22	3.14	22.72	32.32
WET 1	27.95	22	3.00	22.24	32.33
WET 2	26.98	22	2.49	21.76	29.66

Figure 6.1 Long-term minimum and maximum temperatures (degrees Celsius) by quarter. Bars represent mean of three monthly means for each quarter. Data from 13 (wet 1, dry 1 and dry 2) or 14 (wet 2) years between 1975 and 1995. Lines on bars represent standard deviations between years.

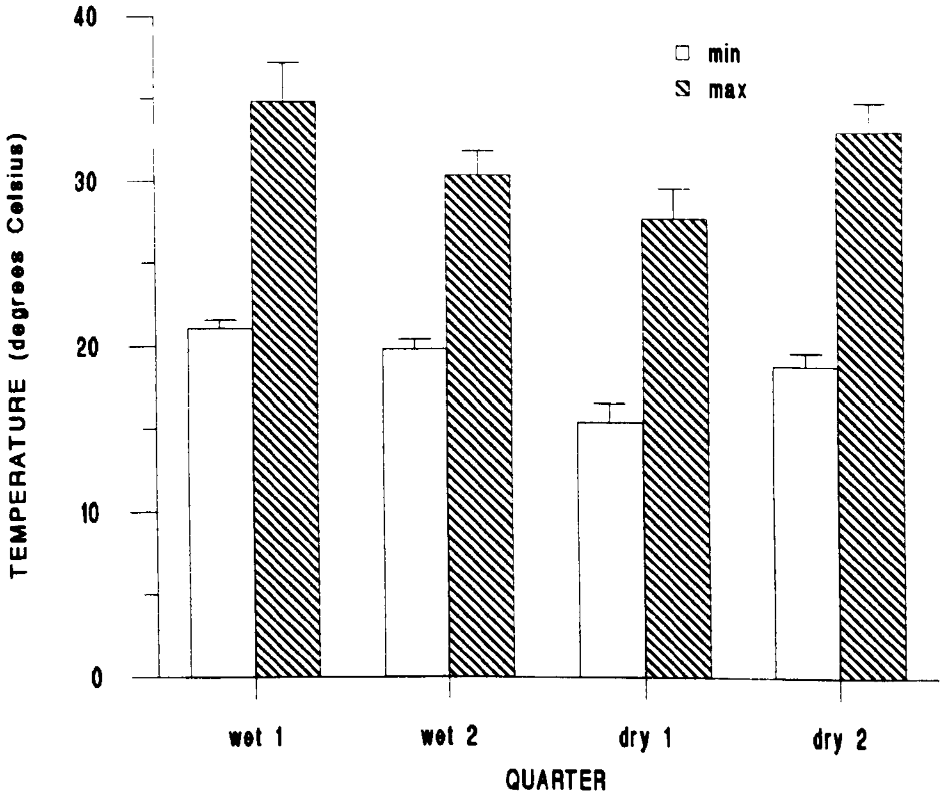


Table 6.4 Environmental features of seasonal quarters in Mikumi National Park. Food measures, visibilty and shade based on findings of Chapter 4 (see e.g., Table 4.3).

FEATURE	DRY 1	DRY 2	WET 1	WET 2
Rainfall	Dry	Dry	Wet	Wet
Overall Temperature	Cool	Hot	Hot	Medium
Afternoon Temperature	< 30 degrees C	> 30 degrees C	> 30 degrees C	< 30 degrees C
Food Measures	Low	Low	High	High
Visibilty	Poor	Good	Good	Poor
Shade	Medium Low	Low	High	High

6.1.3.2 Within days

The half hourly records of temperature taken in the field when following baboons permit a more detailed assessment of temperature change during daylight hours. The pattern is similar in all quarters; the days start cool and reach a peak around 14:30 (Fig. 6.2).

6.1.3 Climate & Behaviour

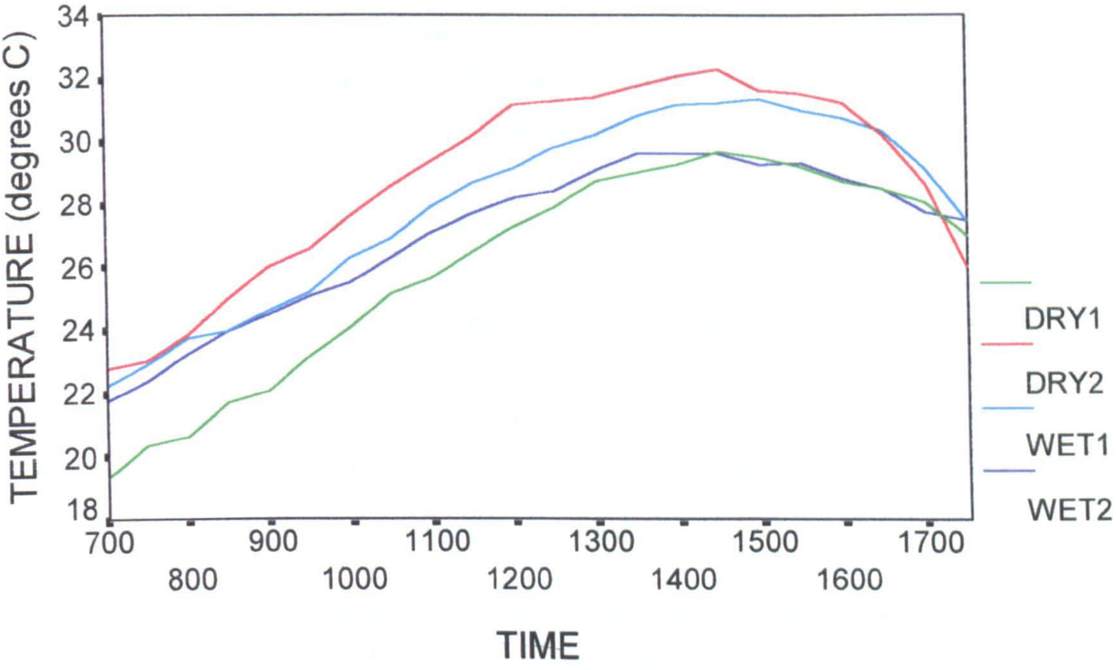
The potential effects of climate on time budgets were reviewed in Chapter 2 (section 2.5.3.2) and are summarised in Table 6.5. They fall into two main categories: direct and indirect. Table 6.4 summarises, by seasonal quarter, the general climatic features and other key ecological features that may mediate indirect effects (Chapter 4).

A wet/dry quarter dichotomy not only occurs for rainfall but also for food and shade measures; rainfall, food measures and shade measures are all higher in wet quarters than in dry. However, in terms of temperature and visibility, dry 1 is more similar to wet 2 and dry 2 more similar to wet 1 (ie., a dry 1, wet 2 / dry2, wet 1 dichotomy).

Table 6.5 Potential mechanisms by which climate can affect behaviour. These are discussed in more detail in Chapter 2 (sections 2.5.3.1 & 2.5.3.2).

	DIRECT	INDIRECT
RAINFALL	Rainfall can affect behaviour directly because in heavy rain primates tend to become inactive.	Rainfall can affect behaviour indirectly via its influence on plant growth and availability of drinking water.
TEMPERATURE	Temperature can affect behaviour directly because it determines thermoregulatory needs, eg., resting to avoid over heating.	Temperature can affect behaviour indirectly via its influence on plant growth & insect activity.

Figure 6.2 Daytime temperatures by quarter during study period.
Data from half hourly records taken in field between 7:00 and 17:30; sample sizes for each half hour range from 1 to 62 with a mean of 31.



6.2 METHODS

A comprehensive description of raw data collection is given in Chapter 3. Chapter 3 also includes definitions of behaviours (Tables 3.7 & 3.8), periods (Table 3.6) and seasonal quarters (Table 3.1). The term wet season or dry season refers to the two wet quarters or two dry quarters combined, respectively. This section contains only additional methodological information relevant to the analyses performed for this chapter.

6.2.1 Calculation of Individual Time Budgets

Only the main time budget components (feeding, moving, resting and socializing) of adult females were considered. Data on males were excluded in order to avoid the potentially confounding influence of sex differences (Chapter 5). Time budgets were calculated for days within quarters and seasons (section 6.2.1.1) and periods within days (section 6.2.1.2).

6.2.1.1 Daily time budgets

The percent of time spent in different activities was calculated for each individual in each quarter or season in two stages. First, the mean of follows in each period of the day (Table 3.6) was calculated; then, the mean of these four periods was determined. Thus each period of the day contributed equally to the final value. Individuals not sampled in all periods in a quarter were excluded from the analyses, except for dry 2 of year 1. This exception was made because of small size of the dataset for this quarter (section 3.3.2.2).

6.2.1.2 Within day time budgets

The percent of time spent in different activities was calculated for each individual for each period of the day in each quarter. Individuals not sampled in all periods in a quarter were excluded from the analyses for that quarter, except for dry 2 of year 1. Again this exception was made because of the limited dataset, specifically the lack of data on adult females in period 2.

6.2.2 Group Activity

In addition to data on the focal individual, the predominant activity of the group was also recorded on each instant. The advantage of these data over that of the individual data are that they can be used to look at individual days without incurring confounding effect of comparing data from different individuals.

The percent of time spent the group activity was recorded as feeding, moving, resting and socializing was calculated for each follow then the mean for each period of each day was taken. The overall time for each day was calculated as a mean of the values for the four periods for that day. Such data were available from 135 complete days.

6.2.3 Statistical Analyses

6.2.3.1 Individual time budgets

Nonparametric tests were used to assess whether the time budgets differed significantly between:

- The same quarters in different years;
- Different quarters in the same year;
- Different seasons in the same year;
- Different periods of the day in the same quarter of the same year.

Mann-Whitney U tests were used for comparing two categories and Kruskall Wallis ANOVAs for comparing three categories. Time budget components were treated as dependent variables and periods, quarters or years as independent variables.

6.2.3.2 Group activity

The total time spent feeding in a day was correlated (Spearman's nonparametric test) with the total time spent moving, resting and socializing. Correlations of time spent in each activity in each period with the same activity in different periods were also calculated.

6.3 RESULTS

Details of statistical analyses (name of test, sample size/degrees of freedom, value of statistic, probability H_0 is true) are given in the legends of the figures. The word "significant" in the text means statistically significant at the 0.05 significance level.

6.3.1 Between Years

Time budgets varied little between years (Fig. 6.3). Of the total of sixteen comparisons made by quarter, only one significant difference was found i.e., significantly more social behaviour in late wet quarter in year 2 of the study than in year 1 (a potential consequence of the troop fusion). No significant differences were found when years were compared by season.

In order to evaluate the level of variation of time budgets measured on different time scales it is useful to consider the range of values produced in more detail. The mean difference between time spent feeding in the same quarter in year 1 and 2 was 7.42%. The greatest range, 11.45, was for feeding dry 2 (year 1 = 37.36%, year 2 = 48.81%) and the smallest, 3.83, for dry 1 (year 1 = 43.14, year 2 = 46.98). The mean difference for moving, resting and socializing was 1.78%, 5.54% and 3.30% respectively.

6.3.2 Within Years

Time spent feeding and time spent resting varied significantly within years, both by quarter and by season. The time spent in these activities was inversely related. In wet quarters, the baboons fed less and rested more than in dry quarters (Fig. 6.3a & c).

There was no discernable within year pattern to time spent socializing (Fig. 6.3 d); neither by quarter nor by season analyses produced significant results. Similarly, there was no clear pattern for time spent moving within year; although quarters were significantly different in year 2 with a peak possible occurring in wet 1 (Fig. 6.3b).

The level of variation generated by comparing quarters within years is greater than that generated by comparing the same quarters in different years. In year 1, feeding was highest in dry 1 (43.13%) and least in wet 1 (30.56%) - a range of 12.57%. In year 2, the range was even bigger at 19.71%. The minimum value was recorded in wet 2 (29.10%) and the maximum in dry 2 (48.81%). In year 1, the range for resting was 10.25% (29.92-40.17%) and 23.43 (19.87-43.31) in year 2. Moving varied 9.77% (14.06-23.83%) between quaters in year 1 and 8.46% (11.33-19.79%) between quarters in year 2. Socializing varied 5.80% (7.94-13.74%) in year 1 and 6.51% (8.73-15.24%) in year 2.

Figure 6.3 Time spent in different activities by quarter.
Bars represent mean of individual daily time budgets. Error lines represent standard deviations between individuals. Results of statistical analyses are given separately for each activity. Sample sizes are given in brackets followed by the value for the statistic and the probability. Bold type indicates a significant result. Mann Whitney U tests were used to compare 2 categories and Kruskal Wallis ANOVA's to compare 3 or 4 categories.

Fig. 6.3a FEEDING

Quarters in different years: Dry 1 (10, 8, 6) χ^2 =1.82, p=0.40; Dry 2 (7,7) U=24, p=0.90; Wet 1 (5,7) U=12, p=0.37; Wet 2 (10,7) U=20, p=0.14. Seasons in different years: Dry (17,15) U=110, p=0.50; Wet (15,14) U=100, p=0.83. Seasons within years:Year 1 (17,15) U=74, **p=0.04**, Year 2 (15,14) U=8, **p<0.01**. Quarters within years: Year 1 (10,7,5,10) χ^2 =4.65, p=0.20, Year 2 (8,7,7,7) χ^2 =21.02, **p<0.01**.

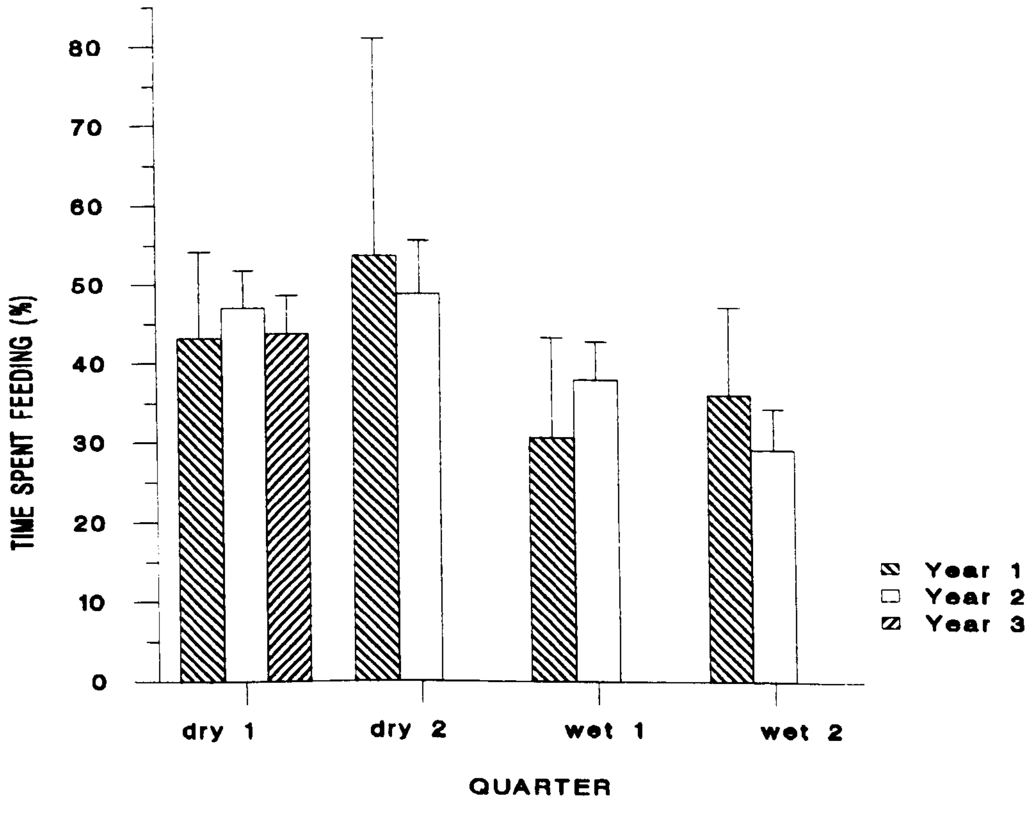


Fig. 6.3b MOVING

Quarters in different years: Dry 1 (10, 8, 6) χ^2 =3.53, p=0.17; Dry 2 (7,7) U=15, p=0.22; Wet 1 (5,7) U=12, p=0.37; Wet 2 (10,7) U=20, p=0.14. Seasons in different years: Dry (17,15) U=93, p=0.19; Wet (15,14) U=91, p=0.54. Seasons within years:Year 1 (17,15) U=93, p=0.19, Year 2 (15,14) U=86, p=0.41. Quarters within years: Year 1 (10,7,5,10) χ^2 =6.77, p=0.08, Year 2 (8,7,7,7) χ^2 =12.95, **p<0.01**.

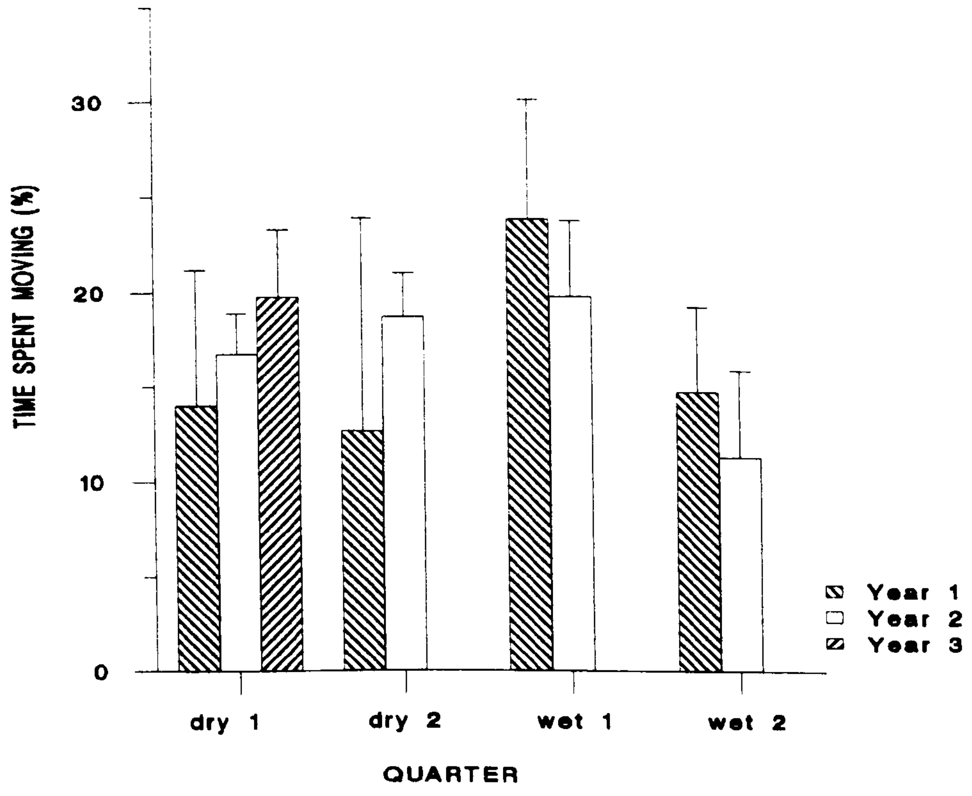


Fig. 6.3c RESTING

Quarters in different years: Dry 1 (10, 8, 6) $\chi^2 = 1.51$, $p=0.47$; Dry 2 (7,7) $U=12$, $p=0.11$; Wet 1 (5,7) $U=17$, $p=0.94$; Wet 2 (10,7) $U=28$, $p=0.49$. Seasons in different years: Dry (17,15) $U=80$, $p=0.07$; Wet (15,14) $U=103$, $p=0.93$. Seasons within years:Year 1 (17,15) $U=59$, **$p=0.01$**, Year 2 (15,14) $U=10$, **$p<0.01$**. Quarters within years: Year 1 (10,7,5,10) $\chi^2 = 7.58$, $p=0.06$, Year 2 (8,7,7,7) $\chi^2 = 21.39$, **$p<0.01$**.

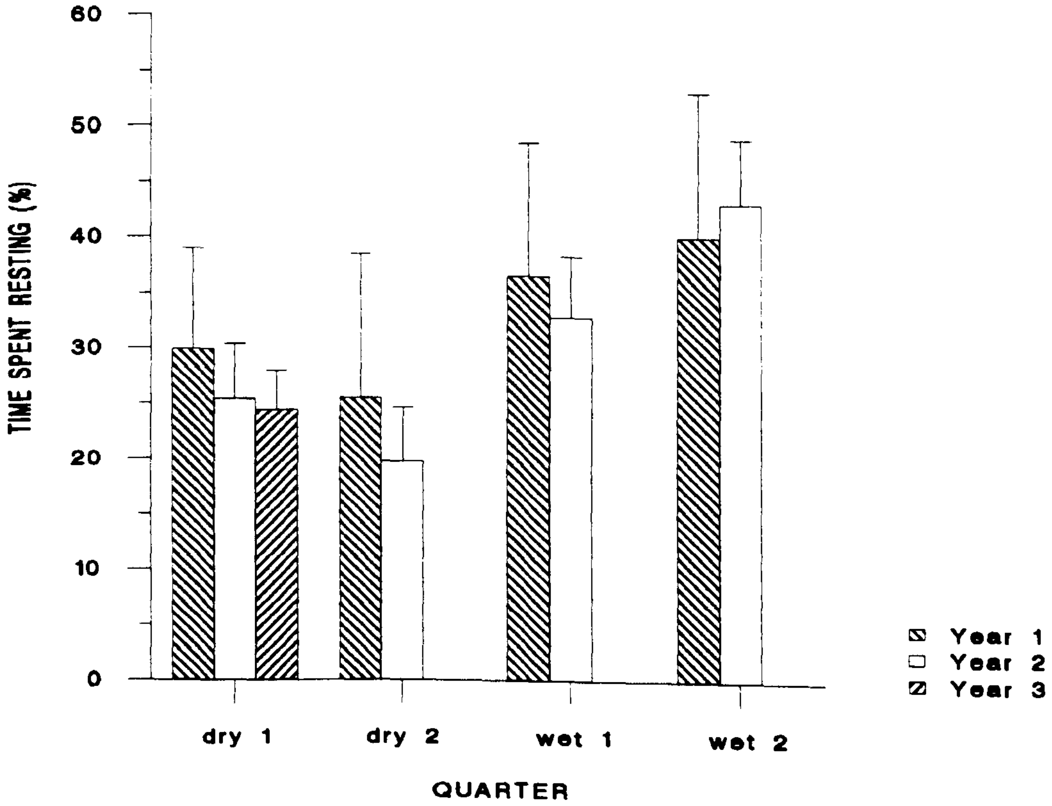
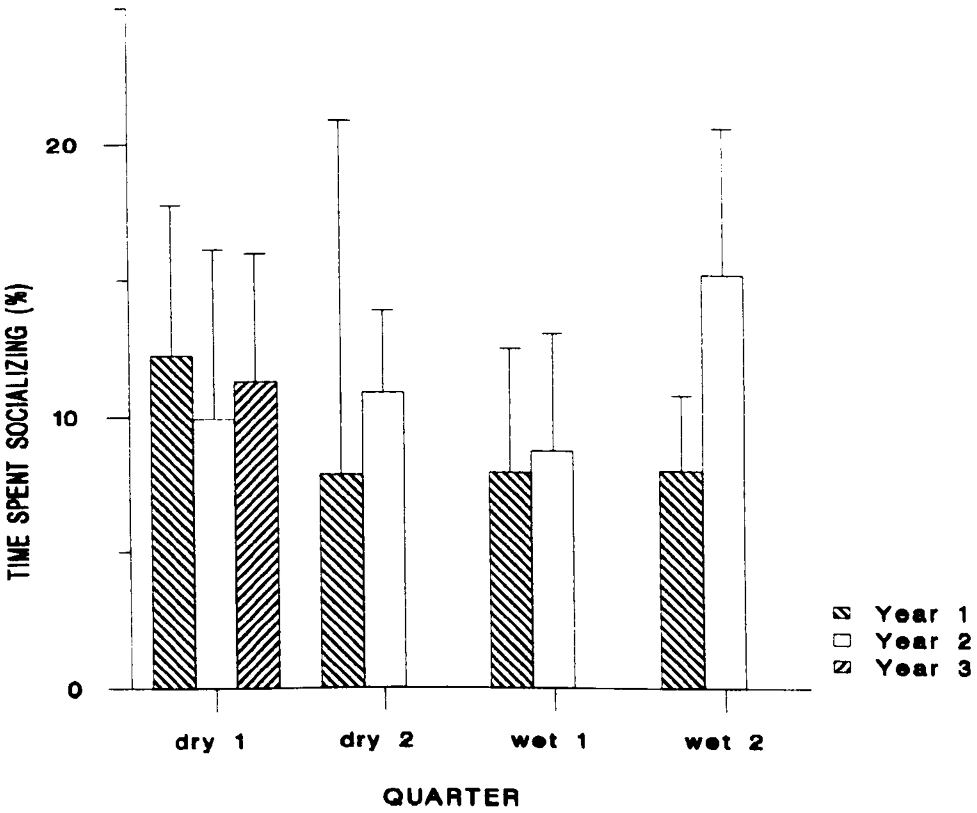


Fig. 6.3d SOCIALIZING

Quarters in different years: Dry 1 (10, 8, 6) χ^2 =2.05, p=0.36; Dry 2 (7,7) U=14, p=0.17; Wet 1 (5,7) U=16, p=0.81; Wet 2 (10,7) U=7, **p=0.01**. Seasons in different years: Dry (17,15) U=119, p=0.75; Wet (15,14) U=61, p=0.55. Seasons within years:Year 1 (17,15) U=105, p=0.40, Year 2 (15,14) U=85, p=0.38. Quarters within years: Year 1 (10,7,5,10) χ^2 =6.39, p=0.09, Year 2 (8,7,7,7) χ^2 =6.15, p=0.10.



6.3.3 Within Days

The percent of time spent feeding, moving, resting and socializing, in different periods of the day for each quarter in each year are shown in Figure 6.4. The most important features are:

- For most activities in most quarters, there was a change in time use throughout the day.
- These patterns were characteristic to each quarter.
- The patterns for feeding and resting were most similar for dry 1 and wet 2 and differed markedly from dry 2, with wet 1 taking an intermediary position. The data did not show the wet/dry dichotomy evident for overall daily time budgets.

Sixty four percent of the thirty six between period analyses conducted (four activities for each of nine quarters) indicated significant within day differences. Significant differences between periods were found for each quarter in at least one year for each activity except for moving in dry 2 and wet 1 and socializing in dry 2. Even where similar statistical results for a particular quarter were not shown in all years, visual assessment of Figure 6.4 indicates consistent patterns of within day use of time between the same quarters in different years. The description below of the daily pattern of time use in the Mikumi baboons is based on these patterns.

Although time spent feeding each day in dry 1 was greater than in wet 2, the pattern was similar throughout the day. Feeding increased through periods 1 to 3 and then levelled off. In wet 1, feeding increased slightly throughout the day, although it was relatively uniform compared to dry 1 and wet 2. In dry 2 the pattern was reversed. Feeding was highest in periods 1 and 2, then decreased as the day progressed. Resting showed a complementary pattern to feeding in all quarters. Socializing was highest in period 1, except in dry 2 where it peaked in period 3. By quarter similarities appear to have been least marked for moving. In general moving increased slightly throughout the day.

The level of variation generated by comparing time budgets within days (Table 6.6) is the greatest of any of the time scales considered. For example the mean range of the four time budget components in dry 1 1993 was 31.8 with a mean standard deviation of 14.5.

Table 6.6 Variation in time use between periods by year (YR.) and quarter (QTR.).
The "min.-max." column indicates the least and the greatest percent of time spent in each activity in a period; the difference between the minimum and maximum values is given in the range column. The standard deviation (sd) of the four periods in each quarter is also given.

		FEED			MOVE			REST			SOC.		
YR.	**QTR.**	**min.-max.**	**range**	**sd**	**min.-max.**	**range**	**sd**	**min.-max.**	**range**	**sd**	**min.-max.**	**range**	**sd**
1	Dry 1	15.0-64.7	49.6	23.0	5.5-20.0	14.5	6.6	14.6-52.7	38.1	17.4	1.6-26.4	24.8	11.2
	Dry 2	30.5-63.3	32.8	16.5	12.2-15.3	3.1	1.5	13.5-42.7	29.2	14.6	14.7-10.7	4.0	2.2
	Wet 1	27.9-34.2	6.31	2.8	17.2-27.8	10.6	5.2	34.4-41.7	7.4	3.2	3.1-15.8	12.7	5.3
	Wet 2	21.3-47.6	26.3	11.4	8.1-21.8	13.7	5.6	25.7-52.2	26.5	11.0	4.0-17.4	13.4	6.2
2	Dry 1	21.7-60.2	38.4	17.0	8.7-22.8	14.1	6.2	12.1-45.6	33.5	14.3	3.9-23.7	19.7	9.4
	Dry 2	38.6-59.7	21.2	10.3	15.1-24.8	9.8	4.3	15.6-25.2	9.6	4.6	7.8-16.5	8.7	4.1
	Wet 1	24.1-48.6	24.5	10.4	14.6-24.2	9.6	4.3	22.9-46.4	23.4	9.8	5.3-14.7	9.5	4.1
	Wet 2	5.0-48.5	43.5	19.7	4.02-17.4	13.4	5.7	25.2-61.5	36.3	15.4	7.0-29.5	22.5	10.0
3	Dry 1	13.9-58.4	44.6	20.9	7.32-25.21	17.9	8.5	12.6-47.5	35.1	16.1	3.8-30.8	27.1	13.1

Figure 6.4 Individual activity by period for different quarters.
Results of Kruskal Wallis ANOVA tests for differences between periods are given separately for each activity. Sample sizes are given in brackets followed by the value for the statistic and the probability. Bold type indicates a significant result. In keys y1, y2 or y3 indicate year of study; d1 = dry 1 (green), d2 = dry 2 (red), w1 = wet 1 (light blue), w2 = wet 2 (dark blue). The lines join the means for each quarter.

Fig. 6.4a FEEDING

Year 1, dry 1: (11,14,14,12) $\chi^2 = 21.93$, **$p<0.01$**. Year 1, dry 2 (4,4,4) $\chi^2 = 4.70$, $p=0.10$. Year 1, wet 1 (8,12,12,9) $\chi^2 = 1.11$, $p=0.77$. Year 1, wet 2 (11,11,11,10) $\chi^2 = 10.40$, **$p=0.02$**. Year 2, dry 1 (8,9,8,9) $\chi^2 = 15.74$, **$p<0.01$**. Year 2, dry 2 (7,7,7,7) $\chi^2 = 9.84$, **$p=0.02$**. Year 2, wet 1 (7,7,7,7) $\chi^2 = 9.84$, **$p=0.02$**. Year 2, wet 2 (7,7,7,7) $\chi^2 = 21.57$, **$p<0.01$**. Year 3, dry 1 (6,6,6,6) $\chi^2 = 13.81$, **$p<0.01$**.

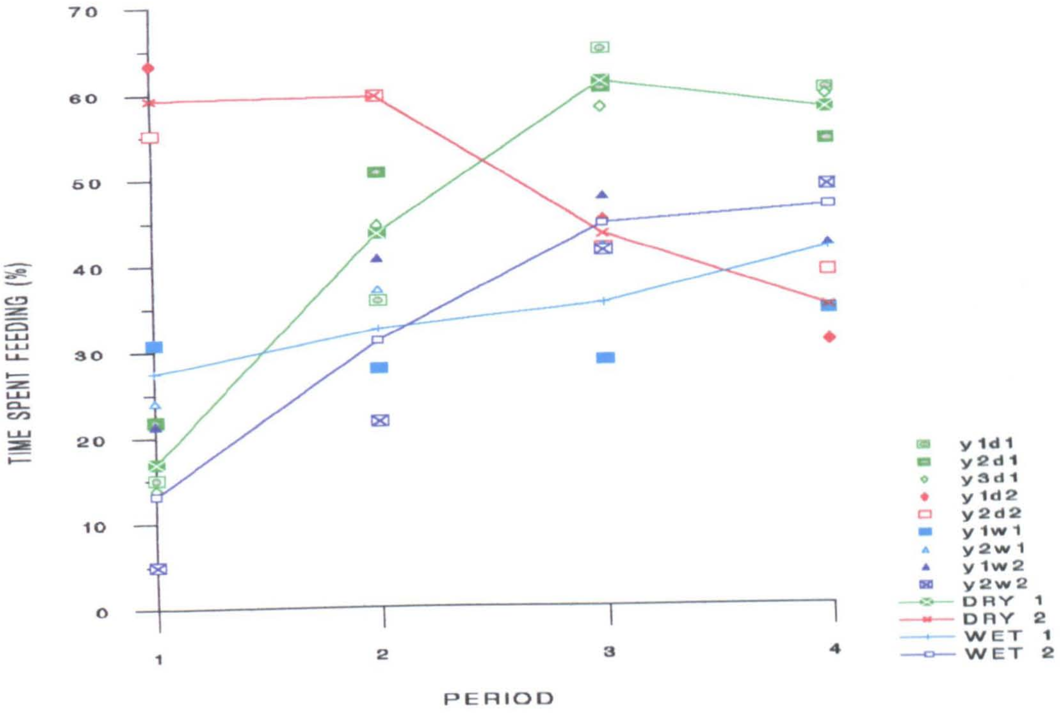


Fig. 6.4b MOVING

Year 1, dry 1 (11,14,14,12) χ^2 =9.59, **p=0.02.** Year 1, dry 2 (4,4,4) χ^2 =0.47, p=0.78.Year 1, wet 1 (8,12,12,9) χ^2 =1.83, p=0.61.Year 1, wet 2 (11,11,11,10) χ^2 =11.74, **p=0.01**. Year 2, dry 1 (8,9,8,9) χ^2 =12.74, **p=0.01**. Year 2, dry 2 (7,7,7,7) χ^2 =5.78, p=0.12. Year 2, wet 1 (7,7,7,7) χ^2 =5.97, p=0.11. Year 2, wet 2 (7,7,7,7) χ^2 =9.97, **p=0.02**. Year 3, dry 1 (6,6,6,6) χ^2 =10.19, **p=0.02**.

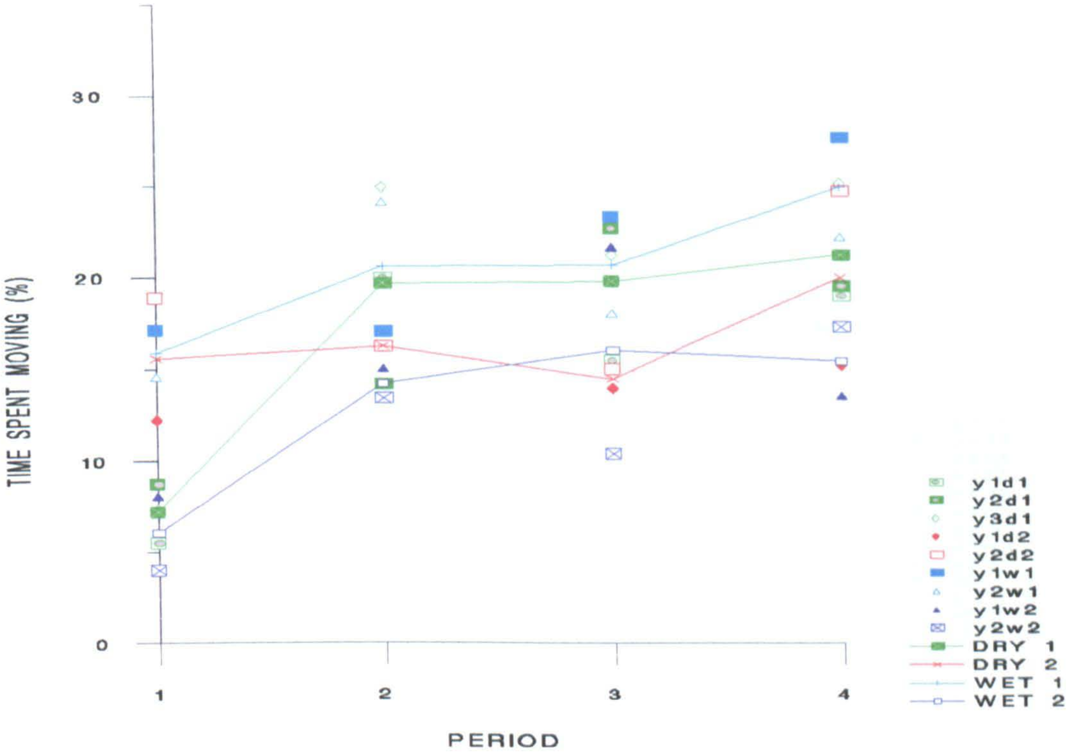


Fig. 6.4c RESTING

Year 1, dry 1: (11,14,14,12) χ^2 =19.93, **p<0.01**. Year 1, dry 2 (4,4,4) χ^2 =4.27, p=0.11. Year 1, wet 1 (8,12,12,9) χ^2 =1.08, p=0.78. Year 1, wet 2 (11,11,11,10) χ^2 =6.67, p=0.08. Year 2, dry 1 (8,9,8,9) χ^2 =15.61, **p<0.01**. Year 2, dry 2 (7,7,7,7) χ^2 =3.87, p=0.27. Year 2, wet 1 (7,7,7,7) χ^2 =10.17, **p<0.01**. Year 2, wet 2 (7,7,7,7) χ^2 =17.18, **p<0.01**. Year 3, dry 1 (6,6,6,6) χ^2 =13.66, **p<0.01**.

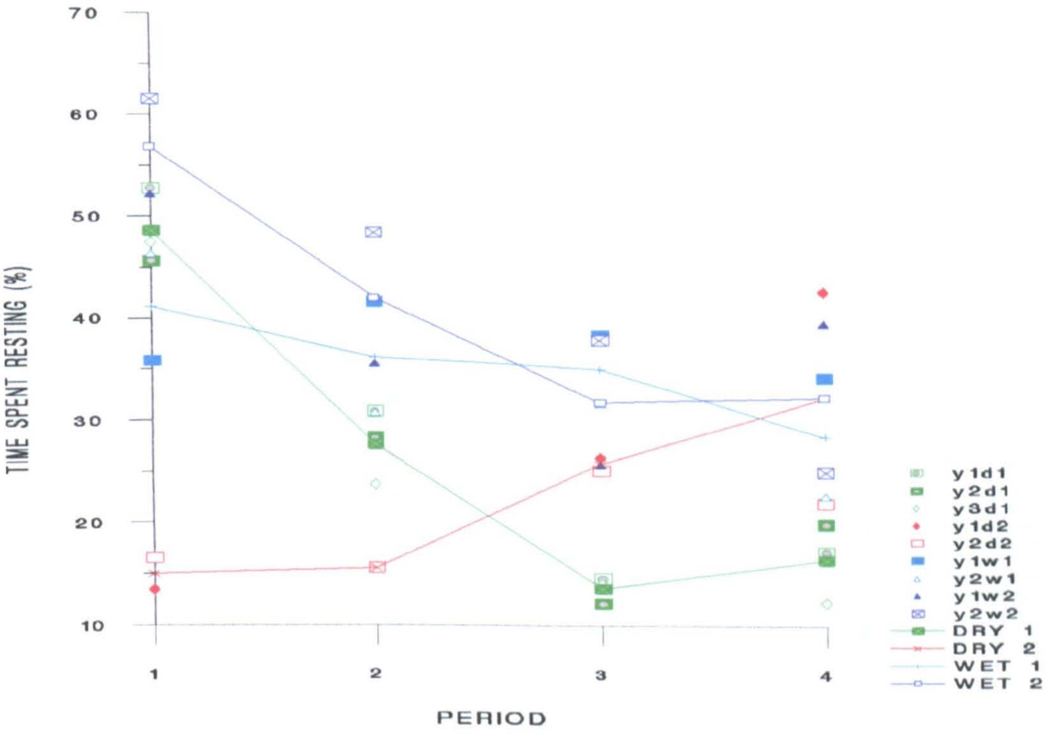
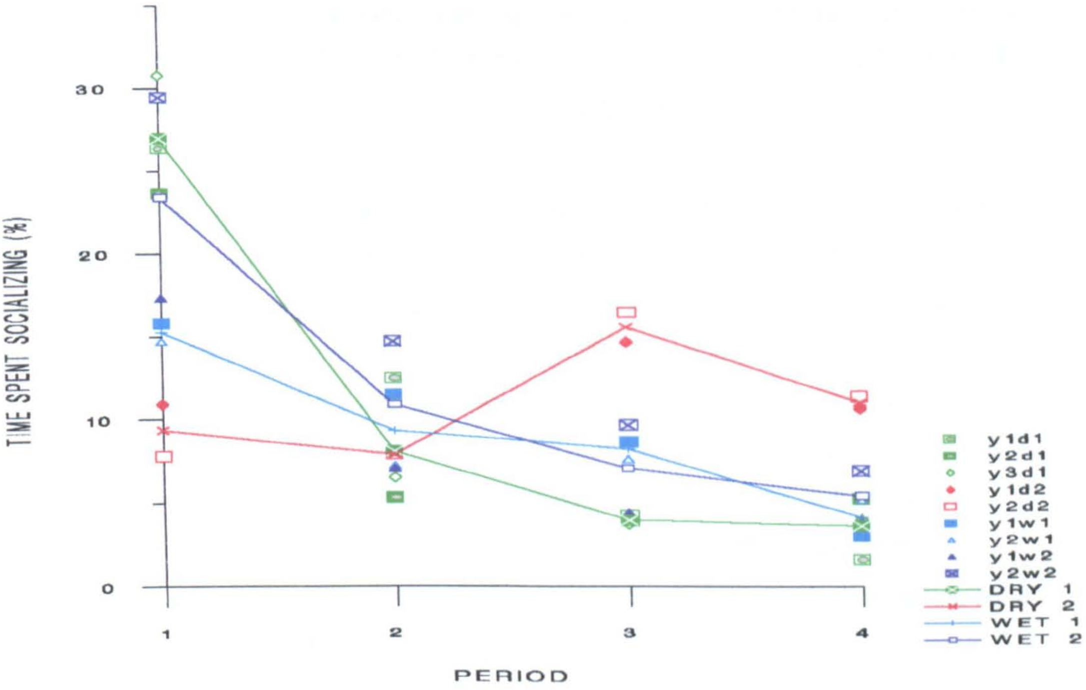


Fig. 6.4d SOCIALIZING

Year 1, dry 1: (11,14,14,12) χ^2 =16.68, **$p<0.01$**. Year 1, dry 2 (4,4,4) χ^2 =0.73, $p=0.69$. Year 1, wet 1 (8,12,12,9) χ^2 =5.96, $p=0.11$. Year 1, wet 2 (11,11,11,10) χ^2 =12.90, **$p<0.01$**. Year 2, dry 1 (8,9,8,9) χ^2 =9.81, **$p=0.02$**. Year 2, dry 2 (7,7,7,7) χ^2 =3.94, **$p=0.27$**. Year 2, wet 1 (7,7,7,7) χ^2 =1.65, $p=0.64$. Year 2, wet 2 (7,7,7,7) χ^2 =12.52, **$p=0.01$**. Year 3, dry 1 (6,6,6,6) χ^2 =13.81, **$p<0.01$**.



6.3.4 Group Activity

Group activity by period for each quarter showed the same pattern as described above for individuals (Fig. 6.5). This provides further confirmation of differences between quarters in the use of time within days and the complementary nature of resting and feeding. The latter is further supported by the highly significant negative correlation between the amount of time spent feeding and the amount of time spent resting in a day (n=135, r_s=-0.57, **p<0.01**). The correlation of the amount time feeding and socializing was also negative, although the coefficient was much weaker and the result only just significant (n=135, r_s= -0.13, **p=0.04**). Feeding and moving were not correlated (n=135, r_s= -0.08, p=0.15).

The pattern of time use within days suggests that there is compensation, between periods, for time spent feeding e.g., if they feed a lot in the morning they do less in the afternoon. This is supported by correlations of group feeding in different periods of the same day. Feeding in period 1 was positively correlated with feeding in period 2 (n=135, r_s=0.47, **p<0.01**) while, feeding in periods 1 and 2 were negatively correlated with feeding in period 4 (n=135, r_s=-0.24, **p<0.01**; n=135, r_s=-0.21, **p=0.01**). Resting showed significant positive correlations for adjacent periods (periods 1 & 2 n=135, r_s=0.46, **p<0.01**; periods 2 & 3 n=135, r_s=0.18, **p=0.03**; periods 3 & 4 n=135, r_s=0.22, **p=0.01**) but the negative correlations between morning and afternoon periods that would be expected if resting time was complementing feeding time, were not found.

Figure 6.5 Group activity by period for different quarters.
Lines connect the mean percentage of instants per day that the behaviours indicated were the predominant activity of the group.

Fig. 6.5a FEEDING

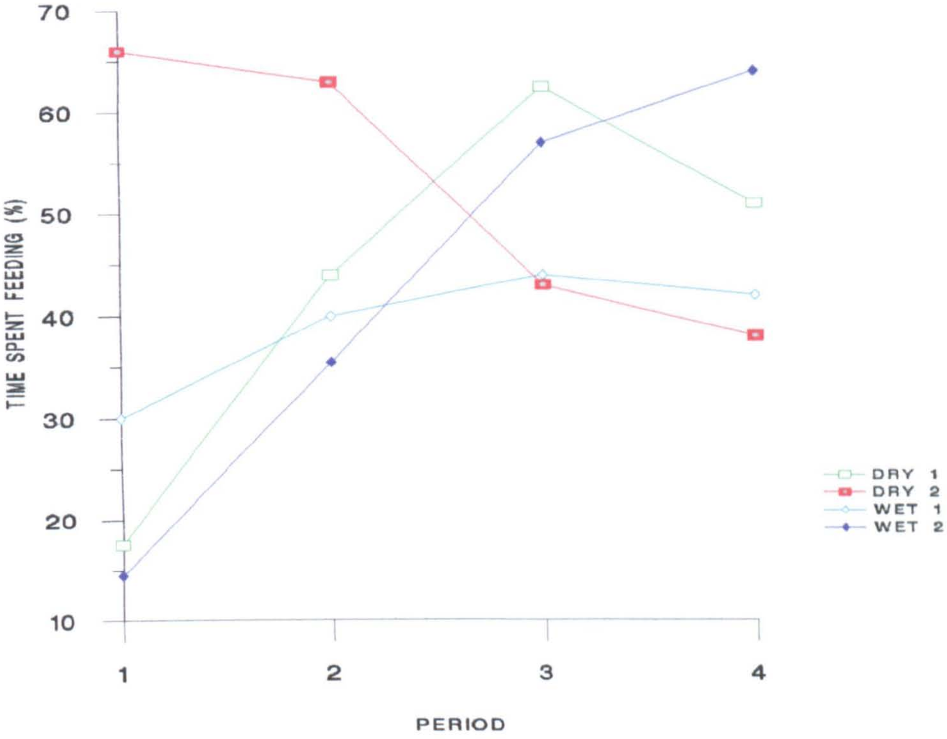


Fig. 6.5b MOVING

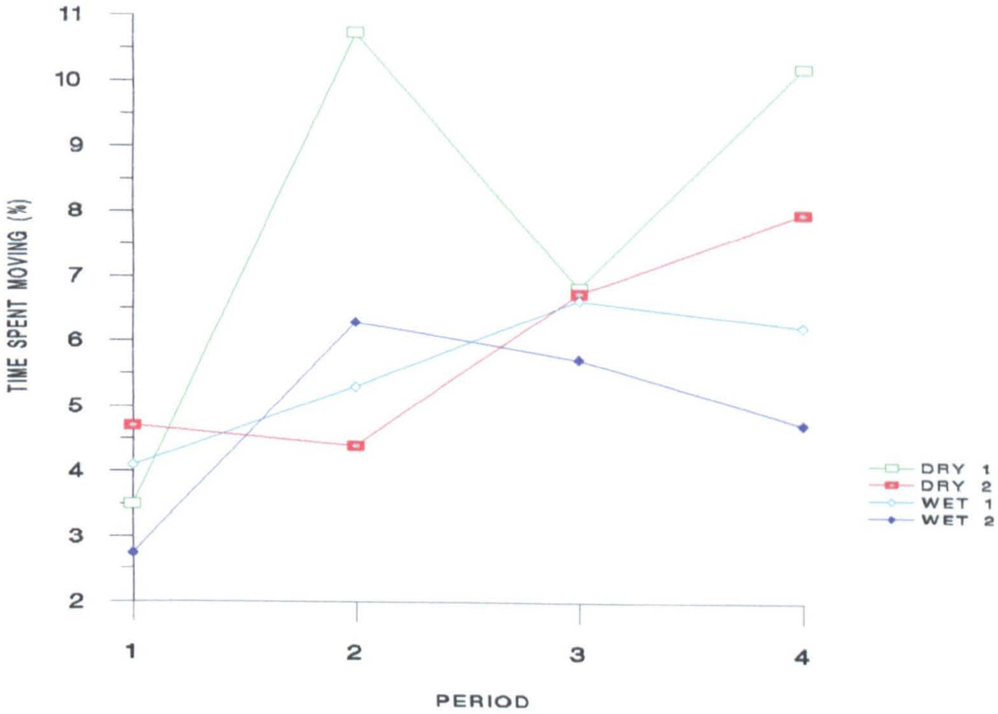


Fig. 6.5c RESTING

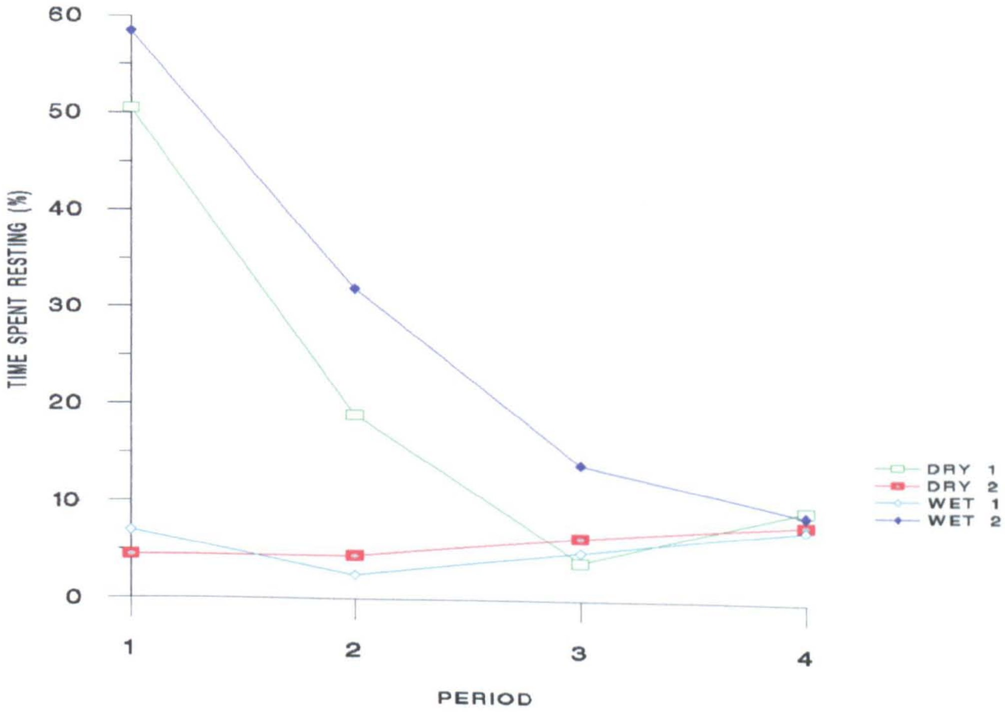
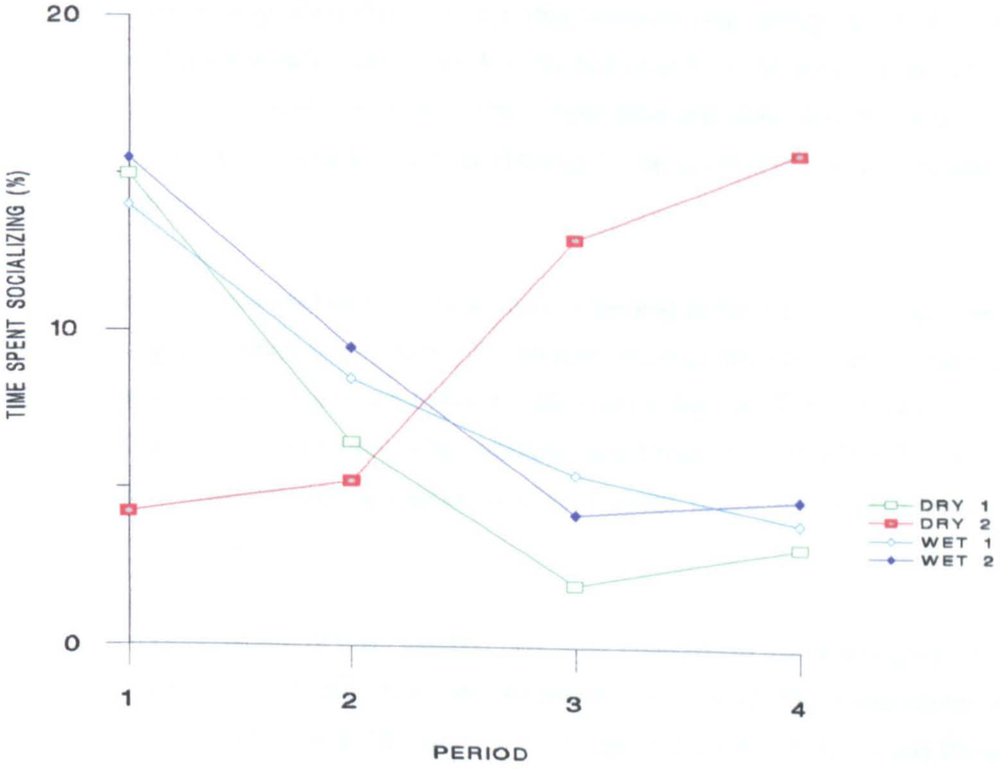


Fig 6.5d SOCIALIZING



6.4 DISCUSSION

6.4.1 Temporal Variation & Previous Research

This study found within year and within day, but little between year, temporal variation in the time budgets of adult female baboons in Mikumi National Park. Moreover, the within day pattern varied from quarter to quarter. When more time was spent feeding, less was spent resting. This section seeks to put these findings in the context of previous research, particularly on baboons.

Clutton-Brock (1977a) reviewed seasonal variation in feeding behaviour, including time spent feeding, in a wide range of primates. Subsequent studies have also found that time budgets vary within years; for baboons these studies include Barton (1989), Post (1978) and Sharman (1981). The result here, that baboons spend more time feeding at drier times of year, is consistent with most other baboon studies (Dunbar 1992a; this is discussed further in section 6.4.2.1).

While a bi or tri modal pattern of daily feeding has been detected in many primates (Barrett 1995; Clutton-Brock 1977a), most other baboon studies have found little evidence for any daily pattern in activity (Altmann & Altmann 1970; Dunbar & Dunbar 1974; Clutton-Brock 1977a). In contrast, Aldrich-Blake et al. (1971) found a gradual increase in feeding throughout the day, similar to the pattern found for dry 1 and wet 2. Aldrich-Blake et al's study took place over 3 months (equivalent to a single quarter in this study) during the long rains with min/max temperatures similar to wet 2. In this study, within day patterns were characteristic of each quarter. For example, the pattern of resting and feeding in dry 1 was the reverse of that found in dry 2. Perhaps patterns of daily activity have been lost in the longer term studies on baboons as a result of lumping data across seasonal quarters; a point also made by Post (1978).

A number of studies have considered seasonal shifts in daily pattern as well as changes in overall daily time budget (Barrett 1995; Clutton-Brock 1974; Post 1978, 1981; Robinson 1984; Sharman 1981; Strier 1987). For example, Sharman's (1981) assessment of guinea baboons' time budgets by season showed differences in the time at which the baboons switched from socializing to feeding and moving. In his words: "In summary, the behaviour characterizing the troops at different times of day differed with the season. In the wet season the baboons socialized until mid-morning and began to move and feed later in the day. In the dry season social activity gave way to moving and feeding before 09:00." However, none of these previous studies have found seasonal shifts as dramatic as those described for this study of the Mikumi baboons.

Altmann & Altmann (1970) report that studies, including their own, reveal peaks of social behaviour after descent and before entering sleeping sites. In this study, social behaviour occupied 15% or more of period 1 in dry 1 and both wet quarters and decreased thereafter. The relative uniformity of time spent socializing during the day in dry 2 would not drown out this pattern if the data were lumped across quarters. There is no evidence of a pre sleeping site peak in this study. This could be a result of population or methodological differences, the latter being due to data collection in Amboseli extending to slightly later in the day (ie., 1800 rather than 1700).

The noticeable inverse relationship between feeding and resting, both within years and within days, supports the hypothesis that resting is used as the main reservoir of extra time for feeding in preference to social behaviour. The correlations of feeding with resting and socializing for group activity also support this hypothesis since feeding was more strongly negetatively correlated with resting than socializing. The within day pattern for individuals for dry 2 suggests that, only once resting time is reduced to around 10% in period 1, is extra time for feeding is taken from social behaviour. These findings are consistent with the majority of other baboon studies (e.g., Bronikowski & Altmann 1996; Dunbar 1988, 1992a; Iwamoto & Dunbar 1983). A minority of studies have found seasonal changes in feeding to be related inversely to socializing rather than to resting (Post 1982; Sharman 1981).

Other aspects of the Mikumi baboons behavioural ecology is known to vary dramatically between years. For example, multiyear studies of both diet (Norton et al. 1987) and ranging (G.W. Norton unpublished data) show that differences between years can be great. This contrasts to the lack of variation between years in time budgets found for the nine quarters considered by this study.

6.4.2 Causal Factors Proposed

In this study both time budgets and climate varied little between the same quarters in different years. This is consistent with the hypothesis that climate has a causal relationship with temporal variation, but does not help distinguish between specific mechanisms. These are more usefully investigated by considering within year and within day patterns of variation.

Feeding time was longer in dry quarters than in wet ones. Since food measures also showed a wet/dry dichotomy, this suggests that food resources are an important factor underlying this pattern. The data are consistent with the hypothesis that when food measures are low baboons have to feed for longer in order to fulfill their nutritional requirements (Dunbar 1992a). However, accepting this as the primary explanation for seasonal variation in time spent feeding begs an important question: Why do the baboons minimize their feeding time - why don't they feed for longer in the wet season and gain weight as captive primates do in the presence of plentiful food (pers. obs.)? This may be because as long as they maintain themselves above a certain threshold, improved nutrition does not translated into increased in reproductive success i.e., there is no further benefit to be gained which would make them time minimizers sensu Schoener (1971). However, evidence from the effects of provisioning on reproductive parameters suggests that primates in the wild are generally below this threshold (Cowlishaw & Dunbar in press; Loy 1988). The alternative explanation, that the cost:benefit ratio is constrained by increased costs associated with increased feeding, therefore seems more likely.

Data collected by this study enable an evaluation of two types of cost. Firstly, direct thermoregulatory costs imposed by high ambient temperature, especially those over 30°C (section 2.5.3.2). Secondly, indirect costs of climate mediated by poor visibility. Considering seasonal shifts in daily patterns of time use in relation to these costs suggests that they are indeed influential in constraining feeding time.

Heat stress thermoregulatory costs are most likely to be incurred during the afternoons of dry 2 and wet 1. In both these quarters the baboons feed less in periods 3 & 4 than they do in cooler quarters. This is consistent with the proposal that feeding time when temperatures are high is costly.

Costs associated with poor visibility include increased risk of predation and increased chances of losing group cohesion. This could be reflected in a reluctance to leave the vicinity of sleeping sites. In addition to increasing the chances of losing group cohesion as they travel away from a sleeping site, the trees provide known escape routes and means of monitoring neighbours as well as hazards in the environment. That resting is greatest and feeding least in period 1 when visibility is poor (i.e., dry 1 & wet 2) is consistent with this possibility. In addition, the observation that social behaviour tends to peak most in period 1 of these quarters may reflect a benefit to socializing in the security of sleeping trees.

Further evidence for the argument that costs are important in producing seasonal patterns of time use comes from interpopulation comparisons. Data in Dunbar (1992a his table 2) indicate that longer feeding time in the dry season is common in *Papio*. In 8 out of 10 studies, feeding time in the dry season was greater than in the wet season, by an average of 9%. In the other two studies, the difference in the opposite direction was much smaller (average 3%). If seasonal patterns are enabled by differences in resource base but imposed by thermoregulatory cost, a relationship between temperature and the magnitude of seasonal differences would be expected. Specifically, the difference would be expected to increase with mean ambient temperature. A plot to examine this prediction based on data in Dunbar (1992a) indicates that this trend does occur (Fig. 6.6) although the relationship is non-significant according to a Spearman rank correlation ($n=10$, $r_s=0.38$, $p=0.29$).

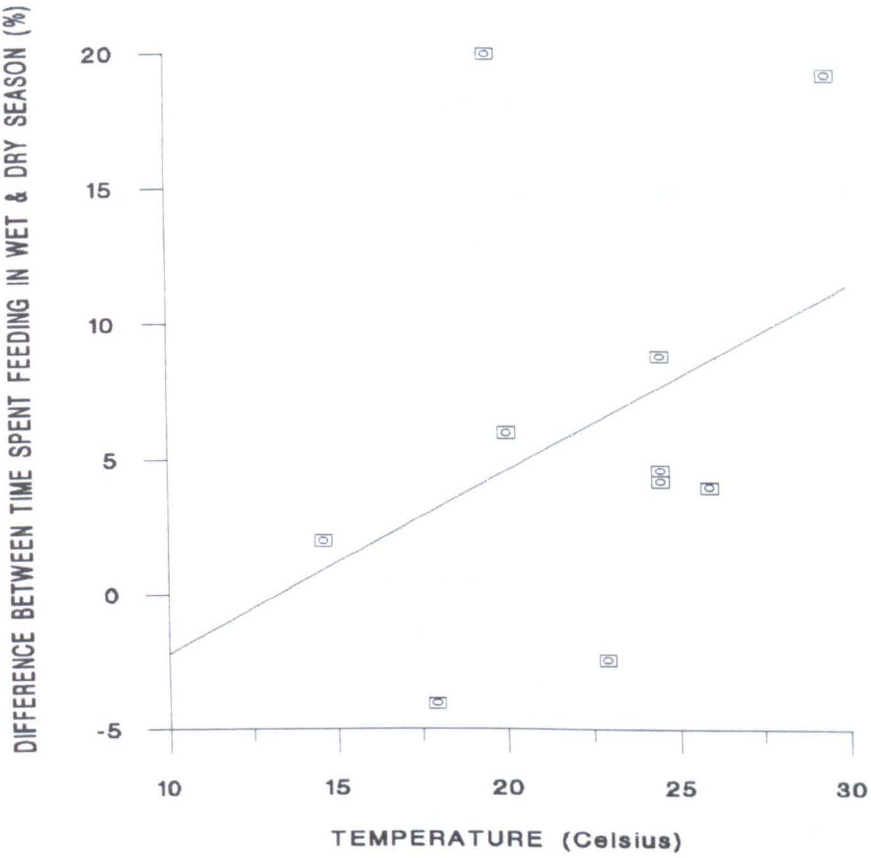
Barton's doctoral study is one of the two in Dunbar's (1992a) table in which the animals appear to feed for slightly longer in the wet season (references cited by Dunbar were Barton 1989 & pers comm.) In addition to having lower temperatures than Mikumi, this study site is on a cattle ranch and therefore the grass presumably never gets tall because of grazing effects. In other words, Chololo is likely to have lower visibility related costs. Moreover, Chololo has few predators and water is available all year round from cattle troughs. The need to keep feeding time to a minimum may therefore not be a strategy which maximizes the benefit:cost ratio in Chololo. (NB: Barton measured food resources directly and found the baboon food biomass was greater in wet months than dry).

Table 6.7 summarizes, by quarter, how the factors discussed in this section can be invoked to explain the patterns of temporal variation found by this study.

Table 6.7 Proposed factors underlying temporal variation in time spent feeding in this study.

Dry 1
In dry 1 food measures are low and visibility are poor but afternoon temperatures are tolerable. Each day a lot of time must be devoted to feeding because food measures are low. Visibility is poor and therefore the cost of leaving the sleeping site is high. However, afternoon temperatures remain below 30 degrees Celsius thus, the baboons can feed extensively later in the day. This promotes a strategy of feeding mostly in the afternoon.
Dry 2
In dry 2 food measures are low and afternoon temperatures are high but, visibility is good. As for dry 1 a lot of time each day must be devoted to feeding. However, afternoon temperatures are very high thus there is a high thermoregulatoy cost to afternoon feeding. Visibility is good and therefore the costs of leaving the sleeping sites to feed are less. This promotes a stategy of feeding mostly in the morning.
Wet 1
In wet 1 food and visibility are good but, afternoon temperatures are high. Food measures are higher therefore the baboons can fulfill their nutritional needs in a shorter amount of time than in the dry season. Afternoon temperatures are high and limit the amount of feeding that can be done at this time. However, visibility is still good and therefore the costs of morning feeding are less. This promotes a strategy of feeding throughout the day.
Wet 2
In wet 2 visibility is poor but afternoon temperatures are tolerable. As for wet 1 overall daily feeding time can be less than in the dry season. However, the costs of morning feeding are higher (poor visibility) and afternoon feeding lower (max temperatures less than 30 degrees Celsius) that in wet 1. This promotes a strategy of increased feeding throughout the day. This pattern is similar to dry 1 except that overall feeding time is less.

Figure 6.6 Seasonal difference in time spent feeding against temperature. Data from Dunbar (1992a, Table 2). Seasonal difference calculated as time spent feeding in dry season minus time spent feeding in wet. Time spend feeding in wet season calculated as two times the annual value minus the value for the dry season only. Line of best fit added using cricket graph facility (Computer Associates 1990).



6.4.3 Other Considerations

The previous section discussed the main causal factors that data from this study suggest underlie temporal variation in the use of time by the Mikumi baboon. This section discusses other factors which may contribute to, or be an alternative explanations of, the observed patterns.

6.4.3.1 Correlations

The null hypothesis that there is no cause and effect relationship between climate and behaviour must be considered. Any associations found could merely indicate correlations as a result of both behaviour and climate covarying with some third variable eg., daylength. However, alternative causal mechanims seem less plausible. Daylength, for example, varies little at Mikumi's low latitude and does not follow a pattern consistent with the wet/dry dichotomy found in daily time budgets.

6.4.3.2 Insect feeding

Correlational effects must also be considered for the more specific mechanisms by which climate may effect behaviour. For example, herbivorous insect populations fluctuate with the biomass of vegetation on which they feed, leading to a greater number of insects in wet quarters in than in dry quarters (pers. obs.). It is possible that it is the presence of insects rather than of vegetable foods that allows the shorter feeding times in the wet season but, it seems more likely that both factors with insect effects being of secondary importance. The findings of previous research on insect feeding in Mikumi supports this proposition. Consumption of insects by the Mikumi baboons has been found to be positively correlated with monthly rainfall (Rhine et al. 1986). Moreover, although important, insects form only a relatively small proportion of the diet of the Mikumi baboons (Rhine et al. 1986; Norton et al. 1987).

Insect activity throughout the day is known to vary with temperature, being greater at warmer temperatures (Unwin & Corbet 1991). Agetsuma (1995a) has suggested that this increases encounter chances and thus the chances that insects will be eaten. In this case, insect mediated effects of temperature would work in the opposite direction to direct thermoregulatory effects and may mitigate some of its costs. Further investigation into this would be interesting.

6.4.3.3 Other characteristics of food resources

The measures used indicate the amount of food present but do not take into account palatability and nutritional value, which could be important in explaining feeding differences between wet and dry seasons. The limitations of the food measures used in this study are considered in section 4.4.4. As also discussed in Chapter 4, the measures used give little indication of the distribution, or patchiness, of food resources. In other words, the food measures used only take into account the first of the three resource characteristics - quantity, quality and distribution - identified as important in section 2.5.3.1. The variation in food measures found by this study may covary with other characteristics of food resources and it may be these other characteristics which are important in determining feeding time. For example, in most years the Mikumi baboons feed heavily on tamarinds during dry 1. Tamarind trees are patchily distributed but usually contain many fruit food items of high nutritional value. In this case, longer feeding time is likely to reflect greater time required for processing (opening pods and peeling seeds) rather than low food presence per se.

In addition, because of the complex nature of the Mikumi habitat, some important food trees were undoubtedly undersampled (section 4.2.1). More intense sampling may have produced higher food indices, especially in dry 1. This would have affected the correlation of food presence with other characteristics of food resources not directly measured by the indexes used, but potentially responsible for the variation found in time budgets.

6.4.3.4 Fire

The role played by fire in producing within and between year patterns of visibility and food was discussed in Chapter 4. By removing vegetation fire leads to both a reduction of food and improved visibility. The timing of fires is strongly influenced by climate, both directly and indirectly. Climate affects fire patterns indirectly via plant growth and thus production of fuel. Indirect effects are mostly mediated by rainfall since rain makes vegetation wet, and thus burn less easily, and an unknown proportion of fires are started by lightening. The pattern of fire within years, therefore, covaries with climate and is likely to contribute to the associations found between climate and behaviour in this study.

6.4.3.5 Direct effects of rain

Data on the direct effects of rainfall on behaviour were not collected by this study but personal observation indicates that during heavy rain the baboons do become less active. While this factor merits more detailed investigation, it seems unlikely that it underlies the regularity of temporal variation found. In contrast to Kibale, where rainstorms generally occur at midday and may enhance noon time peaks of resting in wet months (Barrett 1995), the temporal pattern of rainfall between and within days during the wet season in Mikumi is highly unpredictable (pers. obs.; G.W. Norton pers. comm.) .

Ambient temperatures never get very cold in Mikumi (see minimum temperatures in Table 6.3) and while overheating has been considered, it has been assumed that the problem of overcooling is not generally encountered. However, even if temperatures remain reasonably high, wind chill and the cooling effect of water evaporating from damp fur, may mean the baboons do in fact experience this problem. In dry 1 and wet 2, when grass is tall, their fur can get particularly wet from morning dew on long grass (as do the trousers of researchers walking to sleeping sites to find the baboons). This factor could contribute to the slower starts to feeding typical of the daily pattern of time use during these quarters. The grass makes "popping" noises as it dries out (pers. obs.) during period 1 and is normally completely dry by mid morning. Again the effects of wind chill and damp grass on behaviour would make interesting further study.

6.4.3.6 Water resources

An important climate dependent feature of the environment that has not been mentioned so far is the availability of drinking water. With the onset of the rains in wet 1 (or late dry 2), free standing water becomes widely available. For most of dry 1, free standing water is widely available in permanent water holes, watercourses, depressions and buffalo wallows. However, by the end of dry 2, it is reduced to permanent waterholes to which the baboon make almost daily trips to drink. In addition, this is a hot quarter and so the baboons are liable to sweat more, thus increasing their water requirements. In combination, these factors may impose important constraints on their use of time.

6.4.4 Levels of Variation

In Chapter 5 (section 5.4.2; Table 5.9) the level of variation generated by interindividual differences was considered and its implications for intra and inter population comparisons discussed. This section deals with similar issues in relation to the levels of variation generated by temporal variation. The range of time spent in different activities was greatest between periods within days. The range of the mean daily time budgets in different quarters of the same year was also considerable whereas the range between the same quarters in different years was relatively slight. The variation between periods is comparable to that produced by comparing the annual time budgets of different populations (Table 5.9; Dunbar 1992a).

Given that time budgets can vary considerably over time, comparisons must be based on compatible time scales, especially with respect to time of day. In general, studies have recognised this problem. There are, however, three issues that merit further attention.

Firstly, when only parts of years are compared, they are generally matched according to rainfall patterns eg., wet season compared to wet season. Ideally, matching should be based directly on resource characteristics. Although it seems that they are generally more favourable in the wet season this is not necessarily the case (Clutton-Brock 1977a).

Secondly, the definition of a day varies between studies. Examples used in primate studies are set times (e.g., 700 to 1700 as used in this study), dawn to dusk (e.g., Davidge 1978), sleeping tree to sleeping tree (e.g., Sharman 1981), alert period (e.g., Chivers 1977) and unstated (e.g., Isbell & Young 1993). Given the degree of variation that occurs within a day, even small differences in definition could result in misleading comparisons.

Thirdly, annual time budgets calculated from studies lasting less than a year, e.g., 6 or 9 months, could be biased by seasonal effects and not represent a true annual mean. Ideally behavior should be sampled evenly throughout a full annual cycle before annual time budgets are calculated.

6.5 SUMMARY

The use of time by adult female baboons in Mikumi National Park showed considerably temporal variation within years and days but, not between years. Both daily time budgets and use of time during different periods of a day varied from quarter to quarter. Controlling for such temporal variation is vital for valid intra- and inter- population comparisons.

The data suggest multiple causal mechanisms underlie the temporal variation found. In particular, they suggest that minimum feed time required is determined by food resources but that feeding time is kept to this minimum because of costs associated with poor visibility and heat stress. These factors can be related either directly (heat stress) or indirectly (visibility & food; Chapter 4) to climate. Other factors not investigated here may also be important, especially those related to characteristics of food resources not reflected in the food indexes used. The baboons respond not only to the changing costs and constraints in their environment by altering their daily time budgets but, also by adjusting their time use throughout the day.

CHAPTER 7. TROOP FUSION

7.1 INTRODUCTION

7.1.1 Aim

Almost exactly midway through the data collection period of this project, on July 28th 1994, the two main study troops of yellow baboon in Mikumi National Park fused. This chapter investigates immediate changes in individual behaviour (specifically, adult female time budgets, feeding competition and vigilance) in relation to the sudden doubling of group size caused by this fusion. The aim of this chapter is to evaluate these changes in terms of the costs and benefits of group living and to provide an initial assessment of why and how this event occurred.

7.1.2 Troop Fusion

Fissioning of primate groups has been well documented (just for baboons e.g., Eley et al. 1989; Henzi et al. 1997; Nash 1976; R.J.Rhine & G.W.Norton unpublished data; Stoltz 1972) but cases of fusion appear to be far rarer, having previously been recorded in only three populations (Table 7.1). In Amboseli National Park, a single fusion between two troops of yellow baboon was observed in 1972 (Altmann 1980; Altmann et al. 1985) and six fusions occurred among vervet groups between 1984 and 1988 (Cheney & Seyfarth 1987; Isbell et al. 1991). In Polonnaruwa Reserve, a fusion between two troops of Toque monkey was observed in 1976 (Dittus 1986, 1987). These records of fusions all occurred during truly long-term (>15 years) field studies after periods characterized by population decline. For the vervets and toque monkeys, intertroop competition was implicated as an important causal factor (Dittus 1987; Isbell et al. 1991).

Given the nature and complex social structuring of female-bonded primate groups (Wrangham 1980) it is not surprising that group fission occurs much more often than group fusion. Breaking social bonds to achieve fission must surely be less difficult than forming new ones to enable fusion. The question then, is not just why a fusion occurs, but how such radical redefining of social relations is achieved.

Table 7.1 Comparison of previous fusion events observed in wild primates; see text for references

FEATURE	Baboons	Vervets	Toque Monkeys
Location	Amboseli National Park, Kenya	Amboseli National Park, Kenya	Polonnaruwa Reserve, Sri Lanka
Duration of study	1963-1964, 1971 - present	1977-1991	September 1968 to March 1984
Date of fusion(s)	Fall 1972	Six fusions between 1984 and 1988.	March 4th 1976
Brief description	A one-male troop (High Tail's) numbering approx., 15 joined a troop numbering approx. 35 (Alto's).	Small troops reduced to one adult and a varying number of juveniles, joined larger troops.	A troop with no adult males (group A) numbering 8, joined a troop of 12 with no adult females (group SG)

7.1.3 Group Size & Individual Behaviour

There is general acknowledgement that there can be both foraging and predation benefits to living in larger groups and that these are generally accompanied by increased costs of intragroup competition (e.g., Lee 1994). However, great debate surrounds the relative importance of these factors in the evolution of group living in primates (e.g., Alexander 1974; Dunbar 1988; Cheney & Seyfarth 1987; Janson & Goldsmith 1995; van Schaik 1994; van Schaik et al. 1993; Wrangham 1980). Patterns of behaviour of extant groups have been variously interpreted but represent the product of forces of natural selection and are not necessarily directly indicative of them (Dunbar 1988). This chapter focuses on changes in individual behaviour (time budgets, feeding competition, vigilance) in relation to a specific event which doubled group size; no attempt is made to directly test hypotheses relating to selective pressures. The changes which might be expected in individual behaviour in relation to the fusion on the bases of potential costs and benefits of group living are discussed below.

7.1.3.1 Time budgets & feeding competition

Measuring competition during feeding was not one of the objectives of this research. However, both standard time budgets components and the relative amount of movement and aggression occurring during feeding, can be used to gain some insight in to changes in intragroup feeding competition.

Foraging efficiency of individuals in larger groups can be improved because they are better able to find food and to defend it from larger troops (Wrangham 1980). Chapter 6 indicated that the Mikumi baboons keep their feeding time to the minimum sufficient to fulfil their nutritional needs. If so, greater foraging efficiency would be expected to manifest itself in decreased time spent feeding and possibly moving. This would leave more time available for resting and/or socializing. The effects of any increased intragroup competition would directly counteract these trends. Empirical findings on the relationship between group size and time budgets were reviewed in Chapter 2 (section 2.5.2.1). The picture is unclear and no general pattern can be described. This probably reflects differential resolution of these counteracting pressures dependent on habitat specific patterns of resources and predation.

Both increased direct and indirect competition (Janson & van Schaik 1988) within groups is expected to manifest itself in increased feeding time. For example, individuals experiencing direct competition may have their feeding bout interrupted and those experiencing indirect competition may have to search harder. The incidence of moving and aggression during feeding will increase with the former, and time spent moving with both. Watts (1985) found displacement during feeding increased with group size, which he took to indicate increased direct competition. He assumed that an increase in direct competition would be accompanied by increased indirect competition.

7.1.3.2 Vigilance

Many species can better detect and defend themselves against predators in larger groups (Alexander 1974). One manifestation of this is that individuals in larger groups can afford to invest less time being vigilant for predators (Caraco 1979a&b; Cowlishaw 1993; de Ruiter 1986; Elgar 1989; Kildaw 1995; Roberts 1995; Ruxton 1996; Yaber & Herrera 1994) because they can rely on the vigilance of conspecifics. In birds, it appears that the time saved is devoted to feeding (Caraco 1979b) but this may be less important in primates (Cowlishaw 1993).

One of the main problems with analyzing vigilance is that animals need to look for, or at, many other aspects of their environment in addition to predators (e.g., Gould et al. 1997). For baboons, these include other troops, conspecifics within the troop, food and substratum. While an individual in a larger group may need to spend less time monitoring its environment for predators, resources (refuges, food & water) and other groups, it may well need to invest more time in behaviours that promote cohesive group movement. With more individuals to monitor and potentially higher intragroup competition, individuals in larger groups may need to invest more looking at other group members. Conversely, since it is easier to lose sight of other group members in small groups (Lagory 1986, 1987), this type of vigilance may decrease with increased group size.

Three types of vigilance behaviour were recorded in this study - sentry, attend and orient. Sentry and orient behaviours monitor the environment outside the group while attend monitors conspecifics within the group. By definition, orient involves a strong directional component and often occurs prior to a group movement. Sentry involves scanning from a raised position and is likely to facilitate detection of predators or other groups but is possibly also used to locate food, water and sleeping sites. Decreased sentry and increased orient would be expected with a sudden doubling of group size. The expected effect of increasing group size on attend would depend on the relative influence of needing to look at conspecifics more because of increased competition, versus the effect of needing to look for them less because the probability of losing contact with other group members is lower.

7.2 METHODS

A comprehensive description of raw data collection is given in Chapter 3. Chapter 3 also includes definitions of the behaviours (Table 3.7) considered in this chapter. This section contains only additional methodological information relevant to the analyses performed for this chapter.

Data from a single quarter (dry 1 1994) only were used so that immediate effects could be identified and confounding effects of seasonal variation minimized. Behaviour pre fusion (1st June 1994 to 27th July 1994 inclusive) was compared to behaviour in the post fusion (28th July to 31st August 1994 inclusive) in this quarter. A related samples design was used to compare the behaviour of six adult females (Table 7.2) before and after the fusion: V1 and V2 contributing 3 individuals each to the pre fusion data set. Although the related samples design, used (section 7.2.2) would have avoided the potentially confounding influence of sex differences revealed in Chapter 5, paucity of data on males prevented their inclusion.

Table 7.2 Demography of V1 and V2 at fusion.
Reproductive states of females on 28th July 1994 are given in brackets.

AGE-SEX CLASS	V1	V2
Adult females	Swali$^+$ (pregnant) Kikubwa$^+$ (lactating) Siafu$^+$ (pregnant) Kuvimba* (full swell)	Mtumishi$^+$ (flat) Heshima$^+$ (flat) Ruaha$^+$ (swelling)
Adult males	Mvua Nyigu Mwitalia	Peke
Subadult males	Hondohondo	Nidhamu
Large Juvenile Females	Kitovu Kuongeza* Kicheko*	
Large Juvenile Males		Dalali Karani
Small Juvenile Females		Hayupo Mfanyakazi Tiririka
Small Juvenile Males	Unko	Muungwana
Infant Females	Kirefu	
Infant Males		

$^+$ data from these individuals used for analyses in this chapter.

* females which transfered in on 23rd July 1994.

7.2.1 Behavioural Variables

The dependent behavioural variables considered in this chapter relate to time budgets, competition during feeding, and vigilance. In all cases the individual was used as the unit of analysis.

7.2.1.1 Daily time budgets

Mean daily time budgets for the pre and post fusion periods were calculated for the main time budget components (feeding, moving, resting and socializing) using instantaneous data from individual follows (section 3.3.2.1). The percent of time spent in different activities for each individual was calculated in two stages. First, the mean of follows in each period of the day (Table 3.6) was calculated, then the mean of these four periods was determined. Thus each period of the day contributed equally to the final daily time budget values for each individual.

7.2.1.2 Feeding competition indexes

One-zero data were used to calculate the mean proportion of intervals in which:

- feeding occurred (FD);
- feeding & agonistic behaviour both occurred (FD&AG);
- feeding & moving behaviour both occurred (FD&MV).

One-zero data were used because they enable temporal association of behaviours to be investigated. Mean daily values for each individual pre and post fusion were calculated as for time budget components (section 7.2.1.1) so that each period of the day contributed equally to the final values.

Two indexes of competition were calculated from these data as follows:

1) $$FDAG = \frac{FD\&AG}{FD}$$

Where FDAG = feed-aggression index.

FD&AG = proportion of intervals in which both feeding & agonistic behaviour recorded.

FD = proportion of intervals in which feeding was recorded.

2) $$\mathrm{FDMV} = \frac{\mathrm{FD\&MV}}{\mathrm{FD}}$$

Where FDMV = feed-move index.

FD&MV = proportion of intervals in which both feeding & moving behaviour recorded.

FD = proportion of intervals in which feeding was recorded.

7.2.1.3 Vigilance

One-zero data were used to calculate the mean proportion of intervals in which sentry (surveying environment from a raised position), orient (directional vigilance) and attend (looking at conspecifics) type vigilance behaviour were recorded. One-zero data were used because the behaviours under consideration were relatively infrequent and event-like. Mean daily values for each individual pre and post fusion were calculated as for time budget components (section 7.2.1.1) so that each period of the day contributed equally to the final values.

7.2.2 Statistical Analysis

The nonparametric permutations test for paired replicates (Siegel & Castellan 1988) was used to test for differences in behavioural variables pre and post fusion (i.e., behaviours were treated as dependent variables and pre/post fusion as the independent variable). The sample size for each test was six (adult females with pre and post fusion data).

7.3 RESULTS

7.3.1 Background

Box 7.1 provides brief notes on events occurring around the time of the fusion between V1 and V2. Although the two troops had slept together before July 28th and had tolerated close proximity of each other during some days, this was the first occasion members of one troop responded to the distress locate calls of members in the other troop. They also intermingled fully, at least temporarily, for the first time (G.W. Norton pers. comm.). In retrospect it was therefore decided this day would be used to mark the transition between V1 and V2 and the new single combined V4 troop. After this time they never slept apart and became increasingly intermingled.

At the time of the fusion, V1 had 13 members, including three transfer females who were first recorded in the group on 23rd July 1994. V2 had 11 members. Three of the four adult females in V1 were pregnant or lactating, while all three V2 females were cycling. There were three adult males in V1 but only one in V2 (Table 7.2).

Preliminary analyses of long-term data records (G.W. Norton & S.K. Wasser unpublished data) indicate that mean monthly day journey lengths (DJL) and home ranges of V1 and V2 in June 1994 were similar to those of V4 in August 1994 (i.e., DJL = approx. 3.5 km; home range = approx. 10 km^2). In July, the DJL of both troops was less than 3 km and the home range less than 6 km^2. Both troops concentrated on the area between the highway and the baboon hills (Fig 3.1). In previous months they had used this area and areas west towards the floodplain. In early August they again used the area between the baboon hills and the highway but, then made a dramatic move east into the wooded hills and valleys towards the centre of the park. They had not used this area since 1985 (G.W. Norton pers. comm.) and in fact went further east than ever before recorded. It was undoubtedly not a coincidence that the area east of the baboon hills had burned earlier in the quarter for the first time for several years.

Box 7.1 Selected notes on events occurring between 12th July and 4th September 1994 (source: personal field notes cross referenced with G.W. Norton & S.K. Wasser unpublished data).

17th July 1994 V1 and V2 found together at sleeping site 32 and remained reasonably close for most of the day, V1 following V2. Siafu (V1) approached V2 and was groomed by Karani and Heshima. (First time any affiliative behaviour shown between V1 and V2, previous encounters passive or agonistic.)

18th July 1994 V1, V2 and Large Mwanambogo all found around sleeping site 32. Troop encounters continued throughout the morning, V1 following Large Mwanambogo.

19th July 1994 V1 and V2 slept together at sleeping site 32. They stayed close all morning but moved apart in afternoon. Siafu (V1) grooms Mtumishi (V2). V1 vocalized at then chased V2.

22nd July 1994 V1 slept at sleeping site 54. V1 and V2 met up mid morning and spent much of day in close proximity, V1 following V2.

23rd July 1994 V1 found at sleeping site 32, V2 just south. V2 follows V1 for a short while then V1 moves north and V2 moves west. V1 and V2 briefly encountered each other later in the day when V1 supplanted V2 from a tamarind tree near the small water hole. New adult female accompanied by two large juvenile females (later named Kuvimba, Kuongeza & Kicheko) first recorded with V1.

24th July 1994 V1 encountered Large Mwanambogo. In late afternoon V1 within 150m of V2.

27th July 1994 Last time V1 and V2 thought to have used different sleeping sites. V1 encountered Large Mwanambogo. V1 and V2 came close mid morning and then spent much of day in close proximity, V1 following V2.

28th July 1994 V1 and V2 slept together at sleeping site 6. Both troops chased off by Large Mwanambogo troop. V1 followed V2 all day, doing distress-locate calls when contact lost, to which V2 responded.

29th July 1994 V1 and V2 slept together at sleeping site 36 and stayed together all day (mostly feeding on tamarinds).

30th July 1994 V1 and V2 slept together at sleeping site 12B. Members of V1 and V2 moved apart up to 120m during day but mostly together, contact reestablished with distress-locate calls.

31st July 1994 V1 and V2 slept together at sleeping site 22 and spent all day together.

15th August 1994 V4 slept at sleeping site 22 then went far east of main baboon hills.

16th August 1994 V4 slept at new sleeping site east of main baboon hills, continued to move east reaching and crossing Rungwa river valley. Slept in another new site.

26th August 1994 V4 moved back west as far as the Dell.

7.3.2 Time Budgets

Significant differences pre and post fusion, were found in the amount of time spent feeding and resting (paired permutation tests n=6 pairs, **$p<0.05$**) but not for moving and socializing (paired permutation test n=6 pairs, $p>0.05$). The amount of time spent feeding decreased and the amount of time spent resting increased after the fusion of the two troops (Fig. 7.1). The level of feeding prior to fusion was higher than normal for this quarter (i.e., 51% for both troops compared to a normal ~ 45%, Chapter 6) but returned to normal levels after the fusion.

Although a significant difference in the time spent socializing was not detected overall, prior to the fusion, time spent socializing by females in V1 was extremely low (~5%) and levels for all three females increased after fusion. A probability of less than 0.05 could not have been found due to the small sample size (Siegel & Castellan 1988) and therefore statistical analyses were not performed on these data. However, this result may still be indicative of time constraints on V1 pre fusion.

7.3.3 Feeding Competition Indexes

No significant difference was found before and after the fusion for either the feed-move index (FDMV) or the feed-aggression index (FDAG) (paired permutation tests n=6 pairs, $p>0.05$; Fig. 7.2).

7.3.4 Individual Vigilance

There were significant changes in the amount of time spent by individuals in orient, sentry and attend before and after the fusion (paired permutation tests n=6 pairs, **$p<0.05$**), although the difference in these categories combined was not significant (paired permutation test $p>0.05$). Attend (looking at conspecifics) and sentry (surveying environment from raised location) decreased while orient (directional vigilance) increased after fusion (Fig. 7.3).

Figure 7.1 Time spent in different activities pre and post fusion.
Differences are significant for feeding and resting only (paired permutation tests n=6 pairs, $p<0.05$ indicated by asterisks). Bars represent mean daily time spent in each activity pre and post fusion during the early dry quarter 1994. Errors lines represent standard deviations.

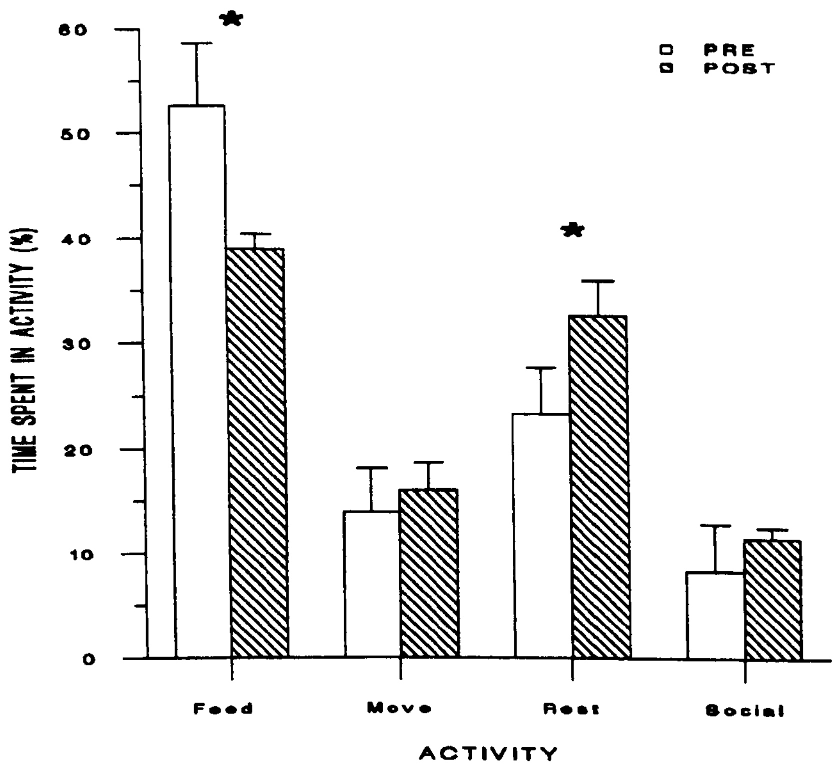


Figure 7.2 Feeding competition indexes (see text for calculation) pre and post fusion. FDAG & FDMV are competion indexes and are explained fully in section 7.2.1.2. Differences are not significant (paired permutation tests n=6 pairs, p>0.05). Bars represent mean daily indexes pre and post fusion during the early dry quarter 1994. Errors lines represent standard deviations.

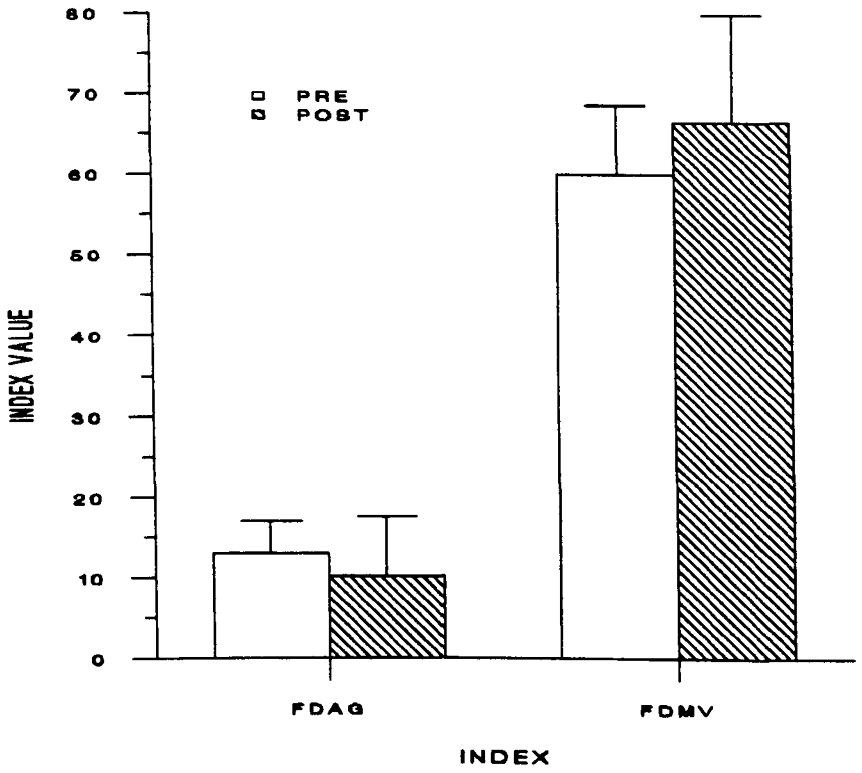
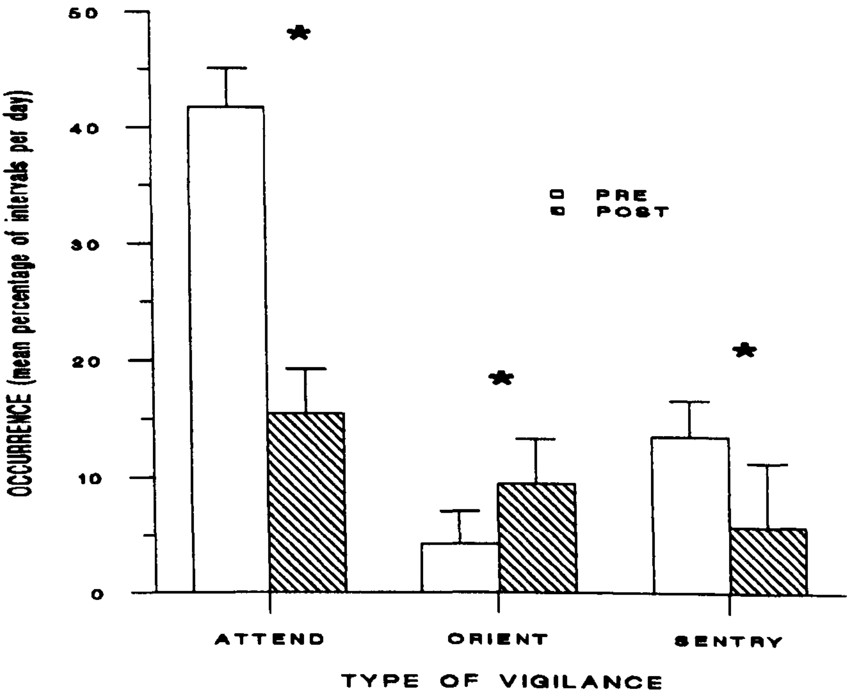


Figure 7.3 Occurrence of vigilance behaviours pre and post fusion.
All differences are significant (paired permutation tests n=6 pairs, **p<0.05** indicated by asterisks). Bars represent mean percent of intervals per day pre and post fusion during the early dry quarter 1994. Errors lines represent standard deviations.



7.4 DISCUSSION

7.4.1 Comparison to Other Studies

The fusion event that took place in Mikumi National Park in 1994 had the following features in common with other recorded occurrences of troop fusion in primates.

1. It was observed during a truly long-term (>15 years) study.
2. It occurred after a period characterized by population decline.
3. In Mikumi, one of the groups involved had only a single adult male. In Amboseli, the baboon fusion and two of the vervet fusions, involved one troop with only a single adult male. In the remaining Amboseli vervet fusions and the Polonnaruwa toque monkey fusion, one troop had no adult males at all.
4. In common with the toque monkey fusion, the Mikumi groups were of relatively similar size even though there was notably asymmetry in the sex ratio of adults. In both studies these group sizes were below the median for the population. In each case of fusion in Amboseli, groups were asymmetrical in size but at least one group was below the median size for the population.
5. Also in common with the toque monkeys, the fused Mikumi troop made a major range change.

Wrangham's (1980) model of female-bonded societies would predict that fusion is more likely to occur between closely related groups. V1 and V2 were the descendants of two troops formed by a fission event in 1978 and thus were more closely related to each other than to neighbouring troops (R.J.Rhine & G.W.Norton unpublished data). The origin of the two toque monkey troops was unknown but, they had been independent groups since the start of the study eight years earlier. A similar situation applies to the Amboseli baboon fusion except that the independence of the groups had only been documented for one year. For the vervets, fusion often occurred between troops known not to be the most closely related.

7.4.2 Costs & Benefits of the Fusion

7.4.2.1 Feeding competition

Three lines of evidence suggest that an increased cost of feeding competition was not incurred as a result of the troop fusion.

1) Neither of the indexes (FDMV and FDAG) measuring relative disruption and aggression during feeding changed.

2) Feeding time decreased and moving time remained the same.

3) Attend vigilance (looking at conspecifics) behaviour decreased.

Group size may have to exceed a threshold size before the costs of group living start to impinge on individual group members (Waser 1977). This threshold is likely to depend on the patch characteristics of the environment. Intragroup competition may not have increased in Viramba baboons after the fusion because group size remained below this threshold.

Before the fusion, time spent feeding in both troops was very high and, especially in V1, not much time was devoted to socializing. This implies that the baboon's use of time was highly constrained and that the fusion averted a potential time budget crisis (Dunbar 1992a). Group fission has already been identified as a mechanism by which time budget constraints can be relieved (Henzi et al. 1997). The results here show that fusion can bring about similar benefits.

7.4.2.2 Foraging efficiency

In Chapter 6 it was proposed that the Mikumi baboons keep their feeding time to the minimum needed in order to obtain sufficient nourishment for survival and reproduction. They may be able to do this because, for example, food quality is higher or feeding rates faster. Whatever allows shorter feeding times, the implication for feeding efficiency if the same; if they are able to fulfill their nutritional needs in a shorter period then they are being more time efficient. Thus the finding that feeding time decreased after the fusion indicates that benefits of improved foraging efficiency were gained.

7.4.2.3 Vigilance

Sentry (surveying the environment from a raised position) decreased after fusion as expected. The many eyes effect means that group levels of environmental surveillance in larger groups can be as high or higher than in the smaller groups even if individuals invest less time in this type of vigilance. Therefore while individuals may have invested less in sentry behaviour, sentry by V4 as a whole may not have declined. However, the frequent intertroop encounters between V1 and V2 prior to the fusion may have lead to elevated sentry behaviour by the groups as a whole; after they joined and no longer needed to monitor one another.

Orient (directional vigilance) also changed as expected - increasing after fusion. Individuals in the larger V4 troop, which were unused to moving together and ventured into new areas, probably needed to orient more in order to co-ordinate movement.

Attend (looking at conspecifics) decreased dramatically after fusion. The result for attend is not only consistent with a lack of increase in intragroup competition as already discussed but, suggests that individuals in V4 were less concerned about monitoring other group members. This is consistent with the proposal that the probability of an individual losing contact with its group is less if the group is larger group.

Combined levels of the three types of specialized looking behaviors did not change. This implies that fusion resulted in no overall time saving benefit in terms of vigilance. However, even if time had been saved, it is not clear if the effect of this would have been important. Firstly, the time saved may be negligible, as Cowlishaw (1993) found for chacma baboons. Secondly, unlike birds on which most work in this area has been conducted (e.g., Caraco 1979a&b), primates can be vigilant without disruption to feeding. In other words, vigilance is not necessarily costly.

7.4.3 How & Why?

In this section, an initial speculation of why and how the fusion took place is made based on the findings of this study and observations made at the time of the fusion event. Detailed analyses of long-term data (G.W. Norton & S.K. Wasser unpublished data) will enable additional tests to be conducted in the future.

Just prior to the fusion, both troops were restricted to a relatively small area. Intertroop conflict, especially with Large Mwanambogo troop, and tall grass to the south appear to have been influential factors in this respect. This period was also characterized by an unusually high proportion of time spent feeding, suggesting food resources in the area were limited and/or V1 and V2 were being periodically excluded from the best patches by other troops.

The foraging benefits of the fusion enabled individuals to reduce their feeding time significantly. The more favourable status of a larger troop in intertroop competition plus the combined knowledge of the two troops would have enabled them to find and defend better food resources. These factors, plus improved anti-predator benefits afforded by being in a larger troop, could have made the home range change to less familiar areas much safer.

The complexity of restructuring inter and intra group relationships is likely to present a barrier to group fusion, even if there are considerable benefits to be had. Tolerant relations between adult females in a baboon troop are usually established during their development within that troop. Fusion requires an *en masse* conversion of interactions from the entirely agonistic state that occurs between groups to the primarily afflliliative state within groups. Both group size and group composition are likely to be very important factors.

In all cases of documented fusion, one or both troops have been below the median size for the population. In the Amboseli vervets one troop had to be reduced to a single adult before fusion would take place and, in all documented cases of fusions in primates, one troop has been a single-male or no-male troop. Therefore, it seems likely that special demographic as well as ecological conditions must exist for fusion to take place.

Schaffner & French (1997) studied the response of different size groups of captive tamarins and marmosets to the introduction of novel individuals. They found that breeding females from large groups showed higher levels of agonistic behaviour towards the intruding individual than did breeding females in small groups. They suggest this "may facilitate the recruitment of additional group members" to small groups to increase the numbers of helpers in these cooperatively breeding species. However, cooperative breeding does not have to be evoked to explain why small groups benefit from recruitment of new individuals. As discussed, there are foraging and predation benefits to be gained. Therefore, similar behavioural mechanisms could occur in other primates, making small groups more predisposed to fuse than larger ones.

The asymmetry of adult sex ratio in V1 and V2 was largely a consequence of different number of males. However, while the numbers of females were more equitable (V1 had 4 and V2 had 3) the reproductive states of these females were quite different. Three of the females in V1 were pregnant or lactating. In contrast all three V2 females were cycling. In short, one troop had three cycling females and a single male, the other had one cycling female and three adult males. Sexual attraction is a common proximate cause of transfer between groups (Pusey & Packer 1987) and probably played a role in the fusion event between V1 and V2.

As Dittus (1987) suggests, fusion may only occur when a complex set of factors come together in time and space. Ecological factors can create conditions in which fusion would be beneficial but, particular demographic features are necessary in order for troops to be able to overcome established agonistic and avoidance behaviour, and achieve fusion. Evidence from Mikumi and elsewhere suggests that important demographic factors include group size, number of adults (especially adult males) and the reproductive state of adult females.

7.5 SUMMARY

Halfway through this study the two main study groups fused. This provided a fortuitous opportunity to investigate the immediate consequences of a sudden doubling of group size on individual behaviour. Feeding time decreased and resting time increased. Indexes of aggression and displacement during feeding remained unchanged. Sentry (surveying environment from a raised position) and attend (looking at conspecifics) declined but orient (directional vigilance) increased.

From these results, and other observations made around the time of the fusion, it is possible to speculate on the factors promoting this fusion event in Mikumi National Park. As a consequence of the troop fusion, individuals gained foraging benefits without incurring costs of increased intragroup competition and were relieved of serious time budget constraints. Intertroop competition appears to have been an important mediator of these benefits. Anti-predator benefits may have played a role in facilitating both the fusion event and the subsequent exploration of new areas by the resultant single larger troop. Undoubtedly, a variety of ecological factors created a situation in which individuals could gain these net benefits by fusing with another troop. This coincided with the occurrence of demographic conditions which made fusion possible.

CHAPTER 8. FUNCTIONAL EQUATIONS

8.1 INTRODUCTION

8.1.1 Aim

The preceding result chapters have dealt with intra-site variation of the behaviour of baboons (Chapters 5, 6 and 7) and their habitat in Mikumi National Park. The purpose of these chapters was to investigate the behavioural ecology of the Mikumi baboons and to explore assumptions and possible mechanisms underlying functional equations based on biogeographical patterns of time budgets in baboons (section 2.6; Bronikowski & Altmann 1996; Dunbar 1992a, 1996; Williamson 1997); equations generated by Dunbar (1992a,1996) and others (Bronikowski & Altmann 1996; Williamson 1997) from an interpopulation dataset.

In general, the analyses indicate that the assumptions of the functional equation approach are valid although, problems can arise in some cases if sampling regimes are indifferent to potential biasing (as summarized in sections 5.5 and 6.5). However, during the course of this study, as more work was produced on the functional equation approach to predicting time budgets (Bronikowski & Altmann 1996; Dunbar 1996; Williamson 1997), more worrying concerns emerged (Chapter 1). The aim of this chapter is, therefore, to provide a thorough critical review of the procedures used to generate and test the functional equations. This is a necessary prequel to Chapter 9, in which such functional equations are used in relation to changes in behaviour of the Mikumi baboons over three decades.

8.1.2 Background on Functional Equations

The functional equations considered in this chapter are, infact, part of a larger model of primate sociality developed by R.I.M.Dunbar (Chapter 1). Functional equation have been used to establish the maximum ecologically tolerable group size component of Dunbar's model (Dunbar 1992a, 1996; Williamson 1997). The equations, produced by stepwise multiple regression, relate individual time budget components to key climatic variables and group size.

Once generated, the equations have been used to predict time spent feeding, moving, resting and socializing by individuals under any given set of conditions of climate and group size. Dunbar (1992a, 1996) and Williamson (1997) have used this to predict the range of group sizes and climatic conditions under which individuals can keep their essential time budgets totalling equal to or less than 100%, with spare time being taken up by additional resting. They define the largest group size satisfying these criteria for a set of climate conditions, as the 'maximum ecological group size' in that habitat. Above this group size animals are predicted to show signs of 'ecological stress', eventually leading to troop fission (Dunbar 1992a). If total essential time budgets of less than 100% cannot be achieved at any group size, baboons are predicted not to be found in that particular habitat.

The functional equations have been tested in three ways. Firstly, values for time budget components have been predicted for specific locations and have been compared to observed data (Dunbar 1992a, Bronikowski & Altmann 1996, Williamson 1997). Secondly, the range of habitats in which baboons are predicted not to be found have been compared to observed biogeographic patterns (Dunbar 1992a, Williamson 1997). Thirdly, evidence of ecological stress has been looked for in groups exceeding the maximum predicted for a particular habitat (Dunbar 1992a). This chapter deals only with the first of these.

There are now several versions of Dunbar's (1992) original functional equations; the principle ones of these are presented in Table 8.1. The abbreviations used for each set are indicated. "D92" denotes Dunbar's original equations (Dunbar 1992a). "B&A" indicates the equations produced by Bronikowski & Altmann (1996); a reanalysis of Dunbar's original work. "D96" is used to indicate Dunbar's updated equations which he presented at the British Academy in 1996 (Dunbar 1996). "DW" denotes the follow on equations produced by Williamson in her thesis. In summary, differences between the versions can largely be accounted for by alterations and additions to the dataset, and by the use of different inclusion criteria in the multiple regression procedure.

Williamson (1997) generated further sets of equations in order to explore the effects of proximity (i.e., distance from field site) and duration (i.e., long versus short term) of climate data collection and different stepwise multiple regression inclusion criteria.

Table 8.1 Main versions of functional equations relating time budget components to group size and climate.
The first column includes the abbreviations (ABBREV.) used in the text to denote each set of equations. J = day journey length (km); N = group size; P = mean annual rainfall (mm); V = number of months with <50mm rainfall; Z = Simpson's index of rainfall; T = mean annual temperature; F = percent time spent feeding; M = percent time spent moving; R = percent time spent resting; S = percent time spent socializing. FIN/FOUT = entry/removal criteria used in stepwise multiple regression. n1 = number of cases used in regressions for time budget components. n2 = number of cases used in regressions for day journey length. For R^2, F and P values see source texts.

ABBREV.& SOURCE	**EQUATIONS**	BEHAVIOURAL DATA	CLIM. DATA	FIN/ FOUT	n1	n2
D92 Table 3 in Dunbar (1992)	$\ln(J) = 1.344 + 0.784\ln(N) - 0.4731\ln(P)$ $\ln(F) = 7.408 + 4.439\ln(Z) - 0.883\ln(T) - 0.447\ln(V) + 0.581\ln(J)$ $\ln(M) = 2.201 + 0.163\ln(N) + 0.219\ln(V)$ $\ln(R) = 10.550 - 1.333\ln(F) - 0.323\ln(N) - 0.282\ln(P)$ $\ln(S) = -1.599 + 0.488\ln(P) - 4.965(Z)$	Original database. Data and sources given in Dunbar (1992)	Climate data from various sources. Data given in Dunbar (1992), sources discussed in Williamson (1997)	n/a	14	18[1]
B&A Table 6 in Bronikowski & Altmann (1996)	$\ln(J) = 2.68 + 0.68\ln(N) - 0.61\ln(P)$ $\ln(F) = 6.39 + 5.12\ln(Z) - 0.68\ln(T)$ $\ln(M) = 2.15 + 0.15\ln(N) + 0.28\ln(V)$ $\ln(R) = 7.57 - 1.26\ln(F)$ $\ln(S) = 1.15 + 0.47\ln(P) - 0.54\ln(F)$	As for D92 except for modifications to Amboseli data.	As for D92 except for modifications to Amboseli data.	2.00/ 1.996	14	17
D96 Dunbar (1996)	$\ln(J) = 1.344 + 0.784\ln(N) - 0.473\ln(P)$ for $T<30^{o}C$: $\ln(F) =6.866 + 4.077\ln(Z) - 0.750\ln(T) - 0.390\ln(V) + 0.155\ln(J)$ for $T>30^{o}C$: $\ln(F) =1.768 + 4.077\ln(Z)+ 0.750\ln(T) - 0.390\ln(V) + 0.155\ln(J)$ $\ln(M) = 2.201 + 0.163\ln(N) + 0.219\ln(V)$ $\ln(R) = 0.97 - 7.923\ln(Z) + 0.601\ln(V)$ $\ln(S) = -2.275 + 1.32\ln(Z) - 0.0445(\ln(N))^2$	As for D92.	As for D92 with improved data for Amboseli.	n/a	14	18
DW Table 3.11 in Williamson (1997)	$\ln(J) = -2.183 + 0.401\ln(V) + 0.691\ln(N)$ $\ln(F) = 6.187 + 3.886\ln(Z) - 0.667\ln(T)$ $\ln(M) = 2.195 + 0.195\ln(V)$ $\ln(R) = 8.609 - 1.415\ln(F) - 0.859\ln(N) - 1.718\ln(Z) + 0.362\ln(P)$ $\ln(S) = 4.837 - 0.684\ln(F)$	As for D92 with corrections for Chololo data and addition of 1982-1991 Amboseli data.	As for D92 with modifications to Amboseli data.	3.84/ 2.71	14[2]	10

[1] "...not 21 as implied in Dunbar 1992" (Dunbar 1996:12).

[2] Degrees of freedom reported in Williamson (1997) suggest only 12 sites used for resting equation.

8.2 THE DATASET

The dataset originally compiled and used by Dunbar (1992a; his table 2) consisted of data on time budget components (% of day spent feeding, moving, resting and socializing), percent of time spent feeding in the dry season, group size, day journey length and meteorological variables (mean annual rainfall, number of months with less than 50mm of rain, Simpson's index of rainfall diversity) for 23 sites across Eastern and Southern Africa. Not all data were available from all sites.

Dunbar (1992a) divided these sites into "main data" (14 sites), "subsidiary sample" (4 sites) and "day journey sample" (4 sites). Dunbar (1992a) used the main data to generate his equations for time budget components which he then tested using the subsidiary sample. He used the day journey sample, in combination with ten sites from the main sample for which day journey length data were available, to generate an equation for day journey length.

Bronikowski & Altmann (1996) criticize the dataset compiled and used by Dunbar (1992a) in the following ways:

1. Travel distance data were assumed to have been collected from to dawn to dusk for all studies.
2. The meteorological data can either not "be found in the cited references or contradict the values given in these references" (Bronikowski & Altmann 1996:20).
3. The sources of meteorological data are unclear.
4. The Simpson Index is not the best measure of the evenness of rainfall.

Points 2 through 4 have been effectively dealt with by Williamson (1997). Her work addresses these criticisms or challenges their validity, such that they do not need to be considered further here. However, other areas of possible concern remain and are explored below:

1. Bronikowski & Altmann's (1996) second point applies not just to the meteorological data presented by Dunbar (1992a) but also to baboon related variables. Many values quoted by Dunbar's (1992; his table 2) for time budgets, day journey length and group size come from personal communications to this author and are absent from or contradict the values given in the published references cited.

2. The potentially confounding effects of sampling of individuals from different age-sex classes or of temporal variation were not assessed for compatibility. Such factors have

been considered in Chapters 5 and 6 of this study. Bronikowski & Altmann (1996) raise this point in relation to the travel distance and daily observation period but again, this criticism applies more widely to all of the behavioural data. While in many cases the variation generated is relatively slight, variation within days, for example, can be considerable. However, providing that sampling is reasonably even from dawn to dusk even this is unlikely to be of major importance.

In addition there are a number of mistakes and inconsistencies relating to the datasets printed in Dunbar (1992a) and Williamson (1997). For example, Williamson (1997) reports a mistake by Dunbar (1992a) in the data for Chololo: "..., moving and resting time values (were) interchanged" (Williamson 1997: 107). However, Dunbar's (1992) figures are, moving = 33.1% and resting = 17.4% while in Williamson (1997) they are moving = 35.8% and resting = 14.7%. Another example is that the value of 3.1km quoted for day journey length of baboons in Mikumi by Dunbar is not consistent with long term records and observations made at the time (R.J.Rhine & G.W.Norton unpublished data, G.W.Norton pers. comm.). It is almost certain that the figure reported is in miles and that the actual day journey length at this time was 5.5km.

The impact of each mistake in isolation is likely to be minimal. Williamson (1997) has shown the functional equations to be robust to minor errors in the data (Williamson 1997). Moreover, I found using the corrected value for DJL in the Mikumi data for generating DJL equations made only minor differences to coefficients and constants and made no difference at all to the variables included (Table 8.2 note 2). However, in combination a series of such mistakes might have a significant effect.

Table 8.2 Versions of functional equations relating time budget components to group size and climate produced by this author. The equations were generated using SPSS stepwise multiple regression with the F entry/removal criteria (FIN/FOUT) set at 3.84/2.71. The data used were as appears in table 2 of Dunbar (1992) without modification or correction. J = day journey length (km); N = group size; P = mean annual rainfall (mm); V = number of months with <50mm rainfall; Z = Simpson's index of rainfall; T = mean annual temperature; F = percent time spent feeding; M = percent time spent moving; R = percent time spent resting; S = percent time spent socializing.

EQUATIONS	**R^2**	**F (df)**	**P**
$\ln(J) = 2.51 + 0.69\ln(N) - 0.60\ln(P)$	0.77	18.85 (2,11)	**<0.01**
$\ln(F) = 4.56 + 6.75\ln(Z)$	0.35	6.58 (1,12)	**0.02**
$\ln(M) = 2.15 + 0.15\ln(N) + 0.27\ln(V)$	0.69	12.34 (2,11)	**<0.01**
$\ln(R) = 7.57 - 1.26\ln(F)$	0.66	23.48 (1,12)	**<0.01**
$\ln(S) = 1.15 + 0.47\ln(P) - 0.54\ln(F)$	0.58	7.50 (2,11)	**0.01**

Notes:

1. Although the number of sites used for the day journey length equation was the same as for the time budget component equations, these were not the same 14 sites. Day journey length data were not available for 4 of the sites in the main sample used for time budget components. Day journey length, but not time budget, data were available from 5 other sites. Data on V and Z were not available for 1 of these 5 sites. Therefore, only 4 were used to generate the equation shown. However, as V and Z do not appear in this equation, including this site makes little difference except to increase the sample size to 15.

2. The equation for day journey length given was generated using the uncorrected J value for Mikumi. Using the corrected data made little difference: $\ln(J) = 2.16 + 0.75\ln(N) - 0.57\ln(P)$, $R^2 = 0.83$, $F_{2,11} = 25.51$, $p<0.01$.

3. Dunbar (1992) substituted values for J generated by his equation for day journey into his main sample data for the 4 sites were no empirical day journey length data. I followed this precedent but, found that J was still not included in any of the time budget components.

8.3 GENERATING FUNCTIONAL EQUATIONS

8.3.1 Review of Procedures

Bronikowski & Altmann (1996) express concern over Dunbar's use of stepwise multiple regression to produce functional equations of time budgets in relation to climate and group size. Again, Williamson (1997) effectively counters their argument, reminding us that "the purpose of stepwise multiple regression is to find the smallest set of predictor variables that still does an adequate job of prediction" (Williamson 1997:95). Although Bronikowski & Altmann (1996) used stepwise multiple regression to generate equation comparible to those of Dunbar (1992a), they avocate that "a balance between univariate analysis and multiple regression should be used to determine significant predictor variables" (Bronikowski & Altmann 1996:14). This approach is appropriate for comparing, as for example they did in their table 4, the effects of climate and group size on different groups within Amboseli. However, when equations are being sought for the purposes of prediction, stepwise multiple regression, while not ideal, is the best option (Sokal & Rohlf 1981; Williamson 1997).

Bronikowski & Altmann (1996) also express concern that Dunbar (1992a) did not explicitly acknowledge the *a priori* statistical dependence of two meteorological independent variables: number of dry months (V) and total annual rainfall (P). Williamson (1997:95) points out that "variables left out of the predictor set may be important, but omitted because they correlate with the other variables in the predictor set". Awareness of this possibility when interpreting the equations is important.

The residuals in a multiple regression are assumed to be normally distributed. This implies the dependent variable will be normally distributed if all the explanatory variables are. Dunbar (1992a) performed natural log transformations on all data "to ensure normality" (Dunbar 1992a: 37). As Williamson (1997) points out, the arcsine transformation is generally more appropriate for proportional data such as percentages used for time budget components (Sokal & Rohlf 1981). However, to be consistent with Dunbar's work both Williamson (1997) and Bronikowski & Altmann (1996) use natural log transformation on all variables.

I explored both the untransformed and the natural log transformed data for normality using procedures in SPSS (SPSS 1993). The results were inconclusive and transformation had little effect. This is consistent with Dunbar's finding that transforming the data "does not have a significant effect on the coefficient of determination" (Dunbar 1992a:37). With only fourteen data points, inspecting for normality is very likely to be inconclusive (Sokal & Rohlf

1981). The normality of the data used to generate the functional equations, before and/or after transformation, has been accepted as an assumption, even though it is difficult to test.

8.3.2 Generating Equations with Appriopriate Standard Errors

In the next section (8.4), the need to use the standard errors of predictions in the procedure for testing the functional equations is justified. Standard errors of predictions have not been reported by previous authors. However, they can be easily generated during the regression procedure of SPSS (SPSS 1993). I therefore generated my own set of equations (Table 8.2) in order to obtain the standard errors of the predictions for the four subsidiary sites (Table 8.3a) used in the test procedure.

My equations are very similar to those produced by Bronikowski & Altmann (1996). Temperature is absent from the feeding equation but, otherwise the equations are similar except for some minor differences in the values of constant or coefficients.

Table 8.3a Observed and predicted values (natural logs) for time budget component for subsidary sites: my equations.
Observed values from table 2 in Dunbar (1992a). Predicted values and their standard errors generated by SPSS during stepwise multiple regression procedure to produce equations in Table 8.2.

SITE	FEED			MOVE			REST			SOCIAL		
	Obs	**Pred.**	**SE Pred.**	**Obs**	**Pred.**	**SE Pred.**	**Obs**	**Pred.**	**SE Pred.**	**Obs**	**Pred.**	**SE Pred.**
Badi	3.26	3.08	0.21	2.21	3.36	0.05	3.84	2.87	0.10	2.76	2.38	0.11
Metahara	3.66	3.51	0.09	3.27	3.32	0.05	3.17	3.68	0.16	2.29	2.55	0.17
Awash	3.39	3.39	0.11	3.32	3.32	0.06	3.45	3.14	0.09	2.60	2.34	0.10
Giligil'73	3.35	3.91	0.15	3.02	3.19	0.04	3.06	3.29	0.10	2.31	2.35	0.12
MEAN			0.14			0.05			0.11			0.13

Table 8.3b Observed and predicted values (natural logs) for time budget component for subsidary sites: D92 equations.
Observed values from table 2 in Dunbar (1992a). Predicted values calculated from D92 equations (Table 8.1) using an Excel 97 spreadsheet. Standard errors of predictions estimated as mean of values in Table 8.3a.

SITE	FEED			MOVE			REST			SOCIAL		
	Obs	**Pred.**	**SE Pred.**	**Obs**	**Pred.**	**SE Pred.**	**Obs**	**Pred.**	**SE Pred.**	**Obs**	**Pred.**	**SE Pred.**
Badi	3.26	2.84	0.14	2.21	3.32	0.05	3.84	2.84	0.11	2.76	2.84	0.13
Metahara	3.66	3.38		3.27	3.33		3.17	3.38		2.29	2.34	
Awash	3.39	3.10		3.23	3.24		3.45	3.10		2.60	2.44	
Giligil'73	3.85	3.93		3.93	3.24		3.06	3.93		2.31	2.01	

Table 8.4 Results of Fisher's test for combining probabilities from independent tests of significance. Observed and predicted values and their sources given in Table 8.3. Test calculations carried out using an Excel 97 spreadsheet. Significant p-values ($\alpha = 0.05$) shown in bold. Degrees of freedom = 8 (with Badi) or 6 (without Badi).

		TIME BUDGET			
		FEED	**MOVE**	**REST**	**SOCIAL**
ORIGINAL METHOD					
D92	sum	-3.63	-8.79	-3.07	-1.16
with	χ^2	7.25	17.58	6.13	2.31
Badi	p	0.51	**0.02**	0.63	0.97
REVISED METHOD					
D92	sum	-10.00	-30.85	-10.82	-5.53
with	χ^2	20.00	61.70	21.63	11.07
Badi	p	**0.01**	**<0.01**	**0.01**	0.20
D92	sum	-5.80	-8.38	-4.26	-4.94
without	χ^2	11.59	16.76	8.51	9.88
Badi	p	0.07	**0.01**	0.20	0.13
DH	sum	-3.46	-32.35	-4.35	-11.09
with	χ^2	6.92	64.71	8.70	22.18
Badi	p	0.55	**<0.01**	0.37	**<0.01**
DH	sum	-2.58	-9.50	-3.26	-5.86
witout	χ^2	5.16	19.00	6.53	11.73
Badi	p	0.52	**<0.01**	0.37	0.07

Note: "D92" denotes Dunbar's original equations (Table 8.1; Dunbar 1992a). "DH" denotes my equations (Table 8.2).

8.4 TESTING THE EQUATIONS

8.4.1 Review of Procedure: Dunbar & Williamson

Dunbar (1992a) assessed the predictive abilities of his equations using data from four subsidiary studies not included in the dataset used to generate the equations. Time budget data from two of these sites, Badi and Metahara, were based on wet season data only and the other two, Awash and Gilgil '73, on dry season data only. These sites were excluded from the original dataset because of their seasonal bias. However, after comparing an equation for feeding based on dry seasons only (which he presents for 10 of his 14 sites in his main sample) Dunbar (1992a) concluded that the differences between wet and dry season data are relatively small and that seasonally biased data could be used to test the equations.

Seasonal variation within Mikumi was considered in Chapter 6. The baboons fed more and rested less in the dry season; time spent socializing and moving did not change. Variability across seasons within Mikumi was less than across populations, but an analyses of seasonal difference against temperature suggests that seasonal variation increases with mean ambient temperature (Fig. 6.5). Three of the four subsidiary sites used by Dunbar (1992a) to test his equations had temperatures similar to, or lower than, Mikumi. Badi, however, is several degrees hotter and inclusion of dry season data would be expected to lower the annual figure by about 6 % (estimating from the line of best fit on Fig. 6.6).

Dunbar (1992a) used the four subsidiary sites, mentioned above, to test his equations in the following way. First, he used his equations to predict the time budget components of the baboons at the subsidiary sites. He then found the difference between the observed and predicted values and divided this by the standard deviation of the data from the 14 main sites to produce z-scores. Next, he used Fisher's procedure for pooling independent tests (Fisher's combined probability test; Sokal & Rohlf 1981:779-782) to obtain an overall probability that the observed and predicted values are not significantly different. The result indicated a very high probability ($p>0.95$) supporting this null hypothesis. However, as Williamson (1997: 131) points out, combining all four time budget components in this way violates the assumption of independence required to ensure the validity of Fisher's test.

Williamson (1997) followed Dunbar's protocol to compare the predictive abilities of different versions of the functional equations but, added an additional step of calculating Fisher's combined probability test for each time budget component for each set of equations. The results of these analyses (Williamson 1997: her table 3.17) and comparable probabilities calculated from for the D92 equations (Table 8.4, top row "original method") indicate that the equations predict observed values well for all components except moving. The poor result for moving is largely accounted for by data from Badi where observation conditions are likely to have led to an underestimation of moving time (Dunbar 1992a).

In Williamson (1997) the standard deviation for social behaviour is given as 13.03 (her table 3.15) but standard deviation of the data for the 14 main field sites (her table 3.6) is in fact 5.37. To establish if this was just a typographical error, I divided the difference between the observed and expected values for social behaviour by the z values given in the table. Unfortunately this produced no consistent number e.g., for Metahara the value of the standard deviation estimate in this way ranged from 4.6 to 186.1. I reanalysed of the social behaviour data in Williamson's table 3.15 using a standard deviation of the 5.25 as for Dunbar (1992a). This made no notable impact on the results of the Fisher's test for combining probabilities was detected.

Errors of calculation in the original work (R.I.M. Dunbar pers. comm.) may also account for the discrepancies between the predicted values I generated for the subsidiary sites (Table 8.3) and those quoted by Dunbar (1992a) and Williamson (1997). Repeating the tests with my predicted values again had little impact on the results of the Fisher's test for combining probabilities.

Dunbar (1992a, 1996) and Williamson (1997) both transformed data to ensure they were normally distributed for use in multiple regression. However, they used the same data untransformed in the z-test which, also requires normality. As discussed in section 8.3.1, the natural log transformation used has little effect and normality is merely assumed. This apparent inconsistency is therefore likely to be of little consequence.

The problems so far discussed are relatively minor. However, the use by Dunbar (1992a) and Williamson (1997) of the standard deviation of the observed dependent y variable in the calculation of z scores is a more serious concern. This standard deviation is not a true reflection of the variability relevant to the difference between the observed and predicted value. Once values have been substituted into a regression equation the variability of the y value is constrained (Sokal & Rohlf 1981). The appropriate values to use are the standard errors of the predictions. These will be less than the standard deviations of the original y values values and will therefore produce larger z scores. Larger z scores will lead to lower probabilities being calculated for Fisher's test and thus a greater likelihood of rejecting the null hypothesis that the observed and predicted values do not differ significantly.

Moreover, since the true population variability is not known, the *t* statistic should be used rather than z scores. The appropriate degrees of freedom to use with this *t* value are the residual degrees of freedom associated with the multiple regression equation fitted for each time budget component (found in the ANOVA table produced for the multiple regression for each time budget component).

The new procedure outlined in the next section (8.4.2) addresses these last three points, by using transformed data, standard errors of prediction and the *t* statistics. However, a further two issues, not solved by this new method, are worth considering.

Firstly, the independent combination of results means that the testing procedure fails to pick up any trends among the new data points that taken together might indicate a difference from the existing predictive equations. However, with only four new points, developing a new procedure which takes this into account is not possible.

Secondly, the probability of making a type II error (accepting a false null hypothesis) is of more interest in relation to these tests than the probability of making a type I error (rejecting a true null hypothesis). The probability of making a type I error is defined by the significance level; for the studies considered here this is 5%. The probability of making a type II error is generally harder to calculate or, as under the circumstances for testing the functional equations, not possible. The probability of making a type I error and the probability of making a type II error are not simply related (Sokal & Rohlf 1981). Improving this aspect of the testing procedure is thus constrained by the philosophical approach of traditional hypothesis testing statistics and our inability to calculate the probability of making a type II error.

8.4.2 Review of Procedure: Bronikowski & Altmann

Bronikowski & Altmann (1996) tested the functional equations by evaluating whether they accurately predicted year to year variation in the time budgets of three groups of baboons in Amboseli. They concluded that the observed and predicted data differ significantly and thus the equations are not biologically useful. However, as outlined below, the statistical procedure that they used is invalid and the data not sufficiently comparable, to that used to generate the equations, to be an appriopriate test.

Firstly, the statistical procedure used by Bronikowski & Altmann (1996) was a chi-squared goodness-of-fit test which they used to compare observed and predicted time budgets.

However, they appear to make the fundamental error of using percentage data in this test. Chi-squared tests are only valid for frequency data (Sokal & Rohlf 1981).

Secondly, the data used by Bronikowski & Altmann (1996) are not comparable with that used to generate the functional equations for two main reasons:

1. The data used to generate Dunbar's original equations were generally derived from different populations. Studies carried out on the same population were included only if they were "undertaken at least 5 years apart and there had been a significant change in group size or climate between the two studies" (Dunbar 1992a:35). Bronikowski & Altmann (1996) applied the equations to variation from one year to the next in a single population.

2. Although Bronikowski & Altmann (1996) state, in reference to the time budget data in Dunbar (1992a) that "each population was represented by a single group" this is in fact not so in several cases. Referring back to the source literature, it is evident that Dunbar's (1992) figures are based on data from the mean values for group size and time budget components when data from more than one group are available. For example the time budget components in Dunbar's (1992; his table 2) for Mt. Assirik are the mean of the values for two groups (see Sharman 1981 his table 3, chapter 4). Bronikowski & Altmann (1996) applied the equations to data from three co-existing groups separately. Moreover, one of these troops was a garbage raiding troop. Food in garbage pits is characteristically in discrete, easy to locate, regularly replenishing, high quality patches (pers. obs.). These characteristics are determined by human activity and not subject to the same environmental constraints as naturally occurring food. The functional equations have been developed from data collected on groups feeding on resources influenced by climate and other ecological factors. We should, therefore, not expect the time budgets of baboons feeding on garbage to be described by these equations.

Bronikowski & Altmann (1996) suggest that "baboons use a suite of interrelated responses to ecological variability that includes not only changes in activity budgets, but also home range shifts, changes in active period, and changes in group size through fissions" (Bronikowski & Altmann 1996:11). This is undoubtedly true but, the aim of the functional equation approach used by Dunbar (1992a) and Williamson (1997) is to explain broad scale variation in relation to gross variation in ecology and demography. Therefore, even if they were statistically valid, Bronikowski & Altmann's (1996) findings cannot be taken as evidence that the functional equations do not work. Although Bronikowski & Altmann (1996) raise some valid and useful concerns over work done by Dunbar (1992a), none of these justify abandoning the functional equation approach in the way intended by Dunbar (1992a).

8.4.3 Revised Procedure Proposed

The following revised procedure addresses the most serious problems discussed in the previous section (8.3). :-

a. Find the difference between the natural logs of the predicted and observed values.

b. Divide this difference by the standard error of the prediction to obtain a value for *t*.

c. Find the 2 tailed probability associated with this value of *t* using the degrees of freedom indicated for the residual in the ANOVA table (n-p-1; where n is the sample size and p is the number of independent variables in the regression equation).

d. For each time budget component, perform Fisher's test for combining probabilities from independent tests of significance ($\chi^2 = -2\Sigma \mathrm{Ln}P$, df = number of tests x 2; Sokal & Rohlf 1981) to get a single probability for each set of equations. (The null hypothesis being that the observed and predicted value do not differ significantly.)

8.4.4 Revised Procedure in Use

The revised procedure described in section 8.4.2 was used with two sets of equations: Firstly, the set of equations in Dunbar (1992a) referred to as set D92 in Table 8.1 were tested. This was done in order to compare the results of the original and revised testing procedures. Secondly, the revised test was applied to the set of equations I produced from the same dataset (Table 8.2).

For my equations, predictions for the four subsidiary sites and their standard errors were generated using SPSS while carrying out stepwise multiple regression procedures. For the D92 equations predictions were generated by substituting values into the published formulae using an Excel 97 spreadsheet constructed for this purpose. The standard errors of these predictions were estimated by taking the mean for each behaviour of the standard errors of the predictions generated by my equations. For both sets of equations, Excel 97 spreadsheets were used to carry out the testing procedure. Observed data were taken from Dunbar (1992a, his table 2).

The results of the tests for the D92 equations using the original testing procedure indicate that predicted and observed values are significantly different only for moving (Table 8.4: original method D92 with Badi). For the revised procedure significance was obtained for feeding, moving and resting (Table 8.4: revised method D92 with Badi).

However, there are two reasons, introduced in section 8.4.1, that suggest that the Badi data should not be used in the testing procedure. Firstly, the data may be seasonally biased because it is a relatively high temperature habitat. Secondly, observation conditions are likely to have led to an underestimation of moving time (Dunbar 1992a). Without the Badi data, the predicted values generated by the D92 are not significantly different from the observed values for feed feeding and resting as well as socializing (Table 8.4: revised method D92 without Badi).

The results of the test on the equations I generated (Table 8.4: revised method DH with Badi) indicate that predicted and observed values are significantly different for moving and socializing. However, significant results were only obtained for moving when Badi was excluded (Table 8.4: revised method DH without Badi).

In conclusion, I contend that the old method, using standard deviations and z scores, is invalid and the use of the Badi data is not appropriate. The revised procedure produces probabilities below the significance level more often than this old procedure but, the exclusion of the Badi data compensates to a certain extent. Consequently, the proportion of significant results using the new procedure without the Badi data are the same as that obtained using the old procedure with the Badi data. Dunbar (1992a) and Williamson (1997), have set a precedence for accepting this proportion of significance as supporting the validity and biological usefulness of these equations, given that one in twenty results would be below a 5% significance level purely by chance. However, we must consider that this may be insufficiently cautious given the weaknesses to the hypothesis testing approach discussed at the end of section 8.4.1.

8.5 INTERPRETING THE EQUATIONS

If we accept that the functional equations do have reasonable abilities of prediction, the variation apparent between the different versions of the equation (Table 8.1 & 8.2) is of concern. However, it is reassuring to see certain commonalities in the nature, direction and strength of different explanatory variables (remembering the *a priori* statistical dependence of two meteorological independent variables: number of dry months (V) and total annual rainfall (P), as mentioned in section 8.3.1). In this section, these common features are identified and possible underlying causal mechanisms discussed.

Bronikowski & Altmann (1996) state that because coefficients in a multiple regression are partial regression coefficients, "the signs of these coefficients cannot be interpreted as indicating the direction of the univariate effect" (Bronikowski & Altmann 1996:17). However, the sign of a partial coefficient does indicate the strength and direction of influence of its independent variable under the condition that all other explanatory variables remain constant. This holds even when variables are log transformed because this is a monotonic transformation. It is true, however, that it's difficult to say by how much the dependent variable will change just by visually inspecting an equation based on logged values.

The predictive abilities of the equations may, or may not, indicate an underlying causal mechanism (Dunbar 1992a). However, causal mechanisms are easily postulated and will be discussed in relation to the common features of the functional equations in the following paragraphs.

Day journey length increases with increasing group size and decreases with the dryness of the habitat (decreasing P or increasing V). The relationship between group size and day journey length is easily explained. If each individual has to forage over approximately the same area, then larger groups will have to travel farther. With respect to dryness, this could be a reflection of poorer quality and/or more patchily distributed food or of more sparsely distributed water. Moving responds in a similar way to day journey length, going up with group size and down with increasing dryness of the habitat. The underlying reasons for this are likely to be similar.

The Simpson Index (Z) and temperature (T) are common to all feeding equations in Table 8.1. Temperature does not appear in my equation but, the R^2 value is low compared to the other versions. Feeding goes up with decreasing temperature (at least below 30 degrees Celsius) and decreasing evenness of rainfall (i.e., increasing seasonality). (NOTE: Since Z is always less than 1 the log of Z will be negative i.e., the effect of Z on feeding is negative not positive). The mechanism which links feeding and temperature may be direct (via thermoregulatory costs) or indirect (via temperature effects on food quality). In Chapter 6, it was proposed that the Mikumi baboons keep their feeding time to a minimum in order to minimize a variety of costs, including thermoregulatory ones. That they feed longer in the dry season reflects the lower food measures at this time of year. This effect is likely to be greater in more seasonal habitats, leading to higher mean annual time spent feeding. The constraining effect of thermoregulatory costs in higher temperature habitats will lead to an interactive effect of seasonality and temperature: the more seasonal a habitat the more potential for the effect to occur, the hotter a habitat the more likely it is to manifest itself.

Common strands between the equations for resting and socializing are harder to identify, although feeding appears as a relatively strong, or only, explanatory variable in a number of cases. Since feeding typically takes the major proportion of a baboons active period and this active period is limited by daylength, it is not surprising that the time budget for other behaviours is predicted by the amount of feeding. However, that feeding appears in the equations for resting and socializing but not the equation for moving, supports the idea that resting and socializing are reservoirs from which time can be diverted, up to a point, to priority behaviours of moving and feeding. It is hard, however, to draw any meaningful inferences regarding the relationship between climate and group size and these time budget components. This is despite the relationships one might expect; such as more resting at higher temperatures or more socializing in larger groups. Perhaps such relationships manifest themselves only secondarily under the constraining effect of feeding time.

8.6 SUMMARY

The data and procedures used to generate the functional equations suffer certain constraints and assumptions. Increasing the size and quality of the dataset used to generate the equations would be particularly desirable. Nevertheless, they do an adequate job of predicting values at independent (subsidiary) sites according to criteria set by previous authors (Dunbar 1992a, Williamson 1997) and, at present, represent the most statistically and biologically acceptable way of relating time budgets, group size and climate across populations. However, these criteria are lenient and it is premature to embed them in more complex models at this stage.

The procedures used by previous workers to test these equations, on the other hand, are seriously flawed. The revised procedure proposed to address this problem required generating a new set of equations. These equations have a number of features in common with previous versions which are suggestive of underlying causal relationships of behaviour with group size and climate.

In short, this Chapter reaches three main conclusions:

- The approach originally developed by Dunbar (1992a) to relate time budget components to group size and climate using stepwise multiple regression can be accepted with caution but should not, at this stage, be used for or embedded in more complex models.
- The approach used by Dunbar (1992a) and Williamson (1997) to test the predictive abilities of the equations is statistically flawed but can be modified to produce the acceptable method developed in section 8.4.3.
- Bronikowski & Altmann's (1996) work to test predictive abilities of the equations is flawed both through the statistical invalidity of their testing procedure and through the use of inappropriate data. Thus, their work does not provide evidence that the functional equations are not applicable to variation in time budgets at a single site.

CHAPTER 9. LONG-TERM CHANGES

9.1 INTRODUCTION

9.1.1 Aim

This chapter explores variations, in individual time budgets and day journey length of adult yellow baboons, between three separate studies carried out in consecutive decades (1970s, 1980s, 1990s) in Mikumi National Park (Table 9.1). The aim is to relate this variation to group size and climate patterns.

Functional equations, initially developed by Dunbar (1992a), indicate that a significant amount of the variation in time budgets and day journey length between populations can be accounted for by group size, quantity and seasonality of rainfall, and temperature (section 2.6; Chapter 8). In this chapter, the set of functional equations presented in Chapter 8 Table 8.2, is used to predict time budgets and day journey length for each of the three Mikumi studies. Discrepancies between predicted and observed values are discussed in relation to possible short comings of the equations and special features of the Mikumi ecosystem.

Table 9.1 Summary of three studies of the Mikumi baboons generating individual time budget data.

PRINCIPLE INVESTIGATOR	PERIOD OF DATA COLLECTION	TROOPS STUDIED	SOURCE OF INFORMATION
Denis Rasmussen	1970s: March 1975-October 1976	V0	Rasmussen (1978) Dunbar (1992a)
Guy Norton	1980s: June 1980-June 1984	V1, V2* & V3	G.W. Norton (unpublished data) & pers. comm.
Dawn Hawkins	1990s: June 1993-June 1995	V1, V2 & V4	This study

* data collected by Norton for V2 were not used in this study.

9.1.2 Background on Mikumi Studies

Details of the period of data collection and sources of information on the three studies considered in this chapter are given in Table 9.1. Neither Norton nor Rasmussen were interested in individual time budgets per se but, collected these data as part of their studies on other questions. Rasmussen studied the environmental and behavioural correlates of changes in range use (Rasmussen 1978a, 1978b, 1979, 1983) while Norton's study considered home range use and leadership (Norton 1986, G.W.Norton unpublished data).

As already mentioned in section 8.2, the individual time budget data collected by Rasmussen were included by Dunbar (1992a) in his original dataset (Dunbar 1992a: his table 2). Long-term records and observations made at the time (G.W.Norton pers. comm.) indicate that the mean day journey length during Rasmussen's study was between 5-6km per day. Dunbar (1992a) gives a value of 3.4km. It is almost certain that the figure reported is in miles and that the actual day journey length at this time was 5.5km. The functional equations have been shown to be robust to minor errors in the data (Williamson 1997) and I found that correcting this figure made little difference to the day journey length equation (Table 8.2 note 2).

Rasmussen's, Norton's and this study all conform to Dunbar's criteria for being considered independent samples: "Studies carried out on the same population were considered to be independent samples provided they were undertaken at least 5 years apart and there had been a significant change in group size or climate between the two studies" (Dunbar 1992a:35). Since the latter two studies are not part of the dataset used to generate the functional equations, they can be used as independent samples with which to test the equations in the same way that data from Awash, Badi, Metahara and Gilgil were used by Dunbar (1992a; see also section 8.4).

9.2 METHODS

A comprehensive description of raw data collection is given in Chapter 3. Chapter 3 also includes definitions of behaviours (Table 3.6). This section contains only additional methodological information relevant to the analyses performed for this chapter.

9.2.1 Group Size & Climate

Data on group size (section 3.3.1 and Figs. 3.3 and 3.4) and climate were taken from long-term records.

9.2.2 Time Budgets

The mean annual values of the main time budget components (feeding, moving, resting and socializing) only were used in analyses. Data for the 1980-4 study were provided by G.W.Norton (unpublished data). Data for Rasmussen's study come from Dunbar (1992a).

The methods of data collection used in all three studies were similar (Chapter 3; Norton in prep; Rasmussen 1978) and conform to Dunbar's (1992a) criteria of being "obtained by some recognized bias-free sampling procedure" Dunbar (1992a:37). In summary, instantaneous records, using a 5 minute sampling interval, were collected during individual follows lasting 45 minutes or longer. Individuals were sampled randomly across days and seasons.

Chapter 5 recommends that groups should only be compared if data were collected using compatible sampling decisions with respect to which individuals are included. As only values including both adult males and females were available for Rasmussen's study, data on all adults were used in the calculations by Norton and for this study.

For this study and for Norton's data, mean daily time budgets for complete annual cycles were calculated for each individual in three stages. Firstly, the means of follows in each period of the day (Table 3.8) were calculated by season (wet and dry). Secondly, the means of the four periods were determined for each individual. Finally, the means of wet and dry season values were calculated for each individual. Individuals not sampled in all periods within a season or not sampled in both seasons within a year were excluded from further analyses. Thus different periods and different seasons contributed equally to the final values controlling for the potentially confounding effects of temporal variation (Chapter 6).

To obtain mean time budgets for each study, values for individuals were averaged within groups for each year and, where appropriate (Norton's and first year of this study) values for different groups averaged within years to give a single value for each year. For multiyear studies (Norton's and this study) these annual values were then averaged across years.

9.2.3 Day Journey Length

Data for the 1980-4 study were provided by G.W. Norton (unpublished data). Data for Rasmussen's study are modified from Dunbar (1992a) based on long-term records and observation around the time of his study (section 9.1.2).

Day journey lengths for this study were calculated from long-term records of the Mikumi baboon project (G.W.Norton & S.K.Wasser unpublished data). The minimum distances between the centre points of the small grid squares (180m x 180m squares; section 3.2.4) in which the troop was recorded at half hour intervals were calculated. This variable was labelled "shift". The mean shift for each half hour period between 8:00 and 16:30 was calculated for each troop, by year and quarter. These values were then summed to obtain each troop's day journey length. Mean annual day journey lengths were determined by taking the mean of quarterly values. In this way different seasonal quarters contributed equally to the final values. The same method was used by G.W.Norton (pers. comm.) Rasmussen's (1978) field methods were similar but based on the large grid squares (720m x 720m squares; section 3.2.4).

9.2.4 Statistical Analyses

The 1964-1996 rainfall data were analyzed using regression and time series autocorrelation (SPSS 1993).

Kruskall Wallis tests of difference were used to compare climate and group size for the three periods during and immediately prior to each study. The test for group size was done with both study group and study population means (i.e., without and with V2 for Norton's study). Sample sizes for all tests are given in the text. The possibility of obtaining a significant result at the 0.05 level was checked in all cases. For example a significant result can not be obtained with a Kruskall-Wallis test with sample sizes of 3, 2 and 1.

However, with sample sizes of 1, 3 and 3, probabilities of 0.05 can be obtained (Siegel & Castellan 1988).

With a sample size of 3, a Spearman rank correlation will not produce a significant result, at 0.05 significance level, even if the three values are perfectly correlated (Siegel & Castellan 1988). Thus correlations were not be performed across the three studies and only a visual assessment of any trends could be made.

Two sets of predictions were generated from the set of equations presented in Table 8.2; one by substituting long-term (mean for 1964-1996 including flood years; Table 9.2) climate data into the equation, the other by substituting in study specific climate data (Table 9.3). Standard errors for each prediction were also generated.

Predicted and observed values for the 1980s and 1990s data were compared statistically using the revised procedure proposed in Chapter 8 (Section 8.3.3). Rasmussen's data, from the 1970s, were part of the dataset used to generate the functional equations and, therefore, could not be used in the testing procedure.

Table 9.2 Long-term climatic data.
1946-1961 values from Williamson (1997 who cites Anon 1984). 1964-1996 values from park or ABRU records (Norton 1994b; unpublished data)

YEARS	Total annual rainfall (mm)	Number of months <50mm rain	Simpson Index	Shannon Index	Mean min. daily temp.	Mean max. daily temp.	Mean of daily min. & max. temp.
1946-1961	851	6	0.86		18.6	30.1	24.4
1964-1996	860 787*	6.26 6.46*	0.82 0.81*	0.75 0.75*	18.9	31.7	25.3

*excluding flood years

Table 9.3 Climatic conditions just prior to and during the three study periods. Data from park or ABRU records. Group size on the 1st June, means rounded to nearest whole animal. Mean study group size = mean group size of groups from which data were used for this study (number of groups in brackets.) Mean group size = mean group size of groups in Viramba study population (number of groups in brackets.)

ECO. YR. (start)	Total rainfall	Number of months <50mm rain	Simpson	Shannon	Mean min. daily temp.	Mean max. daily temp.	Mean of daily min. & max. temp.	Mean study group size (n)	Mean group size (n)
1975 (Dec 1974)	850.31	7	0.79	0.76				99 (1)	99 (1)
1976 (Dec 1975)	588.26	7	0.81	0.72	19.9	31.6	25.8	113 (1)	113 (1)
Mean 1975-1976	**719.29**	**7**	**0.80**	**0.74**	**19.9**	**31.6**	**25.8**	**106 (1)**	**106 (1)**
1980 (Dec 1979)	870.84	5	0.85	0.79				44 (2)	49 (3)
1981 (Dec 1980)	741.66	6	0.83	0.79	18.0	33.8	25.9	45 (2)	53 (3)
1982 (Dec 1981)	700.03	5	0.86	0.84	18.7	33.5	26.1	45 (2)	52 (3)
1983 (Dec 1982)	697.48	8	0.79	0.73	19.0	32.6	25.8	44 (2)	51 (2)
1984 (Dec 1983)	1222.30	4	0.86	0.83				43 (2)	50 (3)
Mean 1980-1984	**846.46**	**5.6**	**0.84**	**0.80**	**18.6**	**33.3**	**25.9**	**44**	**51**
1993 (Dec 1992)	825.30	6	0.82	0.72	18.2	30.3	24.3	22 (2)	22 (2)
1994 (Dec 1993)	767.08	6	0.79	0.72	18.7	31.5	25.1	14 (2)	13 (2)
1995 (Dec 1994)	809.96	6	0.81	0.73	18.4	31.5	25.0	24 (1)	24 (1)
Mean 1993-1995	**800.78**	**6**	**0.81**	**0.72**	**18.4**	**30.8**	**24.8**	**20**	**20**

9.3 RESULTS

9.3.1 Climatic Patterns

Rainfall data for Mikumi National Park since 1963 were used to calculate total annual rainfall, number of months per year with less than 50mm of rain, Shannon Index of (annual) rainfall diversity, and Simpson Index of (annual) rainfall diversity (Bronikowski & Webb 1997, Chapter 4).

While there is considerable year to year variation in annual rainfall, there appears to be no consistent linear trend up or down. Norton (1994b) analyzed the data to 1993 and found no statistically significant linear trend. This finding is not altered when the data are reanalyzed including the additional two years of this study (Fig. 9.1; regression of total rainfall against ecological year B_1=-0.72, t=-0.194, p=0.86). The mean values for the period 1963-1995 are similar to those reported by Williamson (1997) for the period 1946-1961 which suggests Mikumi has experienced a similar rainfall for at least 50 years (Table 9.2).

The total annual rainfall or diversity of rainfall during and immediately prior to the three study periods under consideration in this chapter (Table 9.3) did not differ significantly, although the result for the Shannon Index is suggestive (Kruskall Wallis tests df=2, n=2,5,3 in all cases: rainfall χ^2=0.3055, p=0.86; months less than 50mm χ^2=2.9647, p=0.23; Simpsons index χ^2=3.6148, p=0.16; Shannon index χ^2=5.6642, p=0.06).

There is some indication of a cyclic pattern in total annual rainfall. The coefficient for 9 years of lag falls just outside the lower 95% confidence limit (Fig. 9.2). As this is a negative correlation it suggests a 18 year cycle. However, by chance we would expect 1 in 20 estimated values to fall outside these limits by chance alone and there are 16 estimated values in this figure. What is more striking is the wave-like pattern in the coefficients themselves indicating a 6 year cyclic pattern in autocorrelation coefficients (Fig. 9.2). Interestingly, Rodgers (1979) reports possible 6-10 year cyclic patterns in the annual rainfall of the adjacent Selous Game Reserve.

Norton (1994b) points out that even if there are no overall trends in climate, certain years, at the extremes of the normal variation, may have important acute effects. It is worth noting in this context that 1976 (during Rasmussen's study) was a particularly dry year (<600mm) and 1984 (the final year of Norton's study) was a flood year (>1000mm). These extreme conditions could be part of the cyclic pattern mentioned above.

Since the data on temperature in Mikumi National Park is far less complete than that for rainfall, similar long-term analyses cannot be performed. Complete data for full annual cycles (ecological years) are available for only seven years (1976, 1981, 1990-1993, 1995). The mean for temperature for these years was 24.87+/- 0.74. This is very similar to the mean reported by Williamson (1997) for the period 1946-1961 (Table 9.2). Statistical analysis provides no evidence that temperature during the study periods under consideration in this chapter (Table 9.3) differed significantly (Kruskall Wallis test df=2 n=1,3,3; χ^2=4.87, p=0.09).

Figure 9.1 Annual rainfall, based on ecological year, in Mikumi National Park from 1965 to 1995. RAIN = total annual rainfall (mm). ECOYEAR = ecological year.

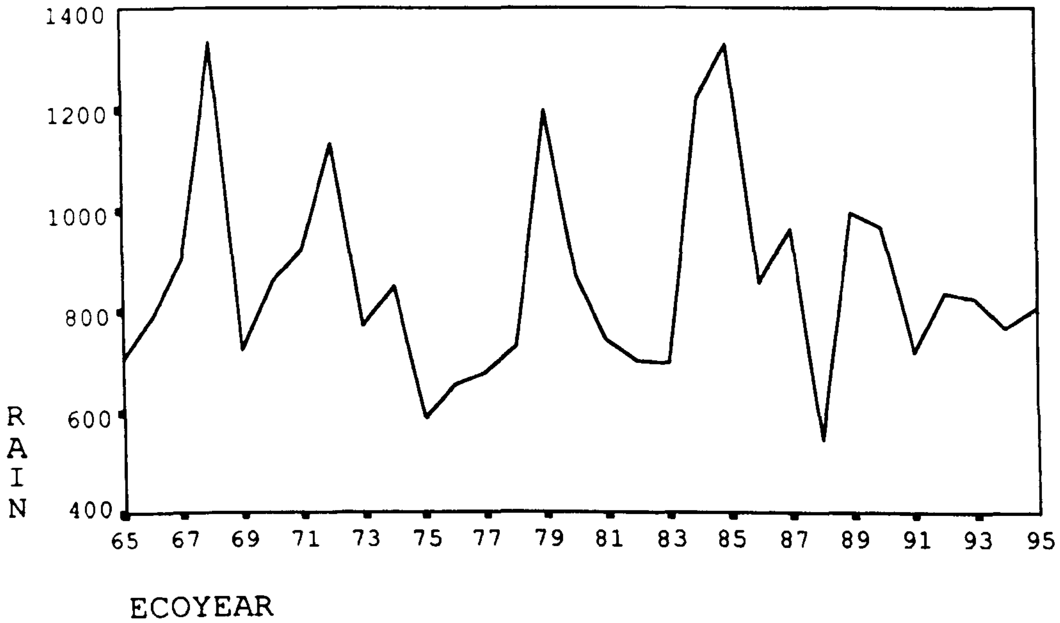
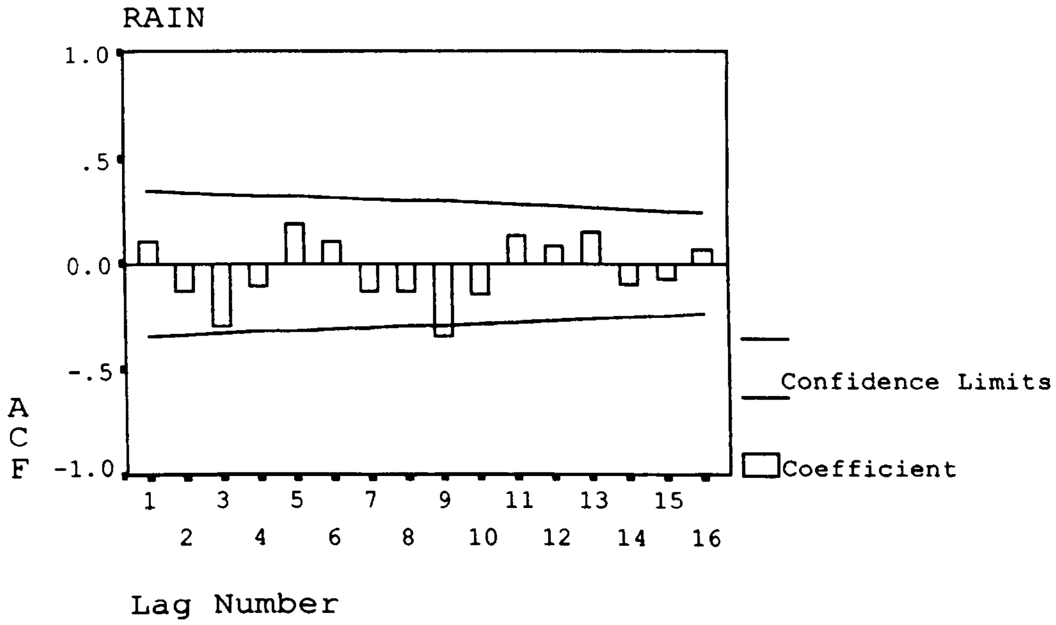


Figure 9.2 Autocorrelation time series analyses on annual rainfall in Mikumi National Park. The bars indicate the autocorrelation coefficients for different time lags of the data. The lines indicate the 95% confidence limits (calculated by SPSS; SPSS 1993) of the autocorrelations coefficients around zero. Where the bars fall within the lines the null hypothesis that the true value of the coefficient is zero can be accepted.



9.3.2 Group Size

Group size varied dramatically between the three studies (section 3.3.1.1). Values for group size on the first of June for each study year are given in Table 9.3. In summary, the Viramba study subpopulation was made up of the following:

- during Rasmussen's there was one large (>100) troop;
- during Norton's study there were two medium (65-75) troops and one small (<25) troop (although only data from one medium, V1, and one small troop, V3, were available for this thesis);
- during this study there were two very small (< 15) which fused to form a small (<25) troop.

Unlike the climatic variables considered in the previous section, the mean group size of the study population during and immediately prior to the three study periods under consideration in this chapter did differ significantly. Statistical results for just the study groups were identical to those on all Viramba groups (Kruskall Wallis tests df=2, n=2,5,3: χ^2=7.64, **p=0.02**).

9.3.3 Time Budgets

Figure 9.3 presents individual time budgets, averaged across groups and years (Table 9.4), for each of the three studies. The only consistent trend is for moving. Time spent moving decreased from one decade to the next. Feeding time changed very little and the most noticeable feature of social time is that it was considerably lower for Rasmussen's study.

Visual inspection of Figure 9.3 indicates observed and equation predicted values are relatively close in most cases, even taking in to account that the y axis is a (natural) log scale. The most notable exception is for time spent socializing in 1970s; the observed value is much lower than the predicted values. However, statistical testing using the 1980s and 1990s data, found that observed and predicted values differed significantly for all time budget components, except socializing (Table 9.5), whether long-term or study specific climate data were used.

Table 9.4 Time budgets by study based on all individuals sampled - see text for details of calculations. Group sizes as of 1st June. PI = principle investigator.

				TIMEBUDGET				
PI	**YEAR (S)**	**MEAN GROUP SIZE**	**DJL (km)**	**FEED**	**MOVE**	**REST**	**SOCIAL**	**TOTAL**
Rasmussen 1990s	1975-6	113	5.5	36.5	26.1	25.0	5.9	93.5
Norton 1980s	1980-4	44	4.5	41.7	20.4	20.0	9.3	91.4
Hawkins 1990s	1993-5	18	3.9	41.1	15.9	33.2	9.1	99.2

Table 9.5 Results of Fisher's test for combining probabilities from independent tests of significance. Results substituting both study specific (Table 9.3) and 1964-1996, including flood years, long-term (Table 9.2) climate data in to the functional equations given Table 8.2, are given. Sum = sum of natural logs of 2 tailed probabilities derived from *t* statistic ($\Sigma \ln P$). Significant p-values ($\alpha = 0.05$) shown in bold. Degrees of freedom for all tests = 4.

		DJL (km)	**TIME BUDGET**			
			FEED	**MOVE**	**REST**	**SOCIAL**
Study specific	sum	-11.63	-13.85	-13.85	-11.86	-2.25
	χ^2	23.26	27.70	27.70	23.72	4.49
	p	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.34
Long-term	sum	-11.93	-9.38	-13.99	-11.86	-2.77
	χ^2	23.85	18.77	27.99	23.72	5.54
	p	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.24

Figure 9.3 Observed and predicted time spent in different activities during three studies. Observed values plotted as bars; predicted values plotted as points. Error bars indicate standard error of each prediction.

...PRED = predicted values generated by substituting study specific climate data (Table 9.3) *in* to the functional equations given *in* Table *8.2.*

...PRED2 = predicted values generated by substituting *1964-1996, including flood years,* long-term climate data (Table 9.2) in to the functional equations given in Table 8.2.

Fig. 9.3a FEEDING

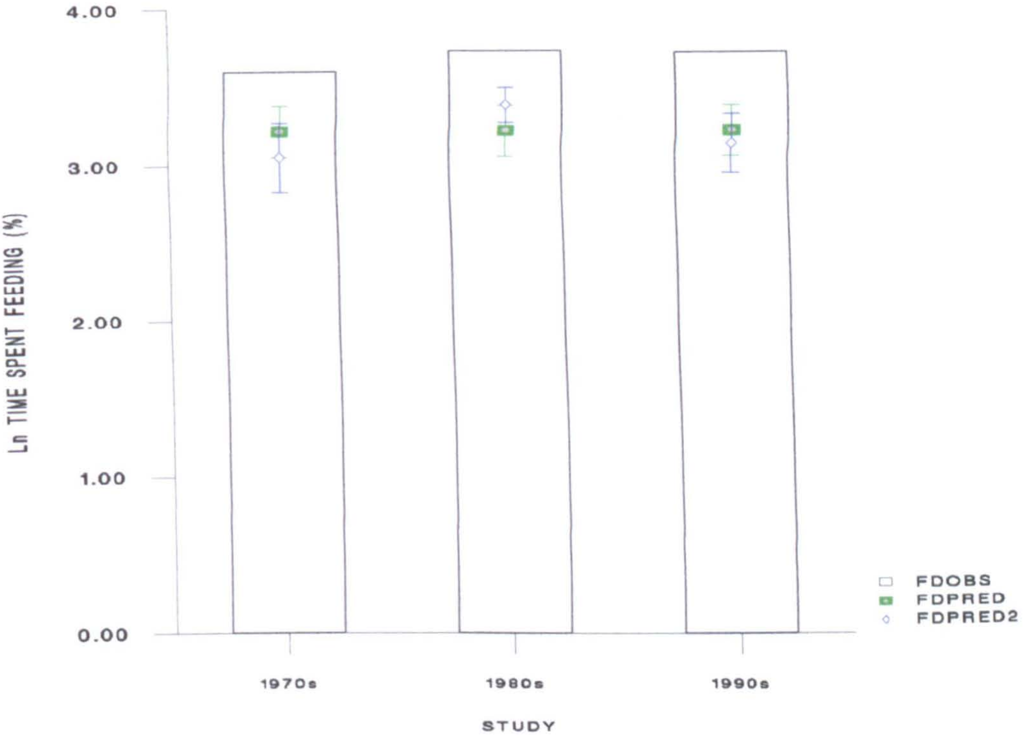


Fig. 9.3b MOVING

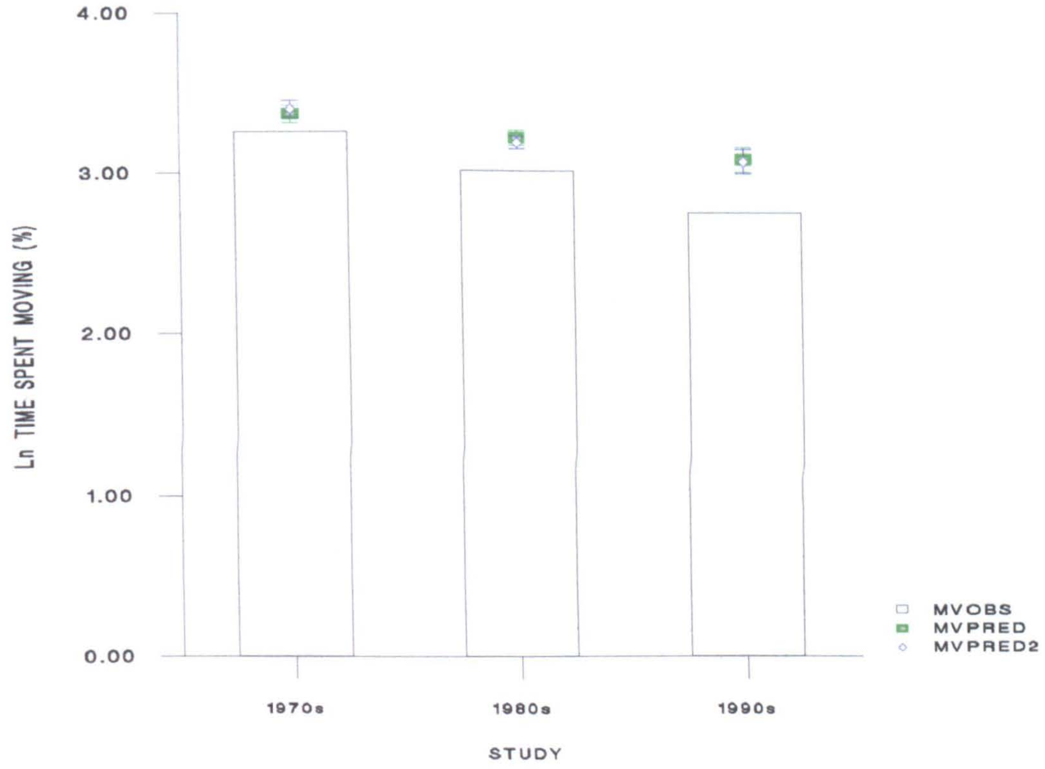


Fig. 9.3c RESTING

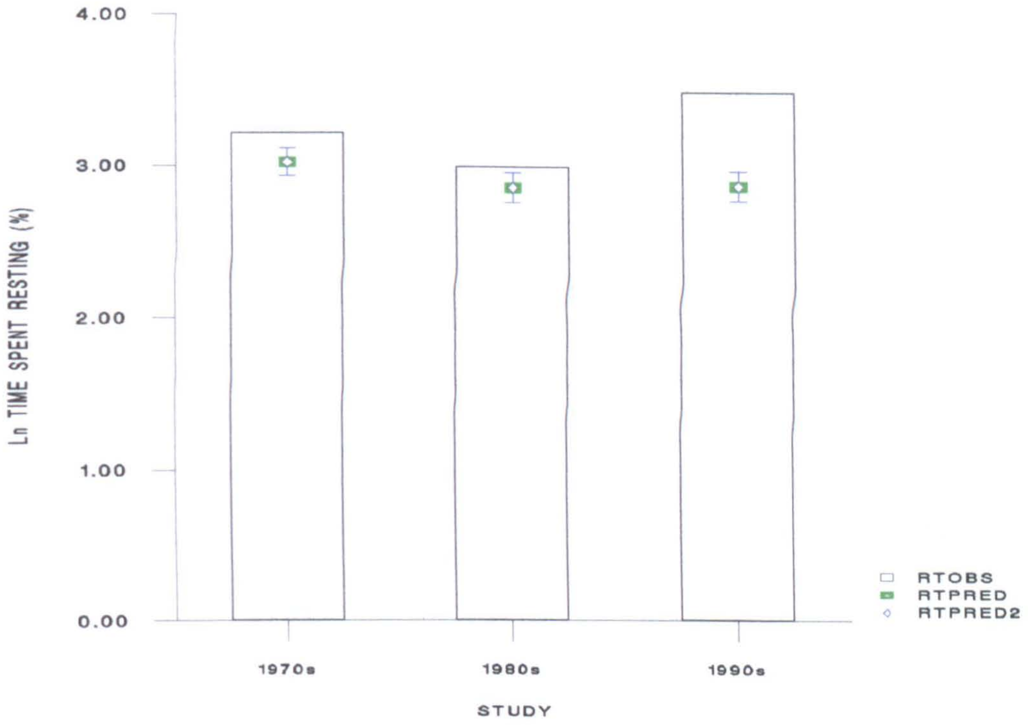
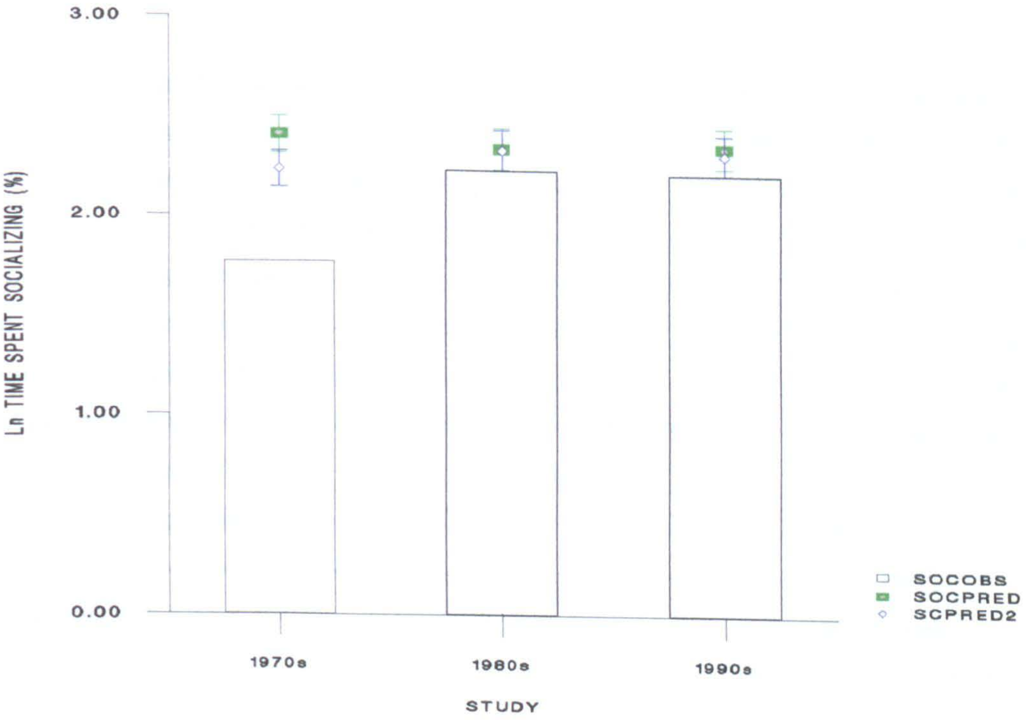


Fig 9.3d SOCIALIZING



9.3.4 Day Journey Length

Figure 9.4 presents day journey lengths, averaged across groups and years (Table 9.4), for each of the three studies; there is a consistent downward trend.

If we assume that day journey length is largely a reflection of movement between patches, the distance travelled can be used to estimate the time spent moving between patches. For example, if baboons move between patches at a speed of 4km per hour, then time spent moving between patches can be estimated by dividing day journey length by 4. This can be converted to a percentage of a 10 hour daily observation period by multiplying by 10. The remaining time spent moving is accounted for by movement within patches. Using these figures, smaller troops are found to spend proportionally less time moving in patches than between them (Fig. 9.5). A speed of travel between patches of 4km per hour is a rough approximation based on personal observation. However, providing the speed of movement between patches is the same for all groups, then the finding that movement between patches is proportionately more important for smaller groups is unchanged. Thus the two key assumptions in this analysis are that day journey length reflects mostly movement between patches and speed of movement between patches is the same for all troops.

A consistent downward trend is shown by the predicted as well as the observed day journey lengths but, observed and predicted values increasing diverge from the 1970s to the 1990s. By the 1990s, the predicted value is much lower than the observed. Statistical evaluation, using just the 1980s and 1990s data, found observed and predicted values differed significantly (Table 9.5) whether long-term, or study specific climate data, were used.

Figure 9.4 Observed and predicted day journey length during three studies. Observed values plotted as bars; predicted values plotted as points. Error bars indicate standard error of each prediction.

...PRED = predicted values generated by substituting study specific climate data (Table 9.3) in to the functional equations given in Table 8.2.

...PRED2 = predicted values generated by substituting 1964-1996, including flood years, long-term climate data (Table 9.2) in to the functional equations given in Table 8.2.

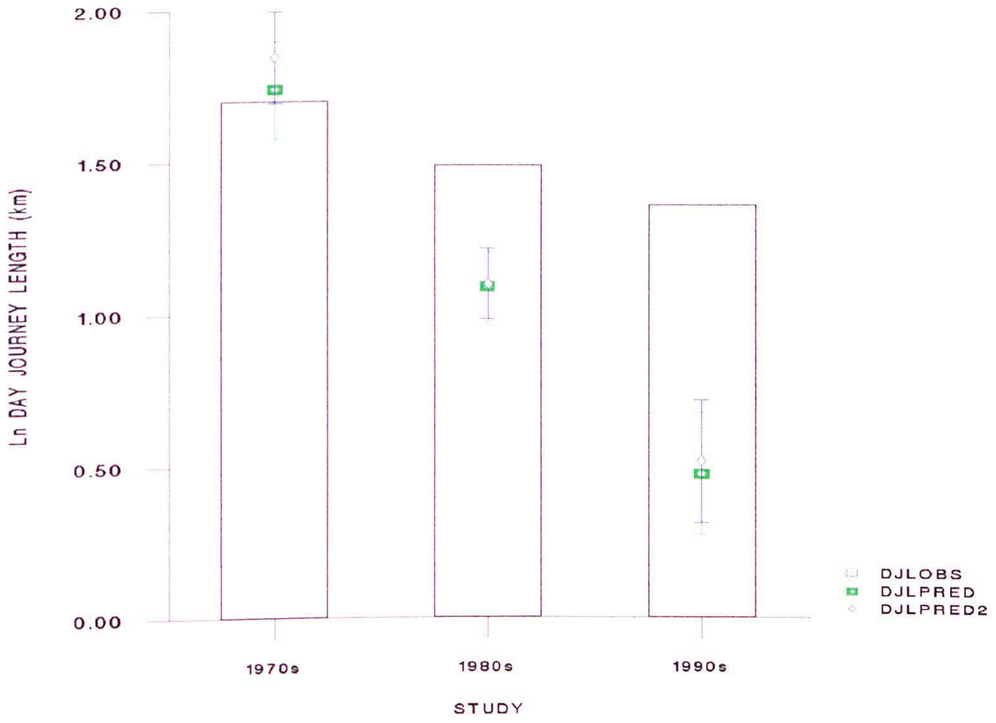
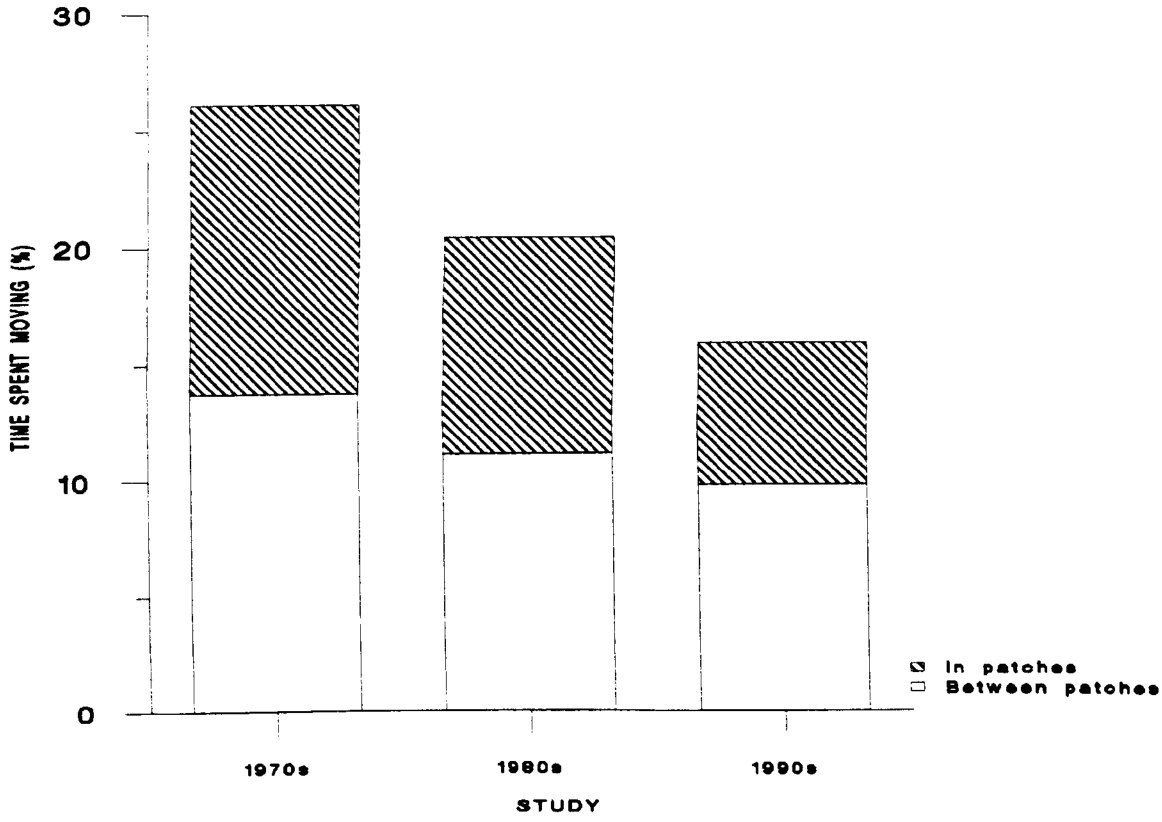


Figure 9.5 Contribution of movement within and between patches to overall time spent moving. Overall time spent moving calculated as percent of 10 hour daily observation period. Time spent moving between patches estimated from day journey length assuming a speed of 4km/hour.



9.4 DISCUSSION

9.4.1 Functional Equations

Qualitatively, the changes predicted by my equations (Table 8.2) match the observed changes in time budgets and day journey length. Climate during and just prior to the three studies was very similar; mean group size, however, declined rapidly. From the general features of the functional equations discussed in section 8.5, we would expect this decline in group size to be accompanied by decreases in moving and day journey length but that feeding should remain relatively unchanged. Increases in resting and/or socializing would be expected, for biological and mathematical (i.e., together feeding, moving, resting and socializing add up to approx. 100%), to accompany any decreases in these higher priority behaviours (feeding and/or moving) (section 8.5). The observed data conform to this general pattern. Moreover, visual inspection of Figure 9.3 reveals that observed and predicted values are relatively close, with two especially notable exceptions:
- day journey length in my study (1990s) being much higher than predicted;
- socializing in Rasmussen's study (1970s) being much lower than predicted.

However observed and predicted values generated by my equations are all statistically significantly different, except for socializing. Thus functional equations appear to predict changes in time budgets and day journey length in Mikumi qualitatively but not quantitatively.

There are a number of possible reasons for this lack of quantitative fit, for example:

1. Cyclic patterns in, and/or extreme years of, climate in Mikumi may be important in predicting baboon behaviour in a way not taken in to account by the equations or the data substituted in to them.

2. Some factor(s) may be responsible for variation in behaviour in a way not simply related to climate. Bronikowski & Altmann (1996) refer to such factors as "extraneous to meteorological models" (Bronikowski & Altmann 1996:23). In Chapter 4, fire and fruiting patterns were identified as two potentially extraneous factors in Mikumi; other possibilities include disease, parasite load and predator-prey relationships. The cause of the major population decline (section 3.3.1.2) between Norton's and my studies could fall into this category.

3. The problems with the data and procedures used to generate the equations discussed in the previous chapter may result in them being insufficiently sensitive to predict changes within sites, even if Dunbar's (1992a) criteria for independent samples are applicable.

Whether a result of inadequacies in the equations or special features of the Mikumi ecosystem, it appears that the functional equations cannot be applied to within site data of Mikumi. Bronikowski & Altmann's (1996) came to a similar conclusion regarding the application of the equations to within site data for Amboseli. However, as explained in Chapter 8, while their paper does draw attention to some important issues, it is not a valid assessment of the application of the equations in this way for a number of reasons. Firstly, the results of the chi-squared goodness-of-fit test they used to compare observed and expected values are invalid because they use percentages not counts (section 8.4.2). Secondly, their work focuses on detailed variation of individual troops (rather than means across troops) over a continuous period of 10 years (rather than studies at least 5 years apart with major changes in climate or group size). At this level, there are indeed many subtleties in the behavioural responses of baboon that will be missed by the broader approach of the functional equations. The functional equations are dealing with a much more coarse grain level of variation. As Bronikowski & Altmann (1996) themselves acknowledge "the options and constraints that pertain for individuals, groups, or populations, from moment to moment, daily, or on longer time frames, are not necessarily the same and may result in different relationships between ecological factors and behavioural response under these different conditions" (Bronikowski & Altmann 1996:23). In short, the equations don't work for Mikumi but the case for all other sites remains untested.

9.4.2 Group Size & Movement

The relationship between group size and movement appears to be consistent for all sets of function equations reviewed in Chapter 8 and for the observed changes in Mikumi: both time spent moving and day journey length decreased with decreasing group size.

Dunbar (1992a) proposes two mechanisms to account for a decrease in time spent moving in smaller groups: (1) if there are fewer individuals in a group they will have to travel to fewer patches in order to find sufficient food resources to feed all members; (2) if there are fewer individuals there will be less disturbance within patches. That day journey length, as well as time spent moving, decreased (Figs. 9.3b and 9.4) suggests that the first mechanism did operate in Mikumi. However, the relatively greater increase in time spent moving in patches compared to between patches (Fig. 9.5) implies that the second mechanism is more important.

To calculate how time spent moving was divided between travelling between patches and moving within them, it was assumed that time spent moving remain constant. This need not necessarily be the case, especially if groups are under time constraints (Dunbar 1992a). If travel speed had increased with decreasing group size this would have diminished, or even reversed, the trend found. If travel speed had decreased with decreasing group size this would have accentuated the trend found. Further investigation into the assumption that speed of movement between patches is the same for all troops and the other key assumption made for this analysis, that journey length reflects largely movement between patches, would be interesting.

The observed relationship between movement in and between patches, is a manifestation of the fact that group size has a stronger effect on time spent moving than day journey length. The functional equations on the other hand predict the opposite. The increasing divergence of the observed and predicted values for day journey length may be indicative of the root of the problem. Four studies in the main sample used to generate the time budget equations did not have day journey length data and were replaced by four alternative studies for which these data were available (but for which time budget data were not) to generate the day journey length equation. The mean of the group size of the four studies used only for time budgets was 46; the mean group size for the four studies that replaced them was 61. That smaller group sizes were less well represented in the dataset for day journey length may account for its poor performance of the day journey length equation at smaller group sizes.

The finding that increases in group size are accompanied by increases in movement, contrasts with that of Bronikowski & Altmann (1996) who found that distance travelled was negatively correlated with group size (their fig. 1). Again, this difference may be due to the temporal (consecutive years) and spatial (individual groups) scale of their data (section 9.4.1). Conversely, their versions of the functional equations for moving and day journey length are consistent; group size appears as a predictor variable with a positive coefficient. That is, if other predictor variables are constant, and group size increases so will the dependent variable.

9.4.3 Troop Fission

In 1978, two years after Rasmussen's study, the Viramba baboons split into two troop (V1 & V2). A year later V1 split into V1 and V3 (Fig. 3.3). The discrepancy between the observed and equation predicted time spent socializing (Fig. 9.3c) is likely to be related to these impending fissions. Spending such little time socializing, individuals would have been unlikely to be service relationships sufficiently to maintain group cohesion and thus fission would have been inevitable (Dunbar 1992a). But, the question is why were they spending such little time socializing.

One proposed explanation is that they were time constrained (Dunbar 1992a, 1996). In summary, the argument is that individuals in larger groups have to spend more time moving. They may compensate somewhat by travelling faster (Dunbar 1992a) but eventually they have to take time away from resting and/or socializing. However, resting and socializing are not unlimited reservoirs of unused time. Individuals cannot function if they don't spend a certain amount of time resting each day for thermoregulatory and other physiological reasons (Dunbar 1992a, 1988; Knight 1998; Secor & Jared 1997). For example, Bronikowski & Altmann (1996) tentatively propose that individuals must spend at least 15% of their time resting in the Amboseli habitat. Once this limit is reached time must be taken solely from socializing. The consequence of which will be that insufficient time is spent servicing social relationships in order to maintain group cohesion and thus fission ensues.

This time constraint hypothesis of fission leads to the prediction that individuals in a troop just about to undergo fission should be resting as near the minimum as possible and socializing less than expected. The latter, as already discussed, is consistent with Rasmussen's data. However, it seems unlikely that 25% represents the absolute lower limit of resting time in these animals.

It is possible that some methodology failing underlies the high level of resting recorded by Rasmussen e.g., if he recorded the animals as resting when they were in fact feeding (if the observer is not able to keep the face of the animal in view then ingestion and chewing can easily be missed). Alternatively, some other factor, such as spatial restrictions (spatial constraint hypothesis of fission) imposed by feeding on patchily distributed food, may have constrained the animals ability to service social relationships sufficiently to maintain cohesion of a large group.

Henzi et al. (1997) have shown that group sizes in savannah baboons in both the Drakensberg and Amboseli are adequately described by a model based on the assumption that the probability of fission increases with troop size. These authors consider their findings as support for the time constraint hypothesis but, increasing probability of fission with group size is consistent with both the time constraint and spatial constraint hypotheses. In the Drakensberg, food is not patchily distributed but because the amount of food available is low inter-individual distances are high e.g. 40m (Henzi et al. 1997) thus spatial constraints could still operate. The way to distinguish between the hypotheses is to compare observed resting time to minimal possible resting time. If observed resting time is considerably above the minimum this would be consistent with the spatial but not the time constraint model. Henzi et al. (1997) do not present resting times. Moreover, it is generally only possible, as Bronikowski and Altmann (1996) did, to roughly estimate minimum resting times.

9.5 SUMMARY

No linear trends in climate were detected but, mean group size declined dramatically from large (>100) during Rasmussen's study, through medium (65-75) during Norton's 1980s study to small (<25) during my 1990s study. This was accompanied by a decline in both time spent moving and day journey length but, time spent feeding changed little. Time spent socializing was much lower in the 1970s than during the other two studies.

A direct causal mechanism between group size and movement is likely with smaller groups having to travel to fewer patches and disturbing each other less once in these patches. As group size decreases the latter becomes relatively less important in causing movement.

Values generated by my set of functional equations provide an adequate qualitative but a poor quantitative prediction of observed patterns over the three decades. This may be due to an unrecognized influence of cyclic or extreme weather and/or the importance of factors extraneous to climate, in shaping the Mikumi ecosystem (e.g., fire, patterns of fruiting). It could also result from short comings of the functional equations as discussed in the previous chapter. Although the equations do not work for Mikumi, the case for other sites, including Amboseli, has still to be adequately tested.

The data support the proposal that lack of time spent socializing (i.e., insufficient time spent servicing social relationships) leads to group fission. However, the Mikumi data favour spatial, rather than temporal constraints, as the underlying causal factor.

CHAPTER 10. CONCLUDING DISCUSSION

10.1 INTRODUCTION

After outlining the special features of this study (section 10.2), this chapter goes on to review the main findings (section 10.3) as discussed in detail in each results chapter. The fourth section (10.4) considers the implications of these findings for the central theme of this thesis: the influence of variable environments and group size on the individual time budgets of baboons. Finally some ideas for future work in this area are discussed (section 10.5).

10.2 SPECIAL FEATURES OF THIS STUDY

This thesis is primarily about the amount of time primates spend in different behaviours during daylight hours. Both the constraints on, and consequences of, time budgeting by yellow baboons in Mikumi National Park have been explored. This has been done to gain a greater understanding of the Mikumi baboons and of the use and abuse of functional equations based on biogeographical patterns of time budgets in baboons (Chapter 8; section 2.6; Bronikowski & Altmann 1996; Dunbar 1992a, 1996; Williamson 1997).

Typically in primate field studies, only a single year of field work is carried out including a period of setting up. This leaves less than a full annual cycle of complete data collection (most studies cited in this thesis except e.g., Agetsuma 1995a; Bronikowski & Altmann 1996; Mitani 1989). Data for this study were collected for a period of just over two years for baboons and a little less for vegetation, excluding pilot work in previous years (Chapter 3). This was made possible because of the existence of the long-term research project in Mikumi and the contribution of many people, past and present. The long-term nature of the Mikumi baboon project also meant that data from two preceding decades (Dunbar 1992a; Rasmussen 1978; G.W. Norton unpublished data) were available for comparison.

Despite the relatively long duration of this study, the investigation of variability between consecutive years was still limited by sample size. At most, data from three years were available for comparison but in most cases only two. In addition, this study suffered sample size constraints related to the number of baboons involved. When the main period of data collection began there were fourteen adult females but, by the end of the first year, this number had dwindled to six. This meant that individuals in different groups had to be pooled and meaningful intergroup comparison could not be made. Work by Bronikowski & Altmann (1996) suggests that intergroup comparisons would be an interesting area for future research. In order to obtain a reasonable sample size, additional troops whose demographic and ecological histories would be much less well known than primary study groups, would have to be habituated.

10.3 REVIEW OF KEY FINDINGS

10.3.1 About the Baboons of Mikumi

10.3.1.1 Interindividual variation

An investigation of time budgets of adult baboons in relation to their sex, reproductive status, social rank and age found only two significant patterns. One was that females socialized more and rested less than males (sections 5.3.1). This supports the proposal that female baboons give greater priority to social behaviour than males because of the female bonded nature of the society. Moreover, it is consistent with the idea that resting is a reservoir of unused time that can be drawn upon if needed. (Table 5.1; section 5.4.1.1). The other significant result was that time spent feeding decreased with age (section 5.3.4). This is consistent with predictions based on knowledge of the effects of ageing on humans but this phenomenon has not been investigated in other wild non-human primates (Table 5.1; section 5.4.1.4). The lack of any significant difference between time spent feeding by males and females (section 5.3.1), despite the larger body size of the male, is consistent studies on a wide range of other primate species. A number of explanations for this have been proposed, including the burden of reproductive costs on females (Table 5.1; section 2.5.1.2).

Time spent moving showed little flexibility between individuals and this raises the interesting issue of what constraints are placed on the time budgets of individuals by group living (section 5.4.1.5). Time spent moving is made up two main components. There is movement to change location and there is movement to change position within a location. For example moving from a tamarind tree to a waterhole involves a change in location, while moving from one branch to another branch in the same tamarind tree involves a change in position. Given the kind of group in which yellow baboons live, the amount of time spent changing location must be very similar for all members of the troop; individuals must spend the same amount of time moving at the same rate in order for the troop to remain a cohesive unit. Once a new location has been reached individuals have more flexibility in their use of time.

In short, group living places special constraints on time spent moving. This could explain why inter-individual differences were not found for moving. It would be interesting to follow up this idea with an investigation of how time spent moving is divided between its two main components (i.e., change in location and change in position) in relation to intergroup variation. Such an investigation could also further test the finding, presented in Chapter 9, that change in location is a relatively bigger component of overall moving time in larger groups (as discussed in more detail in section 10.3.2.3).

10.3.1.2 Temporal variation & environmental constraints

Temporal variation in the time budgets of the adult females within days and within years was considerable (sections 6.3.2, 6.3.3 & 6.4.3). Although differences between years were rare, conclusions were limited by small sample size (section 6.3.1).

The study animals spent less time feeding and more time resting in the wet season (section 6.3.2). This matched seasonal patterns in food resources, which were generally better in the wet season (section 4.3.1.1 & 4.3.1.2). In contrast, patterns of time use throughout days showed a dry 2 and wet 1 versus wet 2 and dry 1 dichotomy (section 6.3.3). This coincided with within year variation in heat stress and poor visibility (section 4.3.1.3). Taken together these results indicate that minimum feeding time is determined by food resources but that the constraining effects of heat stress and poor visibility are instrumental in bringing about the observed within year variation in time budgets (section 6.4.2).

10.3.1.3 The predictive potential of rainfall

Within year patterns of shade, visibility and most aspects of food, were found to be associated with quarterly patterns of rainfall (section 4.3.3). Therefore, rainfall can be used as a broad surrogate for direct measurement of ecological factors within years in Mikumi. Fire is an important ecological factor in the Mikumi ecosystem but, since it covaries with rainfall within years (section 4.3.2.3), this does not undermine the predictive power of rainfall (section 4.3.3.2). However, one important factor that appeared not to be associated with rainfall was fruit and flowering and this could undermine the relationship between rainfall and behaviour in Mikumi (section 4.4.2).

Conclusions on the ability of rainfall to predict between year differences in time budgets were limited by small sample sizes. However, two factors which could potentially undermine a predictive relationship were identified. Firstly, between year variation of fruit and flowering in Mikumi was not associated with rainfall (sections 4.3.3.2 & 4.4.1). Secondly, variation in fire between years may not vary with rainfall (section 4.3.3.3)

An effective way of exploring the relationship between rainfall and behaviour in more detail would be to use time series analysis (Chatfield 1989; SPSS 1993) but data collected for this study were not suitable for such treatment. However, the Mikumi long-term dataset (R.J. Rhine, G.W. Norton & S.K. Wasser unpublished data) includes data that would be suitable for time series analyses of group activity and this would be an interesting area for future work.

10.3.1.4 Troop fission & fusion

Rasmussen's study was conducted just prior to a group fission and halfway through the data collection period of this study the two main study groups fused (Fig 3.3). Stresses were evident in the time budgets of the baboons prior to each of these events. Prior to the fission event in 1978, V0 spent noticeably little time socializing. The data suggest that spatial constraints were important in preventing sufficient socializing to maintain the cohesion of this large group (as discussed further in section 10.3.2.3). Prior to the fusion event in 1994, time spent feeding by V1 and V2 was particularly low for the time of year (sections 7.3.2 & 7.4.3). In addition to a decrease in time spent feeding time, resting time increased in response to the fusion (section 7.3.2). It is evident from these findings that both fission and fusion can relieve pressure on time budgets.

Despite the increase in group size, there was no evidence that intragroup competition increased (feeding time and vigilance at conspecifics decreased whilst indexes of aggression and displacement remained unchanged; sections 7.3.3 & 7.3.4). The amount of time individuals spent surveying their environment decreased (section 7.3.4), consistent with the many eyes hypothesis (Alexander 1974). The amount of directional vigilance increased (section 7.3.4) accompanying co-ordination of movement of a larger group in to new areas. Individuals gained foraging and antipredation benefits from the fusion whilst not incurring costs of increased intragroup competition. This was made possible because certain ecological and demographic factors coincided (section 7.4.3).

Group fusion is a rare event in primates but the fusion event in Mikumi had features in common with the few previously recorded occurrences (section 7.4.1; Altmann 1980; Altmann et al. 1985; Cheney & Seyfarth 1987; Dittus 1986, 1987; Isbell et al. 1991). Specifically, previous investigators also observed group fusion:

- during long-term (>15 years) studies;
- after a period of population decline;
- where at least one group showed atypical demography.

In addition, intertroop competition and a post fusion range shift were features of at least one other observed fusion (Dittus 1986, 1987).

10.3.2 About the Functional Equations

10.3.2.1 Underlying assumptions

The functional equation approach to modelling time budgets (Dunbar 1992a; section 2.6; Chapter 8) assumes that, by averaging out a lot of detail, large scale patterns will be revealed. However, this assumption may not be valid if finer grain variation is on a similar scale to the interpopulation variation, and sampling decisions are not sensitive to this possibility.

The analyses of inter-individual and temporal variation in Mikumi, as outlined in section 10.2.1, suggests that inter-individual differences are less of a potential problem in this respect than differences generated by looking at different time frames within years and within days. However, a review of past studies suggests that researchers are generally more aware of potential problems relating to temporal variation (e.g., Harding 1976 and Post 1978) . An added complication is that methods reported often lack the information to assess temporal and individual sampling fully. Ideally comparisons should only be made between studies using compatible sampling decisions (Chapters 5 & 6).

10.3.2.2 Generation, testing & use

The use of stepwise multiple regression procedures to model time budgets has certain limitations but, represents the most biologically and statistically acceptable approach at the present time (section 8.3). However, methods that have been used previously to test the functional equations are unequivocally invalid (sections 8.4.1 & 8.4.2) and the revised procedure developed in this thesis (section 8.4.3) should be used in future. Even so, the criteria used in this test remain in common with previous methods and are lenient in favour of confirming the predictive abilities of the functional equations (section 8.4.4).

In addition to the limitations of the equation generating procedure and the lenient criteria used in testing their predictive abilities, concerns can be raised over the dataset used to generate the equations (sections 8.2). Considering these problems together, versions of the functional equations currently available should not be embedded in to more complex models until the dataset can be improved and the statistical methods refined (section 8.6).

10.3.2.3 Application to Mikumi

In Chapter 9 the first appropriate attempt was made to apply the functional equations, to long-term changes in a single site (section 8.4.2). The results indicated that the equations predicted observed values qualitatively but not quantitatively (sections 9.3.3 & 9.3.4). This might be due to shortcomings of the functional equations, as discussed in the previous section, or to some special feature of the Mikumi ecosystem such as the unrecognized influence of cyclic or extreme weather conditions and/or factors largely independent of climatic constraints (section 9.4.1). Possible examples of the latter include fire and fruit and flowering patterns (sections 4.3.3.3 & 4.4.2).

Nevertheless, even without a strong quantitative fit, comparisons of equation-predicted and observed values were useful. Two particularly large discrepancies between observed and predicted values were identified. The first of these was that there was much less socializing than predicted in the large group in the 1970s (Rasmussen's study) (section 9.3.3). This was indicative of the impending troop fission. Moreover, by looking at levels of resting it can be concluded that the constraint on this socializing was not lack of time per se. The data were consistent with an alternative explanation of spatial constraints (section 9.4.3).

The second noticeable discrepancy was that day journey length for small groups in the 1990s (this study) was much longer than predicted (section 9.3.4) i.e., the day journey length equation performs badly at small group sizes. This is likely to be because the day journey length equation is based on a dataset biased towards large groups (section 9.4.2). This bias in the dataset also explains why the relatively increasing importance of movement within patches observed as group size decreased (section 9.4.2) is not reflected in the functional equations.

The application of the functional equations to the Mikumi dataset thus proved useful in both understanding the behaviour of the baboons and in understanding the shortcomings of the equations.

10.4 ENVIRONMENT, GROUP SIZE & TIME

If we accept that the functional equations describe biogeographical patterns of time budgets in baboons, then it is important to consider the implications and potential uses of this phenomenon. As discussed in section 8.5, causal relationships may not underlie the predictive abilities of the equations but, it seems likely that they do operate (section 8.5; Dunbar 1992a). It follows from this, that the climatic parameters included in the equation represent the environmental constraints under which baboons in the wild generally operate. Further support for this comes from the findings reported in Chapter 6 and reviewed in sections 10.3.1.2 and 10.3.1.3. Environmental constraints, directly or indirectly related to climate, were implicated as potent factors in bringing about seasonal patterns of time budgets within years in Mikumi.

For the functional equations to work, not only must baboon behaviour potentially be constrained by environmental conditions, it must actually be constraining. If a population is growing it is likely that it is below its carrying capacity and that environmental constraints on it are therefore relieved. Unfortunately, unless data are collected as part of a long-term investigation it is hard to assess the dynamics of the population. Even with a long-term dataset it can be difficult. Turning this line of discussion around, we can argue that if the equations do work adequately this implies that the populations used in the generation of the functional equations were at their carrying capacity.

The application and testing of the functional equations by Bronikowski & Altmann (1996) were invalid for a number of reasons (section 8.4.2). In addition, however, they also failed to consider the population dynamics of the Amboseli baboons. Figure 1 in Altmann et al.'s (1985) paper indicates that this population was increasing during the period analyzed by Bronikowski & Altmann (1996).

The population dynamics of the Mikumi population at the time of Rasmussen's (1975-6) study are hard to judge because his took place at the start of the long-term project. During Norton's study (1980-1984) the population was stable but during the period of data collection for this study (1993-1995) the population was in decline (Fig. 3.4). No change in the key climatic variables, identified by the functional equations as indicative of environmental constraints across the three study periods, was identified (section 9.3.1). Either, environmental constraints were changing in Mikumi in a way not predicted by these variables (e.g., as a consequence of fire effects on ground layer foods). Or, the population decline was not a consequence of changing environmental constraints (e.g., as a consequence of disease). In both cases, the population dynamics would be symptomatic of why the functional equations failed to make adequate quantitative predictions (sections 9.3.3 & 9.3.4). In first case, the equations break down when applied to within site changes in Mikumi because of a special feature of the Mikumi ecosystem. In the second case, the requirement that the population be at its carrying capacity for the equations to work is not met.

Although, the key climatic parameters in Mikumi did not change across the three studies compared, group size did. This was both as a consequence of population decline and of group fission and fusion. Changes in environmental constraints could have been responsible for this even if not reflected in functional equations. For example, if between year changes in fire patterns did alter food availability in ground layer patch size may have become smaller. The following scenario is highly simplified but serves as an illustration: Trees provide food in small relatively discrete patches while sedge fields are large patches with dispersed items. Fire patterns may affect the later but not the former. With a reduction in sedge fields, food resources and average patch size would be reduced dramatically. This would lead to both population decline and smaller optimal group size because intragroup competition within large groups in small patches would be high and hence costly. The functional equations are therefore able to retain some of their predictive powers because environmental constraints are reflected in group size change even if not in climatic variables.

In section 8.5 the role of group size as a constraint in its own right was discussed. Group size appears only in the equations for moving and day journey length except in the set generated by Williamson (1997) in which it also appears in resting (Tables 8.1 & 8.2). Day journey length is a common minor predictor of time spent feeding; in which case group size indirectly effects other time budget components. Day journey length and time spent moving both increased with group size (sections 9.2.2 & 9.2.3). In section 8.5, it was argued that this was because a larger number of animals will have to travel and therefore move further in order to find enough food for all its members.

That group size can act both as an indicator of environmental conditions and as a constraint in its own right is indicative of the interactive nature of optimal group size and environment. This leads us to consideration of what is the appropriate measure of group size to use to generate equations designed to describe and predict interpopulation variation in time budgets and the implications of this for applying the functional equations within sites.

In patchy environments there is likely to be more than one optimal group size. Taking a simple example, a habitat may have small patches (e.g., fruiting trees) which are optimally exploited by small groups, and large patches (e.g., sedge fields) which are optimally exploited by large groups. Large groups can displace smaller groups from any patch but, because intraspecific competition will be intensified in small patches it is not worthwhile for them to do so. Small groups cannot displace large groups but can exploit the small patches which are not economic for large groups to use. In order to have a group size that reflects patchiness of an environment a mean of a representative sample of groups would be most suitable. Unfortunately this kind of data are rarely available. The number of groups studied in any detail is typically only one to three and information on the general population from which the study animals belong is limited (but see e.g., Altmann & Altmann 1970; Henzi et al. 1997; R.J. Rhine, G.W. Norton & S.K. Wasser unpublished data). We are therefore left with the use of study group size, or mean study group size, as our best measure; acting as a mixed measure of both environmental constraints and the constraining influence of the group size. This measure is adequate for investigating broad scale variation. However, perhaps the functional equations would be more fine tuned to working within sites if these two measures could be separated.

The ultimate constraint on time budgets is time itself. The animals only have a limited number of daylight hours in which to fit all the activities they need to survive and reproduce (Dunbar 1992a). If environmental and group size constraints are such that the animals cannot do this then they will not be able to persist. Either, they must move to an area where the environmental constraints are tolerable or, they must undergo changes in group size. As already mentioned both fission (Dunbar 1992a; Henzi et al. 1997; section 10.3.1.4) and fusion (Chapter 7; section 10.3.1.4) can relieve pressure on time.

10.5 IDEAS FOR THE FUTURE

A number of topics for future consideration have been mentioned throughout this thesis including this discussion chapter. In this section, two additional ideas for potentially fruitful research are proposed.

10.5.1 Specialization of Baboon Types

The five types of baboon (yellow, olive, hamadryas, guinea, chacma) included in the functional equation dataset are treated as a single widely spread, generalist species capable of adapting to local habitat conditions (Dunbar 1992a). However, if maps of baboon distribution (e.g., Jolly 1993) are compared with vegetation maps of Africa (e.g. White 1984), a general correspondence is evident. Moreover, canonical variate analysis of tooth shape of yellow, olive and chacma baboons reveals distinct differences in dentition between these three types (Hayes et al. 1990). These differences in dentition and possible habitat selection could lead to environmental constraints operating slightly differently for each baboon type (Norton & Hawkins 1996, 1997a&b).

A proposal can therefore be put forward that, within a broad and adaptable niche, different baboon types do show some degree of specialization. This could be explored by generating functional equations within, as well as across, baboon types. At present this is not possible due to paucity of data. However, if separate sets of functional equations can eventually be provided for each baboon type interesting insights may be gained by comparing them with each other and with equations based on all types combined.

10.5.2 Use of Satellite Remote Sensing

The logistical problems associated with monitoring ecological parameters through ground surveys was mentioned in Chapter 4 (section 4.2.1). Remote sensing data from satellites, which can provide ecological information frequently, over large areas for long periods, are becoming increasingly easy to obtain and process. These data offer opportunities for exploring temporal and spatial variation of habitat and of habitat-climate relationships within and between study site. Moreover, by analyzing archived data, historical patterns can be investigated. The potential use of data from satellite remote sensing in models of behaviour leading to a greater understanding of environmental constraints on baboons, and other animals, is very exciting.

There are two systems of particular interest. The first is the United State's National Oceanic and Atmospheric Administration (NOAA) Polar-orbiting Operational Environmental Satellites (POES; http://isis.dlr.de/guide/NOAA-AVHRR.html). Data from the AVHRR sensors on the NOAA satellites are broadcast at full-resolution (approximately 1km) from the satellites in High Resolution Picture Transmission Resolution (HRPT) form. Data are also recorded on board at full-resolution, known as Local Area Coverage (LAC), and subsampled at 5km, known as Global Area Coverage (GAC). Both LAC and GAC are subsequently transmitted to ground stations. GAC data on Africa have been archived since at least 1982. Archiving of LAC data has not been as comprehensive due to limited storage capacities the receiving station in Nairobi (K. Campbell in litt.; R.H. Lamprey in litt.).

AVHRR data have already been successfully used in a variety of projects mapping and monitoring habitat types, fire and other useful ecological parameters (e.g., Frederiksen et al. 1991; Langaas & Anderson 1991; Langaas & Kane 1991; J. Wellens in litt.; also see the following websites http://ceo-www.jrc.it/mtv-docs/ndvi_africa.html; http://www.uku.fi/Africa.html). In particular, AVHRR data can be used to calculate a Normalized Difference Vegetation Index (NDVI) which reflects primary productivity. Ground surveys are still needed for "ground truthing" of data but assessments in relatively small areas can be extrapolated.

The second satellite system of particular interest is Europe's Meteorological satellite Organisation's (EUMETSAT) Meteosat system (http://www.eumetsat.de/en/area1/topic1.html). Useful information available from Meteosat includes "Cold-Cloud duration" which can be used to provide rainfall estimations (R.H. Lamprey in litt.).

REFERENCES

Agetsuma, N. (1995a) Dietary selection by Yakushima macaques (*Macaca fuscata yakui*): the influence of food availability and temperature. *Int. J. Primatol.* **16**:611-627.

Agetsuma, N. (1995b) Foraging strategies of Yakushima macaques. *Int. J. Primatol.* **16**:595-609.

Alcock, J. (1996) Animal Behaviour: 5th Edition. Sineauer Associates, Inc., Massachusetts.

Aldrich-Blake, F.P.G., Bunn, T.K. and Dunbar, R.I.M. (1971) Observations on baboons, *Papio anubis*, in an arid region in Ethiopia. *Folia primatol.* **15**:1-35.

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

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

Altmann, J. (1980) Baboon Mothers and Infants. Harvard University Press, Cambridge.

Altmann, J., Hausfater, G. and Altmann, S.A. (1985) Demography of Amboseli baboons, 1963-1983. *Am. J. Primatol.* **8**:113-125.

Altmann, J. and Muruthi, P. (1988) Differences in daily life between semiprovisioned and wild-feeding baboons. *Am. J. Primatol.* **15**:213-221.

Altmann, J. and Samuels, A. (1992) Costs of maternal care: infant-carrying in baboons. *Behav. Ecol. Sociobiol.* **29**:391-398.

Altmann, S.A. and Altmann, J. (1970) Baboon Ecology: African field research. University of Chicago Press, Chicago.

Anon (1984) Africa, the Atlantic Ocean South of 35°N and the Indian Ocean (Met. 0.85.d.). Tables of Temperature, Precipitation and Sunshine for the World. Her Majesties Stationery Office, London

Archibold, O.W. (1995) Ecology of World Vegetation. Chapman & Hall, London.

Baldellou, M. and Adan, A. (1997) Time, gender and seasonality in vervet activity: a chronbiological approach. *Primates* **38**:31-43.

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

Barrett, L. (1995) Foraging strategies, ranging behaviour & territoriality among grey-cheeked managabeys in Kibale Forest, western Uganda. Ph.D. thesis, University College London.

Barton, R.A. (1989) Foraging strategies, diet and competition in olive baboons. Ph.D. thesis, St. Andrews University.

Begon, M., Harper, J.L. and Townsend, C.R. (1996) Ecology: individuals, populations and communities: 3rd Edition. Blackwells Scientific, Oxford.

Bekoff, M. and Byers, J. (1992) Time, energy and play. *Anim. Behav.* **44**:981-982.

Bernstein, I.S. (1976) Activity patterns in a sooty mangabey group. *Folia primatol.* **26:**185-206.

Bernstein, I. (1991) An empirical comparison of focal and ad libitum scoring with commentary on instantaneous scans, all occurrence and one-zero techniques. *Anim. Behav.* **42:**721-728.

Binney, R. (1989) The Human Body. Galley Press, London.

Biswas, M.R. and Biswas, A.K. (1979) Food, Climate and Man. John Wiley & Sons Inc., New York.

Bronikowski, A.M. and Altmann, J. (1996) Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behav. Ecol. Sociobiol.* **390:**11-25.

Bronikowski, A.M. and Webb, C. (1996) A critical examination of variability measures applied to annual rainfall. *Behav. Ecol. Sociobiol.* **39:**27-30.

Brown, D. and Rothery, P. (1993) Models in Biology: mathematics, statistics and computing. Wiley, Chicester.

Bryne, R.W., Whiten, A. and Henzi, S.P. (1988) Measuring the food constraints on mountain baboons. Pages 105-122 in M.T. de Mello, A. Whiten and R. Bryne (eds.) Baboons. Selected Proceedings from XIIth Congress of the International Primatological Society.

Bryne, G. and Suomi, S.J. (1995) Development of activity patterns, social interactions, and exploratory behaviour in infant tufted capuchins (*Cebus apella*). *Am. J. Primatol.* **35:**255-270.

Caraco, T. (1979a) Time budgeting and group size: a theory. *Ecology* **60:**611-617.

Caraco, T. (1979b) Time budgeting and group size: a test of theory. *Ecology* **60:**618-627.

Chapman, C.A. (1988a) Patterns of foraging and range use by three species of neotropical primates. *Primates* **29:**177-194.

Chapman, C.A. (1988b) Patch use and patch depletion by spider and howling monkeys of Santa Rosa National Park, Costa Rica. *Behav.* **105:**99-116.

Chatfield, C. (1989) ed. The Analysis of Time Series. Chapman & Hall, London.

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

Chivers, D.J. (1977) The feeding behaviour of siamang. Pages 355-383 in T.H. Clutton-Brock (ed.) Primate Ecology: studies of feeding and ranging in lemurs, monkeys and apes. Academic Press, London.

Clutton-Brock, T.H. (1974) Activity patterns of red colobus (*Colobus badius tephrosceles*). *Folia primatol.* **21:**161-187.

Clutton-Brock, T.H. (1977a) Some aspects of intraspecific variation in feeding and ranging behaviour in primates. Pages 539-556 in T.H. Clutton-Brock (ed.) Primate Ecology: studies of feeding and ranging in lemurs, monkeys and apes. Academic Press, London.

Clutton-Brock, T.H. (1977b) ed. Primate Ecology: studies of feeding and ranging in lemurs, monkeys and apes. Academic Press, New York.

Clutton-Brock, T.H. and Harvey, P.H. (1977) Species differences in feeding and ranging behaviour in primates. Pages 557-584 in T.H. Clutton-Brock (ed.) Primate Ecology: studies of feeding and ranging in lemurs, monkeys and apes. Academic Press, London.

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

Coelho, A.M., Bramblett, C.A. and Quick, L.B. (1976) Resource availability and population density in primates: socio-biogenergetic analysis of energy budgets of Guatemalan howler and spider monkeys. *Primates* **17**:63-80.

Coelho, A.M., Bramblett, C.A. and Quick, L.B. (1979) Activity patterns in howler and spider monkeys: an application of socio-biogenergetic methods. Pages 175-199 in I. Bernstein and E.O. Smith (eds.) Primate Ecology & Human Evolution Garland STPM Press, New York.

Computer Associates (1990) Cricket Graph for Microsoft Windows User Manual.

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

Cowlishaw, G.C. and Dunbar, R.I.M. (in press) Primate Conservation Biology. Chicago University Press.

Crawley, M.J. (1997) Plant Ecology: 2nd Edition. Blackwell Scientific Publications, Oxford.

Crutzen, P.J., and Goldammer, J.G. (1993) eds. Fire in the Environment: the ecological, atmospheric and climatic importance of vegetation fires. John Wiley & Sons, New York.

Dasilva, G.L. (1992) The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *J. Anim. Ecol.* **61**:79-91.

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

Davis, R.T. and Leathers, C.W. (1985) Behaviour and Pathology of Aging in Rhesus Monkeys. Alan R. Liss, New York.

de Ruiter, J.R. (1986) The influence of group size on predator scanning and foraging behaviour of wedgecapped capuchin monkeys (*Cebus olivaceus*). *Behav.* **98**:240-258.

Defler, T.R. (1995) The time budget of a group of wild woolly monkeys (*Lagothrix lagothricha*). *Int. J .Primatol.* **16**:107-119.

Demment, M.W. (1988) Dynamics of exploitation: differential energetic adaptations of two troops of baboons to recent human contact. Pages 25-51 in J.E. Fa and C.H. Southwick (eds.) Ecology and Behaviour of Food Enhanced Primate Groups. Alan R. Liss Inc, New York.

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

Dittus, W.P.J. (1986) Sex differences in fitness following a group take-over among Toque macaques: testing models of social evolution. *Behav. Ecol. Sociobiol.* **19**:257-266.

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

Doran, D. (1997) Influence of seasonality on activity patterns, feeding behaviour, ranging, and grouping patterns in Tai chimpanzees. *Int. J. Primatol.* **18**:183-206.

Drews, C. (1993) Psychological warfare and the management of relationships between male baboons (*Papio cynocephalus*). Ph.D. thesis, University of Cambridge.

Drews, C. (1995) Road kills by public transport in Mikumi National Park, Tanzania, with notes on baboon mortality. *Afr. J. Ecol.* **33:** 89-100.

Dunbar, R.I.M. (1976) Some aspects of research design and their implications in the observational study of behaviour. *Behav.* **58**:78-98.

Dunbar, R.I.M. (1977) Feeding ecology of gelada baboons: a preliminary report. Pages 251-273 in T.H. Clutton-Brock (ed.) Primate Ecology: studies of feeding and ranging in lemurs, monkeys and apes. Academic Press, London.

Dunbar, R.I.M. (1988) Primate Social Systems. Croom Helm, London.

Dunbar, R.I.M. (1990) Environmental determinants of intraspecific variation in body weight in baboons (*Papio spp.*). *J. Zool., Lond.* **220**:157-169.

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

Dunbar, R.I.M. (1992b) A model of the gelada socio-ecological System. *Primates* **69**:69-83.

Dunbar, R.I.M. (1996) Determinants of group size in primates: a general model. *Pro. Brit. Acad.* **88**:33-57.

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

Dunbar, R.I.M. and Dunbar, P. (1977) Dominance and reproductive success among female gelada baboons. *Nature, Lond.* **266**:351-352.

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

Dunbar, R.I.M. and Nathan, M.F. (1972) Social organization of the guinea baboon (*Papio papio*) in Senegal. *Folia primatol.* **17**:321-334.

Dunbar, R.I.M. and Sharman, M. (1984) Is social grooming altruistic? *Z. Tierpsychol.* **8**:299-330.

Eley, R.M., Strum, S.C., Muchem, G. and Reid, G.D.F. (1989) Nutrition, body condition, activity patterns and parasitism of free-ranging troops of olive baboons (*Papio anubis*) in Kenya. *Am. J. Primatol.* **18**:209-219.

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.

Frederiksen, P., Langaas, S. and Mbaye, M. (1991) NOAA-AVHRR and GIS-based monitoring of fire activity in Senegal - a provisional methodology and potential applications. Pages 400-417 in J.G. Goldammer (ed.) Fire in the Tropical Biota: ecosystem processes and global challenges. Springer-Verlag, Berlin.

Fossey, D. and Harcourt, A.H. (1977) Feeding ecology of free-ranging mountain gorilla. Pages 415-449 in Pages 557-584 in T.H. Clutton-Brock (ed.) Primate Ecology: studies of feeding and ranging in lemurs, monkeys and apes. Academic Press, London.

Fowler, C. & Pankhurst, P. (in prep.) The effects of captive management on the behaviour of the mara (*Dolichotis patagonium*) at Marwell Zoological Park, U.K.

Garber, P.A. (1988) Diet, foraging patterns and resource defense in a mixed troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. *Behav.* **105**:18-34.

Gates, D.M. (1993) Climate Change and its Biological Consequences. Sinauer Associates, Inc., Sunderland.

Gautier-Hion, A. (1980) Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *J. Anim. Ecol.* **49**:237-269.

Godfray, H.C.J. and Grenfell, G.T. (1993) The continuing quest for chaos. *TREE* **8**:43-44.

Gould, L., Fedigan, L.M. and Rose, L. (1997) Why be vigilant? The case of the alpha animal. *Int. J. Primatol.* **18**:401-414.

Gutierrez-Diego, V., Norton, G.W. and Hawkins, D.M. (1998) Cheek pouches: an neglected adaptation. XVIIth International Primatological Congress.

Hall, J.B. (1991) Multiple-nearest-tree sampling in an ecological survey of afromontane catchment forest. *For. Ecol. Man.* **42**:245-266.

Hall-Martin, A.J. and Fuller, N.G. (1975) Observations on the phenology of some tree and shrubs of the Lengwe National Park, Malawi. *J. stn. Afr. Widl. Mgmt Ass.* **5**:83-86.

Harcourt, A.H. and Stewart, K.J. (1984) Gorillas' time feeding: aspects of methodology, body size, competition and diet. *Afr. J .Ecol.* **22**:207-215.

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

Harrison, M.J.S. (1983) Age and sex differences in the diet and feeding strategies of green monkey *Cercopithecus sabaeus*. *Anim. Behav.* **31**:969-977.

Hawkins, D.M. (1994) Savannah hedgehogs. *BBC Wildlife* **12**:58.

Hawkins, D.M. (1989) A study of the effects of fire on the ranging behaviour of elephants & baboons in Mikumi National Park, Tanzania, using satellite remote sensing & ground surveys. Unpublished research proposal.

Hawkins, D.M. (1992) The activity of squirrel monkeys (*Saimiri sciureus*) at Whipsnade Wild Animal Park. *Int. Zoo. Yb.* **31**:163-170.

Hawkins, D.M., Lyaruu, H.V. and Norton, G.W. (1996) *Dalbergia melanoxylon* in Mikumi National Park. Pages 44-51 in Proceedings of Maputo Workshop: towards conservation and responsible use of *Dalbergia melanoxylon*, 6-9 November 1995. Flora & Fauna International.

Hayes, V.J., Freedman, L. and Oxnard, C.E. (1990) The taxonomy of savanna baboons: an odontomorphometric analysis. *Am. J. Primatol.* **22**:171-190.

Hayes, V.J., Henzi, S.P., Freedman, L. and Gaynor, D. (1992) The differential use of cheek pouches in a troop of *Papio ursinus*. *Primates* **33**:477-500.

Heideman, P.D. (1989) Temporal and spatial variation in the phenology of flowering and fruiting in a tropical rainforest. *J. Ecol.* **77**:1059-1079.

Henzi, S.P., Lycett, J.E. and Piper, S.E. (1997) Fission and troop size in a mountain baboon population. *Anim. Behav.* **530**:525-535.

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

Isbell, L.A. and Young, T.P. (1993) Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. *Behav. Ecol. Sociobiol.* **32**:377-385.

Iwamoto, T. and Dunbar, R.I.M. (1983) Thermoregulation, habitat quality and the behavioural ecology of gelada baboons. *J. Anim. Ecol.* **52**:357-366.

Jackson, L.J. (1989) Climate, Water and Agriculture in the Tropics Longman Scientific and Technical.

Janson, C.H. and Goldsmith, M.L. (1995) Predicting group size in primates: foraging costs and predation risks. *Behav. Ecol.* **6**:326-336.

Janson, C.H. and van Schaik, C.P. (1988) Recognizing the many faces of primate food competition: methods. *Behav.* **105**:165-166.

Johnson, R. (1989) The feeding strategy of adult male baboons (*Papio cynocephalus*). Ph.D. thesis, University of Cambridge.

Jolly, C.J. (1993) Species, subspecies and baboon systematics. Pages 67-107 in W.H. Kimbel and L.B. Martin (eds.) Species, Species Concepts and Primate Evolution Plenum Press.

Kamal, K.B., Bouq, A.I., Brain, P.F., Ghandour, A., Banaja, A. and Zaid, N. (1995) Time budgets and annual activity patterns of commensal hamadryas baboon (*Papio hamadryas*) in Saudi Arabia. *J. Egypt. Ger. Soc. Zool.* **16**:269-286.

Kenyatta, C.G. (1995) Ecological and social constraints on maternal investment strategies. Ph.D. thesis, University College London.

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

Kleiman, D.G. (1977) Monogamy in mammals. *Quart. Rev. Biol.* **52**:39-69.

Knight, J. (1998) Busy doing nothing. *New Sci.* **35**:32-35.

Kotrschal, K. Hirschenhauser, K. & Mostl, E. (1998) The relationship between social stress and dominance is seasonal in greylag geese. *Anim. Behav.* **55**:119-127.

Kraemer, H.C. (1979) One-zero sampling in the study of primate behaviour. *Primates* **20**:237-244.

Lagory, K.E. (1986) Habitat, group size and behaviour of white-tailed deer. *Behav.* **98**:168-179.

Lagory, K.E. (1987) The influence of habitat and group characteristics on alarm and flight response of white-tailed deer. *Anim. Behav.* **35**:20-25.

Langaas, S. & Anderson, H.S. (1991) Semi-automatic bispectral approach to NOAA AVHRR based detection of savanna fires. 5th AVHRR User Meeting, Tromso, Norway.

Langaas, S. & Kane, R. (1991) Temporal spectral signatures of fire scars in savanna woodland. International Geoscience and Remote Sensing Symposium, Helsinki, Finland.

Larcher, W. (1995) Physiological Plant Ecology: 3rd Edition. Springer, Berlin.

Lee, P.C. (1984) Ecological constraints on the social development of vervet monkeys. *Behav.* **91**:245-262.

Lee, P.C. (1986) Environmental influences on development: play, weaning & social structure. Pages 227-238 in J. Else and P.C. Lee (eds.) Primate ontogeny, cognition and social behaviour. CUP, Cambridge.

Lee, P.C. (1987) Nutrition, fertility and maternal investment in primates. *J. Zool., Lond.* **213**:409-422.

Lee, P.C. (1994) Social structure and evolution. Pages 266-303 in P.J.B. Slater and T.R. Halliday (eds.) Behaviour and Evolution. Cambridge University Press, Cambridge.

Lee, P.C. and Bowman, J.E. (1995) Influence of ecology and energetics on primate mothers and infants. Pages 47-58 in Motherhood in Human and Nonhuman Primates. S. Karger, Basel.

Leger, D.W. (1977) An empirical evaluation of instantaneous and one-zero sampling of chimpanzee behavior. *Primates* **1814**:387-393.

Lehner, P.N. (1996) Handbook of Ethological Methods: 2nd Edition. Garland STMP, New York.

Le Houerou, H.N. and Hoste, C.H. (1977) Rangeland production and annual rainfall relations in the Mediterranean basin and in the Africa Sahelo-Sudanian zone. *J. Range Man.* **30**:181-189.

Linacre, E. (1992) Climate Data & Resources: a reference and guide. Routledge, London.

Lind, E.M. and Morrison, M.E.S. (1974) East African Vegetation. Longman, London.

Linville, S.U., Breitwisch, R., & Schilling, A.J. (1998) Plumage brightness as an indicator of parental care in northern cardinals. *Anim. Behav.* **55**:119-127.

Lovett, J.C. & Norton, G.W. (1989) Afromontane rainforest on Malundwe Hill in Mikumi National Park, Tanzania. *Bio. Cons.* **48**:13-19.

Loy, J. (1988) Effects of supplementary feeding on maturation and fertility in primate groups. Pages 153-166 J.E. Fa & C.H. Southwick (eds.) Food-enhanced Primate Populations. Alan R. Liss, Inc. New York.

MAFF (1976) The Agricultural Climate of England and Wales (technical bulletin 35). HMSO, London.

Marsh, C.W. (1981) Time budget of Tana river red colobus. *Folia primatol.* **35**:30-50.

Martin, P. & Bateson, P. (1986) Measuring Behaviour: an introductory guide. Cambridge University Press, Cambridge.

May, R.M. (1981) ed. Theoretical Ecology: principles and applications. Blackwells Scientific, Oxford.

May, R.M. (1984) Graeme Caughley and the emerging science of conservation biology. *TREE* **9**:368-369.

McFarland-Symington, M. (1988a) Food competition and foraging party size in the black spider monkey. *Behav.* **105**:117-134.

McFarland-Symington, M. (1988b) Demography, ranging patterns and activity budgets of black spider monkeys. *Am. J .Primatol.* **15**:45-67.

McNaughton, S.J. (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecol .Mono.* **55**:259-294.

Milne, G. (1947) A soil reconnaissance journey through parts of Tanganyika Territory, December 1935 to February 1936. *J. Ecol.* **35**:192-265.

Mitani, J.C. (1989) Orangutan activity budgets: monthly variations and effects of body size, parturition and sociality. *Am. J. Primatol.* **18**:87-100.

Muller, E.F., Kamau, J.M.Z. and Maloiy, G.M.O. (1983) A comparative study of basal metabolism and thermoregulation in a folivorous (*Colobus guereza*) and an omnivorous (*Cercopithecus mitis*) primate species. *Comp. Biochem. Physiol.* **74**:319-322.

Muruthi, P., Altmann, J. and Altmann, S. (1991) Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population. *Oecologia* **87**:467-472.

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

Nash, L.T. (1976) Troop fission in free-ranging baboons in the Gombe Stream National Park. *Am. J. Physical Anthropol.* **44**:63-77.

Norton, G.W. (1993) Checklist of the vascular plants of Mikumi National Park, Tanzania: 6th Edition. Report to Tanzania National Parks.

Norton, G.W. (1994a) Long-term baboon behavioural ecology and vegetation monitoring in Mikumi National Park. Report to Tanzania National Parks.

Norton, G.W. (1994b) Rainfall in Mikumi National Park, Tanzania: part 1 monthly and annual patterns (1964 to 1993). Report to Tanzania National Parks.

Norton, G.W. and Hawkins, D.M. (1996) Baboon behaviour and ecology: a long-term perspective. European Workshop on Primate Research, Madrid, Spain.

Norton, G.W. and Hawkins, D.M. (1997a) Baboon biogeography and vegetation patterns. Seminar presentation at the Institute of Zoology, London March 18th 1997.

Norton, G.W. and Hawkins, D.M. (1997b) Population variation in baboon behaviour and ecology: the perspective from Mikumi. Seminar presentation at the Department of Anthropology, University of Cambridge, 19th November.

Norton, G.W., Lyaruu, H.V., Wasser, S.K. and Hawkins, D.M. (1992) Vegetation monitoring Mikumi National Park. Report to Tanzania Natioal Parks.

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

O'Connor, T.G. and Roux, P.W. (1995) Vegetation changes (1949-1971) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: the influence of rainfall variability and grazing by sheep. *J. Appl. Ecol.* **32**:612-626.

Oates, J.F. (1977) The guereza and its food. Pages 276-321 in T.H. Clutton-Brock (ed.) Primate Ecology: studies of feeding and ranging in lemurs, monkeys and apes. Academic Press, London.

Oates, J.F. (1987) Food distribution and foraging behavior. Pages 197-209 in B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds.) Primate Societies. University of Chicago Press, Chicago.

Peters, R.H. (1987) The Ecological Implications of Body Size. Cambridge University Press, Cambridge.

Phillips-Conroy, J.E. (1986) Baboons, diet and disease: food plant selection and *Schistosomiasis*. Pages 287-304 in D. Taub and F. King (eds.) Current Perspectives in Primate Social Dynamics. von Norstrand Reinhold.

Pochron, S.T. (1999) Test of food-selection models in Yellow baboons (*Papio cynocephalus cynocephalus*), Ruaha National Park, Tanzania. PhD thesis, University of New Mexico.

Pollock, J.I. (1977) The ecology and sociology of feeding in *Indri indri*. Pages 38-69 in T.H. Clutton-Brock (ed.) Primate Ecology: studies of feeding and ranging in lemurs, monkeys and apes. Academic Press, London.

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

Post, D.G. (1981) Activity patterns of yellow baboons (*Papio cynocephalus*) in Amboseli National Park, Kenya. *Anim. Behav.* **29**:357-374.

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

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

Prins, H.H.T. (1996) Ecology and Behaviour of the African Buffalo: social inequality and decision making. Chapman and Hall, London.

Pusey, A.E. and Packer, C. (1987) Dispersal and philopatry. Pages 250-266 B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds.) Primate Societies. University of Chicago, Chicago.

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

Rhine, R.J. (1986) Ten years of cooperative baboon research at Mikumi National Park. Pages 13-22 in J.G. Else and P.C. Lee (eds.) Primate Ontogeny, Cognition and Social Behaviour. Cambridge University Press, Cambridge.

Rhine, R.J. and Ender, P.B. (1983) Comparability of methods used in the sampling of primate behavior. *Am. J. Primatol.* **5**:1-5.

Rhine, R.J. and Flanigan, M. (1978) An empirical comparison of one-zero focal-animal, and instantaneous methods of sampling social behaviour. *Primates* **19**:353-361.

Rhine, R.J. and Linville, A.K. (1980) Properties of one-zero scores in observational studies of primate social behaviour: the effect of assumptions on empirical analyses. *Primates* **21**:111-121.

Rhine, R.J., Norton, G.W. and Westlund, B.J. (1984) The waning of dependence in infant free-ranging yellow baboons (*Papio cynocephalus*) of Mikumi National Park. *Am. J. Primatol.* **7**:213-228.

Rhine, R.J., Norton, G.W., Wynn, G.M. and Wynn, R.D. (1985) Weaning of free-ranging infant baboons (*Papio cynocephalus*) as indicated by one-zero and instantaneous sampling of feeding. *Int. J. Primatol.* **6**:491-499.

Rhine, R.J., Norton, G.W., Wynn, G.M., Wynn, R.D. and Rhine, H.B. (1986) Insect and meat eating among infant and adult baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. *Am. J. Physical Anthropol.* **70**:105-118.

Rhine, R.J., Wasser, S.K. and Norton, G.W. (1988) Eight year study of social and ecological correlates of mortality among immature baboons of Mikumi National Park, Tanzania. *Am. J. Primatol.* **16**:199-212.

Rhine, R.J., Norton, G.W., Wynn, G.M. and Wynn, R.D. (1989) Plant feeding of yellow baboons (*Papio cynocephalus*) in Mikumi National Park, Tanzania, and the relationship between seasonal feeding and immature survival. *Int. J. Primatol.* **10**:319-342.

Rhine, R.J. and Westlund, B.J. (1978) The nature of primary feeding habit in different age-sex classes of yellow baboons (*Papio cynocephalus*). *Folia primatol.* **30**:64-79.

Richard, A. (1970) A comparative study of the activity patterns and behaviour of *Alouatta villosa* and *Ateles geoffroyi*. *Folia primatol.* **12**:241-263.

Roberts, G. (1995) A real-time response of vigilance behaviour to changes in group size. *Anim. Behav.* **50**:1371-1374.

Robinson, J.G. (1984) Diurnal variation in foraging and diet in wedge-capped capuchin monkey, *Cebus olivaceus*: implications for foraging theory. *Folia primatol.* **43**:216-228.

Robinson, J.G. (1986) Seasonal variation in the use of time and space by wedge-capped capuchin monkey, *Cebus olivaceus*: implications for foraging theory. *Smith. Contrib. Zool.* **431**:1-60.

Rodgers, W.A. (1979) The ecology of large herbivores in the miombo woodlands of south east Tanzania. Ph.D. thesis, University of Nairobi.

Rodman, P.S (1977) Feeding behaviour of orang-utans of the Kutai Nature Reserve, East Kalimantan. Pages 384-414 in T.H. Clutton-Brock (ed.) Primate Ecology: studies of feeding and ranging in lemurs, monkeys and apes. Academic Press, London.

Ruxton, G.D. (1996) Group size and anti-predator vigilance: a simple model requiring limited monitoring of other group members. *Anim. Behav.* **51**:478-481.

Sakura, O. (1991) On the concept of "group" in primates, with special reference to fission-fusion of chimpanzees. Pages 247-250 in A. Ehara, T. Kimura, O. Takenaka and M. Iwamoto (eds.) Primatology Today. Elsevier Science Publishers, Amsterdam.

Schaffner, C.M. and French, A.F. (1997) Group size and aggression: 'recruitment incentives' in a cooperatively breeding primate. *Anim. Behav.* **54**:171-180.

Schmidt-Nielsen, K. (1990) Animal Physiology. Cambridge University Press, Cambridge.

Schoener, T.W. (1971) Theory of feeding strategies. *Ann. Rev. Sys. & Ecol.* **2**:369-414.

Secor, S. and Diamond,J. (1997) Determinants of the post-feeding metabolic response of Burmese pythons, *Python molurus*. *Phys. Zool.* **70**:202.

Sharman, M. (1981) Feeding, ranging and social organization of the Guinea baboon, *Papio papio*. Ph.D. thesis, University of St. Andrews.

Siegel, S. and Castellan, Jr. N.J. (1988) Nonparametric Statistics: for the behavioral sciences. McGraw Hill, New York.

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. *Int. J. Primatol.* **7**:583-603.

Smith, C.C. (1977) Feeding behaviour and social organization in howling monkeys. Pages 97-126 in T.H. Clutton-Brock (ed.) Primate Ecology: studies of feeding and ranging in lemurs, monkeys and apes. Academic Press, London.

Smith, K. (1975) Principles of Applied Climatology. McGraw Hill.

Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. and Struhsaker, T.T. (1987) eds. Primate Societies. University of Chicago Press, Chicago.

Sokal, R.R. and Rohlf, F.J. (1981) Biometry: 2nd Edition. W.H. Freeman & Co., New York.

Sommer, V. and Mendoza-Granados, D. (1995) Play as indicator of habitat quality: a field study of langur monkeys (*Presbytis entellus*). *Ethol.* **99**:177-192.

Southwick, C.H. (1980) Rhesus monkey populations in India and Nepal: Patterns of growth, decline and natural regulation. Pages 151-170 in M.N. Cohen, R.S. Malpass and H.G. Klein (eds.) Biosocial Mechanisms of Population Regulation Yale University Press Ltd., London.

SPSS (1993) SPSS for Windows: base system user guide release 6.0. SPSS Inc, Chicago.

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

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

Stoltz, L.P. (1972) The size, composition and fissioning in baboon troops (*Papio ursinus* KERR, 1792). *Zoologica Africana* **7**:367-378.

Strier, K.B. (1987) Activity budgets of woolly spider monkeys, or Muriquis (*Brachyteles arachnoides*). *Am. J. Primatol.* **13**:385-395.

Stronach, N. (1988a) The management of fire in Serengeti National Park: objectives and prescriptions. Report to Tanzania National Parks.

Stronach, N. (1988b) Serengeti Fire Ecology Project 1985-1987: final report on management. Report to Tanzania National Parks.

Thompson, L.M. (1975) Weather variability, climatic change and grain production. *Science* **188**:535-543.

Unwin, D.M. & Corbet, S.A. (1991) Insects, Plants and Microclimate. Richmond Publishing Company.

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

van Schaik, C.P. (1994) Why are diurnal primates living in groups? *Behav.* **87**:120-144.

Walter, H. (1973) Vegetation of the Earth: in relation to climate and the eco-physiological conditions. Springer-Verlag, New York.

Waser, P.M. (1975) Monthly variations in feeding activity and activity patterns of mangabey, *Cercocebus albiginea. E. Afr. Wildl. J.* **13:**249-263.

Waser, P.M. (1977) Feeding, ranging and group size in the mangabey *Cercocebus albigena*. Pages 183-222 in T.H. Clutton-Brock (ed.) Primate Ecology: studies of feeding and ranging in lemurs, monkeys and apes. Academic Press, London.

Wasser, L.M. and Wasser, S.K. (1995) Environmental variation and developmental rate among free ranging yellow baboons (*Papio cynocephalus*). *Am. J. Primatol.* **35:**15-30.

Wasser, S.K. (1983) Reproductive competition and cooperation among female yellow baboons. Pages 349-390 in S.K. Wasser (ed.) Social Behavior of Female Vertebrates. Academic Press, New York.

Wasser, S.K. and Norton, G.W. (1993) Baboons adjust secondary sex ratio in response to predictors of sex-specific offspring survival. *Behav. Ecol. Sociobiol.* **32:**273-281.

Watts, D.P. (1984) Composition and variability of mountain gorilla diets in the central Virungas. *Am. J. Primatol.* **7:**323-356.

Watts, D.P. (1985) Relations between group size and feeding competition in mountain gorillas. *Anim. Behav.* **33:**72-85.

Watts, D.P. (1988) Environmental influences on mountain gorilla time budgets. *Am. J. Primatol.* **15:**195-211.

White, F. (1983) The Vegetation of Africa Unesco.

Whiten, A., Byrne, R.W. and Henzi, S.P. (1987) The behavioral ecology of mountain baboons. *Int. J. Primatol.* **8:**367-388.

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

Williams, G.D.V., Joynt, M.I. and McCormick, P.A. (1975) Regression analyses of Canadian prairie crop-district cereal yields 1961-1972. *Can. J. Soil Sci.* **55:**43-53.

Williamson, D.K. (1997) Primate socioecology: development of a conceptual model for the early hominids. Ph.D. thesis, University College London.

Woodward, F.I. (1987) Climate and Plant Distribution. Cambridge University Press, Cambridge.

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

Yaber, M.C. and Herrera, E.A. (1994) Vigilance, group size and social status in capybaras. *Anim. Behav.* **48:**1301-1307.

APPENDIX

The table below shows the total number of minutes individuals were observed during each seasonal quarter of this study. Specific information on data used in different analyses is given in the relevant data chapters. I.D. codes and other information on the study animals is given in section 3.3.1 (see especially Table 3.3a).

	YEAR 1 1993/4				**YEAR 1994/5**				**YEAR 3 1995**
I.D.	**Dry 1**	**Dry 2**	**Wet 1**	**Wet 2**	**Dry 1**	**Dry 2**	**Wet 1**	**Wet 2**	**Dry 1**
24	630		540	720					
26	360	270	360	1080	1575	765	900	1260	540
27	360	270	270						
29	450		360	1170	180				
32	420		540	900	2025	855	765	1305	630
38	540		720	1080	2070	1125	945	1080	720
39	450	90	450						
41	540	90	540	810	990				
50	180								
54	360	90	270	1170	1260	945	990	855	495
55	360		360	1350	1485	675	1305	1080	
56	540		720	900	2205	810	1125	1350	540
58	270	180	450	900					
62	540	180	360	540					
88					855	630	1395	1305	720
134		90		360	1215	405			
136				90	180				
139				270	540	810	720	1035	540
142					90				
146				540	405				
149					90	45			
238	540	180	720	810	1440	810	180		
239	450	90				900			
240	450	360	180	1260	1035			45	
243					225				