From space to species: integrating remotely sensed information on primary productivity into investigations and systems models of vervet monkey (Cercopithecus aethiops) socio ecology

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From space to species:

Integrating remotely sensed information on primary productivity into investigations and systems models of vervet monkey (*Cercopithecus aethiops*) socio-ecology

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Abstract

An in depth investigation of the socio-ecology of the vervet monkey species complex (*Cercopithecus aethiops subspp.*) is presented. Herein, particular emphasis has been placed on evaluating the information content of remotely sensed primary productivity with respect to inquiries into the causal network underlying the behavioural ecology of the species. The principal aim was to construct an inter-populational model of group size and range of distribution for vervet monkeys over the whole of sub-Saharan Africa.

Data were collected on a habituated group of vervet monkeys over a 12 months observation period at the Lajuma Research Centre, South Africa. In addition, behavioural information from other populations was gathered in an extensive literature review. Environmental data were accrued on both a global (inter-populational) and local (intra-populational) level using a combination of remotely sensed data and more traditional field-observation based techniques. Where appropriate, variables were integrated into the powerful modelling environment of a Geographical Information System (GIS).

Biologically intuitive associations between a remotely sensed index of primary productivity (the Normalised Difference Vegetation Index, or NDVI) and climatic conditions were established on the long-term global (annual average values over sub-Saharan Africa) and short-term local level (monthly values over the home range area of the study group). Local NDVI values, moreover, were strong correlates and predictors of field estimates on local phenology and food availability as well as of temporal and spatial variation in parameters of range use and time allocation by the study group. Global NDVI values proved pivotal to the eventual inter-populational time budget model of vervet monkey group size and potential range of distribution. Current results are taken to suggest that several areas of research within primatology may stand a lot to gain from a more widespread and systematic application of the powerful methodological synergism offered by remote sensing and geographical information systems.

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1 Introduction

1.1 Modelling primate socio-ecology

Primate societies display a remarkable degree of inter- and intra-specific variation. One of the most fundamental challenges in primatology may therefore lie in the construction of evolutionary theories to account for this fascinating behavioural diversity. Pertaining to this, a comprehensive understanding of primate social systems is generally believed to critically hinge on the identification of the proximate mechanisms that determine group size and composition (Smuts *et al.*, 1987; Dunbar, 1988). As a result, a multitude of conceptual models has been developed to relate these key aspects to ecological and demographic factors. More recently, the insights gained from these descriptive models have been implemented into more quantitative approaches capable of generating highly specific predictions. The expeditious progress brought about by this synergism between descriptive and predictive tools, has greatly advanced our understanding of primate sociality. A concise treatise of the theories and models that have featured most prominently within primatology over the last couple of decades is offered below as these set the principal framework within which this thesis was written.

1.1.1 Conceptual models of primate social organisation

The earliest models that attempted to identify the proximate mechanisms determining primate group size and composition, regarded the social organisation of a group as an adaptation to local ecological conditions (Crook and Gartlan, 1966; Crook and Goss-Custard, 1972; Eisenberg *et al.*, 1972). Although the reasoning behind these first attempts was flawed by elements of group selection theory, the proposed link between social phenomena and ecological variables was both insightful and constructive and has subsequently become the quintessence of the study of primate socio-ecology. The subsequent recognition of the individual as the correct unit of selection brought about the realisation that behavioural strategies of the animal, rather than the social organisation of the group, should be interpreted in terms of adaptive significance (Hinde, 1983). In combination with the growing awareness of differential selective pressures limiting the reproductive success of the sexes (Trivers, 1972), this engendered the fundamental paradigm of modern primate socio-ecology; spatial distribution and social relationships of females are thought to mainly reflect ecological conditions, in particular the distribution of risk and food (Clutton-Brock and Harvey, 1977), whereas the distribution and social relationships of males are believed to be determined primarily by the spatio-temporal distribution of mating opportunities (Emlen and Oring, 1977; Wrangham, 1980; van Schaik, 1983; 1989; Dunbar, 1988; Janson and Goldsmith, 1995).

A vast number of conceptual models based on this fundamental insight has been developed, each identifying slightly different selective forces that could have favoured the evolution of group living in primates. The first generation of these models suggested that predation risk was an important environmental factor -or indeed the most important (Alexander, 1974)- but also assumed several feeding advantages associated with group living (Jolly, 1972; Altmann, 1974; Clutton-Brock, 1974). In some respect however, these models failed to recognise that female behavioural strategies ordain the range of strategies open to males (*e.g.* Emlen and Oring, 1977) and that, hence, any investigation into the evolution of primate social organisations should start with an examination of the ecological determinants of female social relationships.

One of the most groundbreaking and controversial models to pick up on this, is the ecological model of female-bonded primate groups (Wrangham, 1980). Wrangham (1979), however, dismissed the selective significance of predation risk. Instead, he argued that the distribution of food was the most important determinant of female dispersion and social relationships, both within and between groups. He reasoned that, given a limited number of feeding sites, a clumped distribution of high quality food items would result in competition for access to food. Females that cooperatively defend these food patches would thereby gain a selective advantage over others in that they could effectively monopolize feeding access. An additional evolutionary advantage can furthermore be secured if females associate and cooperate with close relatives, enhancing inclusive fitness through kin selection (Hamilton, 1964). Wrangham (1980) also hypothesised that larger groups of cooperating females would be more successful in monopolising limited resources than smaller ones. As groups grow larger though, increased within group competition gives rise to more pronounced dominance relationships among group members, which can lead to differential food intake (Whitten, 1983). Ultimately, groups will reach a size at which the benefits of cooperation against other groups are outweighed by the costs of intra-group competition. Thus, in Wrangham's model between group food competition sets the lower limit on group size, whereas within group food competition defines the upper limit. The number of males that associate to these female groups is thought to reflect the outcome of the conflict between, primarily, female feeding strategies and male mating strategies and largely depends on the added value of males over females in agonistic between group interactions. This conceptual model, although restricted to female-bonded species, was the first to explain both the evolution of group living in primates as well as the internal structure of primate groups (Wrangham, 1983).

Wrangham's (1979, 1980) view that predation risk was of no significance in the evolution of primate social organisations and that group size and social structure are entirely defined by competition for resources, was challenged by a number of authors (van Schaik, 1983; Terborgh and Janson, 1986; Dunbar, 1988). Perhaps the most elegant and authoritative test between Wrangham's proposition and the prevailing alternative in which group size was taken to be determined by both predation risk and resource competition, was conducted by van Schaik (1983). In an extensive comparative analysis using data from 13 different primate taxa he assessed the explanatory powers of the two theories. His findings suggested that group living is disadvantageous with respect to feeding (*contra* Wrangham, 1980) and that the avoidance of predation confers the only selective advantage to group living in diurnal primates. In this scenario, the minimum permissible group size is set by predation risk whereas the maximum sustainable group size is defined by within group feeding competition.

A further significant enhancement procured by van Schaik (1989) consisted of synthesising the two competing models. In this new conceptual framework, group size and social regime were determined by the interaction between the benefits of group living, *i.e.* either a reduction of predation risk or an increased leverage in between group competition, and the costs of group living, *i.e.* within group competition. The relative importance of predation risk and feeding competition was thought to be species- and habitat-specific and, thus, to depend on ecotype (diurnal, nocturnal or cathemeral activity phase), body size, number, distribution and type of predators and the abundance, distribution and quality of food. Males in this model, were still taken to passively map onto the availability of mating opportunities, although it was suggested that the number of males in primate groups could in addition be related to predation risk (van Schaik and Hörstermann, 1994; Hill and Lee, 1998). The notion of feeding competition was also notably refined. By discerning between scramble competition, in which food intake of all individuals is equally affected, and contest (or interference) competition, in which territory owners or dominant individuals can monopolize access to resources (Nicholsen, 1967; Isbell, 1991) at both the intra- and inter-group level, a distinction could be made between four possible competitive regimes in primate groups (Janson and van Schaik, 1988). These regimes, in turn, exert a profound effect on the nature of female relationships and give rise to four main types of social organisation (Table 1.1): resident-egalitarian, dispersal-egalitarian, resident-nepotistic and resident-nepotistic-tolerant species, respectively (van Schaik, 1989, 1996; Sterck *et al.*, 1997).

Table 1.1 A summary of the relationship between ecological conditions, competitive regime and female social organisation (freely after Sterck *et al.*, 1997)

Ecological conditions	**Competitive regime**		**Female social organisation**		
Food Distribution	*Within Group*	*Between Group*	*Relationships*	*Hierarchy*	*Philopatry*
Dispersed	Scramble	Scramble	Egalitarian	Individualistic	No
Dispersed	Scramble	Contest	Egalitarian	Individualistic	Yes
Clumped	Contest	Scramble	Despotic	Nepotistic	Yes
Clumped	Contest	Contest	Tolerant	Nepotistic	Yes

The most recent extensions have mainly complemented this model by drawing attention to the importance of social factors in the evolution of group living (van Schaik, 1996; van Schaik and Kappeler, 1997; Sterck *et al.*, 1997). Most significant in this respect is the effect of male-female interactions in some species, where male reproductive strategies (infanticide) have had a profound influence on the social organisation of the species by inducing the evolution of female counterstrategies (Sterck, 1995; Sterck *et al.*, 2005). Another powerful selective pressure added to the model is habitat saturation. With the incorporation of these factors, the socio-ecological model of primate societies arrived at its current form (Figure 1.1).

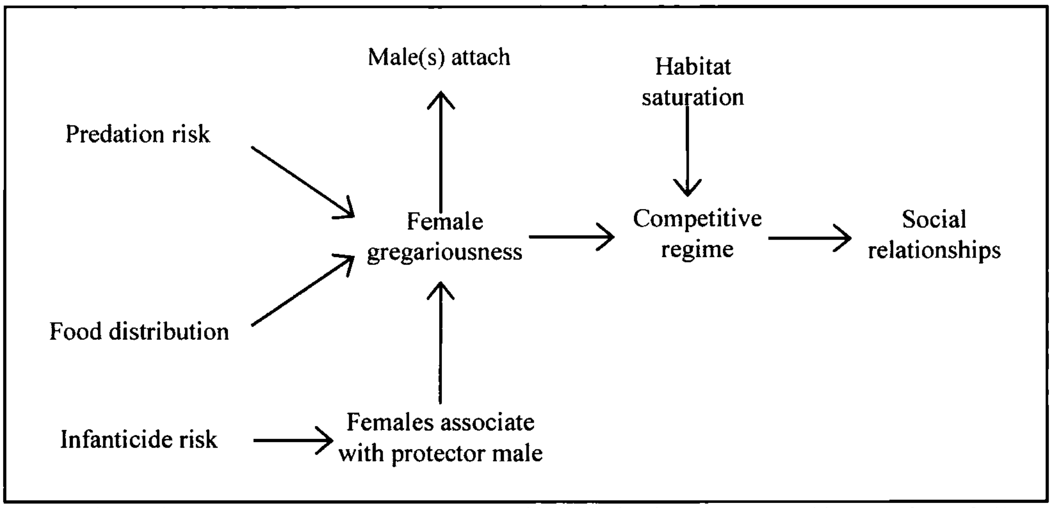


Figure 1.1 The socio-ecological model of primate social organisation as proposed by Sterck *et al.* (1997).

1.1.2 A quantitative model of primate group size

Although key to the identification and conceptualisation of the mechanisms that underlie primate social organisations, the models described so far provide descriptive rather than predictive tools. No explicit statements are made about the extent to which the respective ecological and social factors determine the size or composition of primate groups. The only primatological models to date that specifically do so, are a series of systems models originally developed to account for the marked inter-populational variation in baboon group size (Dunbar, 1992c; 1993a; 1996). These models have been applied with varying degrees of success in a steadily increasing number of studies on both extant (baboon (*Papio spp.*): (Dunbar, 1992c; 1993a; 1996; Bronikowski and Altmann, 1996; Hill, 1999); gelada (*Theropithecus gelada*): (Dunbar, 1992b); hanuman langur (*Semnopithecus entellus*):(Srivastava and Dunbar, 1996); chimpanzee (*Pan spp.*): (Williamson, 1997)Lehmann *et al.*, 2007a); spider monkey (*Ateles spp.*): (Korstjens *et al.*, 2006); colobus (*Colobus spp.* and *Piliocolobus spp.*): (Korstjens and Dunbar, 2007); gorilla (*Gorilla spp.*): (Lehmann *et al.*, submitted)) and extinct species (fossil papionines: (Dunbar, 1992a); fossil theropithecines: (Dunbar, 1993b); fossil hominids: (Williamson, 1997)).

The theoretical framework behind these quantitative models leans heavily on the socio-ecological model of primate organisations (Sterck *et al.*, 1997), or indeed more general models of animal group living (Pulliam, 1973; Pulliam and Caraco, 1984; Caraco, 1979b, a). It starts from the premise that group size in most primate species is the result of a trade-off between local predation risk and within group competition. These two environmental factors define a realisable state-space of potential group sizes between a minimum permissible group size, at which predation is reduced to a sustainable level, and a maximum ecologically tolerable group size, at which within group competition reaches a critical level. The first generation of models also considered a potential cognitive limit on primate group size, set by the maximum number of social relationships an individual can maintain (Figure 1.2; Dunbar, 1992c, 1996). More recent versions of the model, however, have focussed entirely on the habitat-specific maximum ecologically tolerable group size as this has been found to be the most informative component. Moreover, for most primate species there is currently no feasible way to realistically quantify either the minimum permissible or maximum cognitive group size. What follows below, therefore, is a brief elaboration on how the taxon-specific maximum ecologically tolerable group size can be related to, and subsequently predicted from, local ecological conditions.

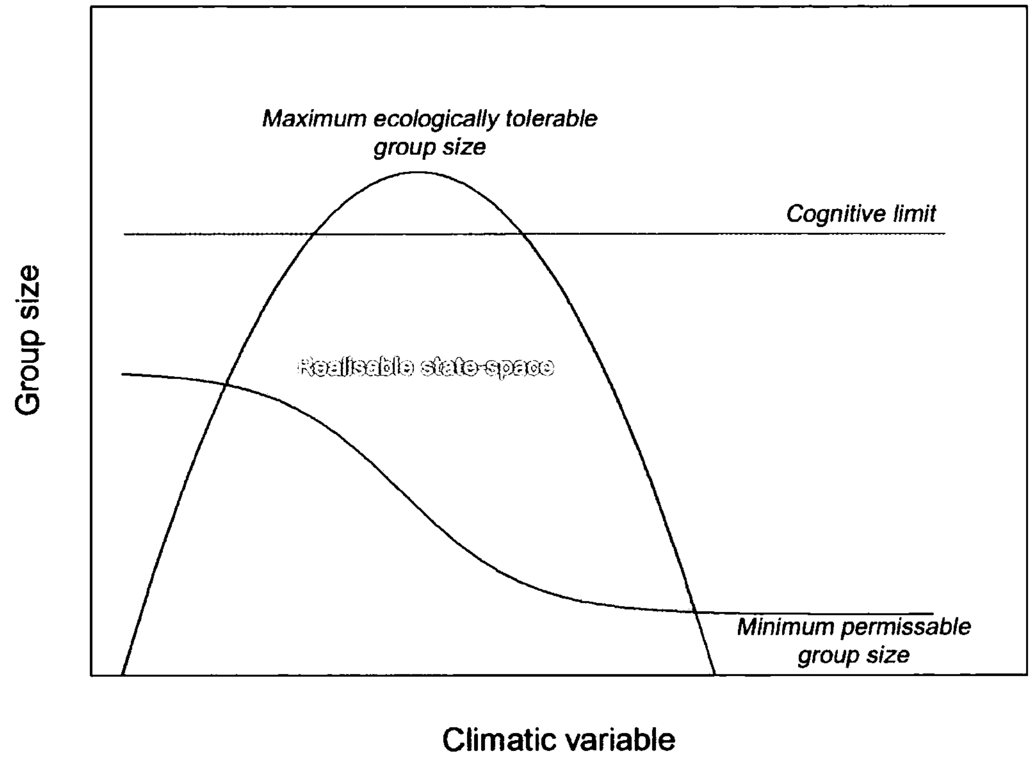


Figure 1.2 Qualitative illustration of how the three model components demarcate a habitat-specific realisable state space of group size. The n-dimensional state-space (where n equals the number of climatic variables used to characterise the local environment) gives the range of possible group sizes (based on Dunbar, 1996).

At the basis of the model lies the observation that time is a fundamental resource affecting primate activity (Dunbar, 1992c). To maximise inclusive fitness, primates do not only have to invest time to meet nutritional and thermoregulatory demands whilst avoiding predation (Schoener, 1971; Pulliam, 1973; Caraco, 1979b; 1979a; Iwamoto and Dunbar, 1983; Mangel and Clark, 1986; Mitchell and Lima, 2002), but also to maintain social relationships within the group (Janson and Boinski, 1992; Dunbar, 1993a; 1996). Based on these elementary demands on the primate time budget, four broad functional categories, or time budget components, are generally recognised within the behavioural repertoire of primates. These are time spent feeding, moving, in social interactions and resting that together typically account for more than 95% of the total activity period of the animals (Dunbar, 1988). Time allocation demands of these time budget components are not only taxon-specific but also strongly determined by local environmental conditions and group size (Dunbar, 1996; Williamson and Dunbar, 1999).

The proportion of the active period that is spent feeding, is mainly determined by body size (Dunbar, 1992c), availability and quality of food resources (Isbell, 1991), and thermoregulatory costs (Hill, 2005). Moving time has been related to, amongst others, day journey length and the spatial distribution and density of food resources (Isbell *et al.*, 1998). Time spent in social interactions is thought to serve in maintaining social relationships and group cohesion and has hence been suggested to primarily be a function of group size (Dunbar, 1991; Dunbar and Sharman, 1984; Lehmann *et al.*, 2007b). Resting time, lastly, consists for unknown proportions of enforced resting time and uncommitted time (Herbers, 1981; Korstjens *et al.*, submitted). Enforced resting time comprises locally defined demands on recuperation, vigilance, digestion and thermoregulation (Herbers, 1981) whereas uncommitted time reflects a surplus of time, available to reallocation over other activities when the need arises (Altmann, 1980; Dunbar and Sharman, 1984; Dunbar and Dunbar, 1988; Dunbar, 1992c). As time budget demands increase with group size (Dunbar, 1992c; 1993a; 1998; Janson and Goldsmith, 1995), the maximum ecologically tolerable group size can thus be defined as the group size at which all uncommitted time has been reallocated to functional behavioural activities while the sum of proportional time budget demands does not exceed 100%.

In order to quantify this maximum group size, the model uses multiple regression analyses to calculate a set of best-fit equations to express the four time budget components as functions of the local environment, group size and (when available) additional behavioural aspects such as diet composition and range use (Dunbar, 1996). For practical reasons the environment in these regression models has always been characterised in terms of direct climatic factors, such as temperature affecting thermoregulation, and indirect climatic proxies of habitat quality and productivity, such as rainfall and rainfall seasonality indices (Dunbar, 1992c; Williamson and Dunbar, 1999). The causal network defining the socio-ecology of the study species thus emerges by combining the individual best-fit regression models into a single time budget model (Figure 1.3).

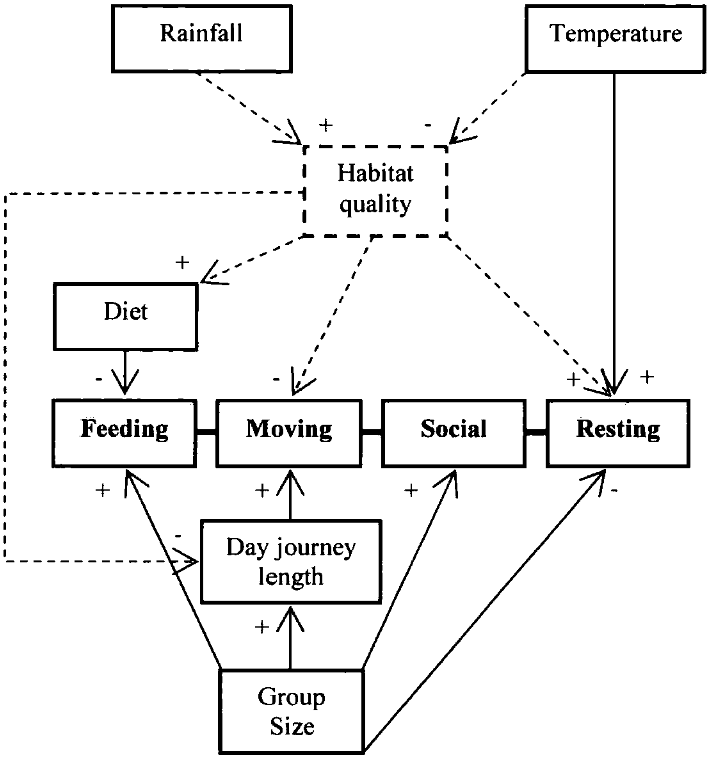


Figure 1.3 Hypothetical flow chart, qualitatively depicting the inferred causal relationships between local environmental conditions, time allocation, group size and additional behavioural variables (diet and range use). The sign and strength of the relationships is encoded in the parameters of the best-fit equations calculated by multiple regression analyses on a set of sample populations (freely after Williamson and Dunbar, 1999).

Some of the relationships clearly involve a causal cascade in which, for example, rainfall affects habitat quality, which influences dietary composition, which in turn determines the local proportion of time that animals, living in a group of a certain size, have to spend feeding. The habitat-specific maximum ecologically tolerable group size can be calculated from this causal network through an iterative process, in which a minimum value is set to resting time (taken to represent the minimum enforced resting time demands) and the sum of the time budget components is calculated for incrementing group sizes until the total exceeds 100%. The largest group at which the sum of the calculated local time budget components is less than, or equal to 100%, is taken to represent the local maximum ecologically tolerable group size. A final point to make is that by calculating the maximum ecologically tolerable group size, the potential range of distribution of a species can also be established. Under those climatic conditions for which the model predicts that time budget requirements can be met, a species can occur if it is capable to maintain group sizes larger than its local minimum permissible group size. As said though, there is currently no feasible way to quantify the value of the minimum permissible group size and thus a minimum viable value is chosen by considerations of life-history variables and the ecology of the species (Korstjens *et al.*, 2006).

From the above, it may have become clear how the quantitative model of primate group size has allowed an unparalleled insight into the mechanisms driving some of the most fundamental aspects of primate socio-ecology. Testament to its continuous utility to primatologists and anthropologists alike may be the latest studies in a series of time budget models that have enhanced our understanding of the socio-ecology, biogeography and conservation biology of some of man's closest living relatives (Lehmann *et al.*, 2007a, submitted).

1.2 Main aims of study and thesis outline

Following this brief introduction to the main theories and models within current primatology, the main aims of this study are now presented. Being part of a greater research project that seeks to use cercopithicine models as a contextual framework for hominin evolution, the principal goal was to construct a systems model for the socio-ecology of vervet monkeys (*Cercopithecus aethiops subspp.*) throughout their natural range. Vervet monkeys make a particularly suitable comparative group in this respect as they share their sub-Saharan African distribution and predominantly terrestrial lifestyle in mostly open woodland and savannahs with Plio-Pleistocene hominins. Be that as it may, this thesis aims to present an account of the behavioural ecology of vervet monkeys in its own right. The focus herein, however, has primarily been on key socio-ecological parameters in the quantitative model of primate group size. In developing a model of vervet monkey socio-ecology the thesis further aspires to investigate the usefulness of some, within primatology relatively unexplored, powerful new methodologies to enhance model performance. For the first time, therefore, investigations and models of the socio-ecology of a primate species were fully integrated within a geographical information system (GIS). Moreover, the wealth of remotely sensed ecological data that is ever increasingly becoming available to the scientific community was consistently explored. The structure of this thesis is briefly outlined below.

Chapter 2 introduces the field site and main study population, alongside with details on the ecological and behavioural sampling methods. Chapter 3 develops spatial datasets for climatic variables and primary productivity that will be implemented into the systems model of vervet monkey socio-ecology in Chapter 7. It uses the compiled data to reinvestigate the relationship between climate and habitat productivity over sub-Saharan Africa and draws attention to the inherent spatial character of ecological data. Chapter 4 then moves one step down the causal cascade underlying primate socio-ecology and looks into the relationships between remotely sensed information on habitat productivity and field observations on phenology and food availability. It does this on a local scale over the home range area of the study group. Chapter 5 is the first of three chapters that explore the potential of remotely sensed data to account directly for aspects of vervet monkey behaviour. Here, some powerful new analytical techniques are applied to quantify temporal and spatial variation in parameters of range use by the study group. These are subsequently related to key environmental conditions, taking an explicitly spatial approach where appropriate. Time allocation by the study group is examined in Chapter 6. Monthly and daily patterns of activity are established and related to local environmental and demographic conditions. An in depth exploration of the functional aspects of the four main time budget components is subsequently undertaken. Chapter 7 integrates findings from all preceding chapters into the development of a systems model for vervet monkey group size throughout sub-Saharan Africa. Remotely sensed information on habitat productivity features prominently in the model. Geographical maps of local time allocation demands, maximum ecologically tolerable group size and the potential geographic range of vervet monkeys are presented. In Chapter 8, lastly, the main results and conclusions of this thesis are integrated into a brief final discussion.

2 Methodology

2.1 Study species

Research was conducted on the socio-ecology of the *Cercopithecus aethiops* species complex, which shall be referred to throughout this script as vervet monkey or, simply, vervet. The vervet is one of Africa's most common and abundant non-human primates (Struhsaker, 1967b; Cawthon Lang, 2006) and is found throughout sub-Saharan Africa, although it is generally absent from the deserts in southern Africa and the rainforests of the Congo basin and West Africa (Fedigan and Fedigan, 1988; IEA, 1998b; Enstam and Isbell, 2007). Its natural geographic range stretches from Senegal in the west to Somalia in the east, and from the southern edge of the Sahara down to the southern tip of South Africa (Figure 2.1).

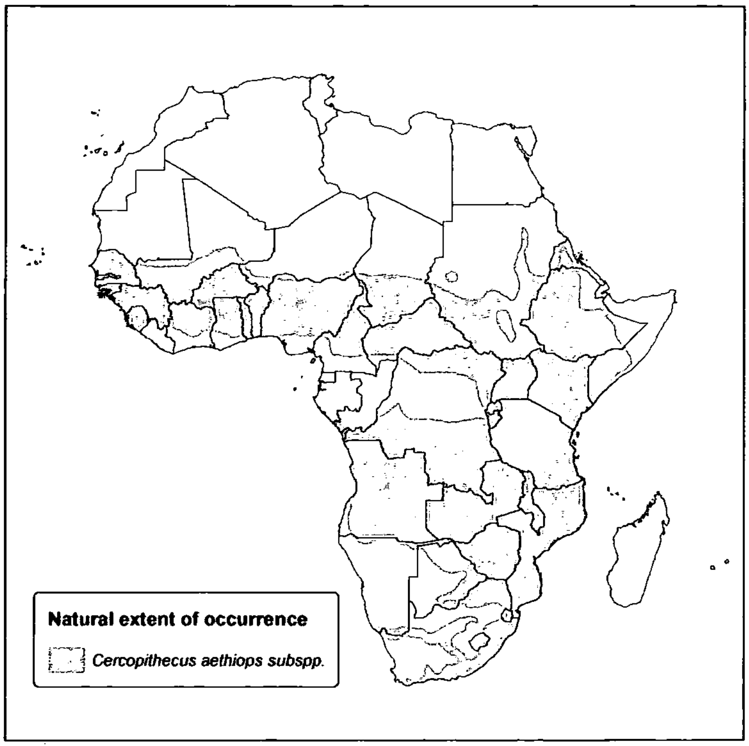


Figure 2.1 Natural geographic range of the vervet monkey (*Cercopithecus aethiops subspp.*) according to the African Mammals Databank (IEA, 1998a).

In addition, vervets have been introduced to several islands in the West Indies (Poirier, 1972; McGuire, 1974; Horrocks, 1986; Horrocks and Hunte, 1986). Natural populations are recorded from sea level up to 4,500m (Cawthon Lang, 2006) and the species displays a remarkable ability to exploit a wide range of habitats, with an apparent preference for riverine environments (Kingdon, 1997; Enstam and Isbell, 2007). The adaptability of vervet monkeys to such varied ecological conditions is thought to be facilitated by an absence of anatomical specialisations, a relative lack of sexual dimorphism and a flexible social structure in combination with a highly diverse behavioural repertoire (Struhsaker, 1967a; Gartlan and Brain, 1968). Morphologically, vervets are quite diverse too (Cardini *et al.*, 2007) and, perhaps consequently, its taxonomical status is highly disputed (Dandelot, 1959; Kingdon, 1997). Recently, taxonomists have suggested to change the genus name into *Chlorocebus* to recognise the species' distinct morphological (Fleagle, 1999; Groves, 2000) and molecular (Tosi *et al.*, 2004) features within the Cercopithecini tribe. This suggestion, however, has been disputed by others (Butynski, 2002), a view adopted here, partly because it is in agreement with the consensus achieved at a IUCN/SSC Primate Specialist Group's Workgroup (*Primate Taxonomy for the new Millennium*, 2000) and partly because further research is pending to justify any major taxonomical revision (Grubb *et al.*, 2003). Currently, 6 subspecies are recognised within the *Cercopithecus aethiops* group (Table 2.1) which contrasts sharply with the more than 20 taxa recognised elsewhere (Napier, 1981; Lernould, 1988; Rowe, 1996).

Table 2.1 A list of the 6 subspecies within the *Cercopithecus aethiops* group recognized at the IUCN/SSC Primate Specialist Group's Workshop (Primate Taxonomy for the new Millennium, 2000)

Nominal taxon	Vernacular name
C. a. aethiops (Linnaeus, 1758)	Grivet
C. a. djamdjamensis (Neumann, 1902)	Bale mountains grivet
C. a. tantalus (Ogilby, 1841)	Tantalus monkey
C. a. sabaeus (Linnaeus, 1766)	Green monkey
C. a. cynosurus (Scopoli, 1786)	Malbrouck monkey
C. a. pygerythrus (F. Cuvier, 1821)	Vervet

In the light of this project, the information amassed from different subspecies was taken to be fully commensurable, since primate behaviour is a habitat specific adaptation to local conditions rather than a (sub-)species specific trait (Eisenberg *et al.*, 1972; Clutton-Brock, 1974). Given that vervet monkeys have been studied throughout their entire geographical range (Figure 7.1) they made an ideal subject for the development of an inter-populational model of primate socio-ecology.

2.2 Study area and field site

Field work was conducted at the Lajuma Research Centre in the western part of the Soutpansberg mountain range, Northern Province, South-Africa (29°26'05''E, 23°02'23''S; Figure 2.2). Lajuma is set in a mountainous environment and on site elevation varies from 1150 m up to the 1748 m high peak of mount Letjume, the apex of the Soutpansberg mountain range. Substantial local variation in abiotic factors such as elevation, slope, aspect and water availability results in numerous microclimates and microhabitats that support a large biotic diversity.

Figure 2.2 Map of South Africa with the geographical extent of the Soutpansberg (red area) and the location of the Lajuma Research Station (white arrow tip) highlighted.

In recognition of its biotic heterogeneity, Lajuma (430 ha) was granted the status of Natural Heritage Site in 1997. In addition, the Research Centre serves as a leopard conservation area and is part of the Soutpansberg Conservancy, the Thavha Ya Muno Private Nature Reserve (5,000 ha) and the recently proposed Soutpansberg to Limpopo UNESCO biosphere reserve (30,700 km^2).

2.2.1 Topography, geology and lithosphere

The Soutpansberg topographical zone constitutes South Africa's most northerly mountain range and has an altitudinal range of 300 m to 1748m. It extends in an east-west direction from the Kruger National Park to the Blouberg mountain, thereby covering a distance of about 210 km at a width of up to 60 km (Berger *et al.*, 2003). Geologically, the Soutpansberg group represents a volcano-sedimentary succession that was deposited during the South African Mokolian stage 2,050 - 90 Mya (Rohde, 2005; Council for Geoscience, 2006). Local rock formations within this group have an age of between 1,975-1,800 million years and are mostly composed of sandstone, quartz sandstone or quartzite with some igneous intrusions (Hahn, 1994; Brandl, 2003). Orogenesis occurred during successive faulting events caused by seismographic activity at the northern rim of the Kaapvaal craton in the so-called Limpopo belt (Anhaeusser, 2002). This process gave rise to the main cliff line of the present mountain range with its steep south-facing bluffs and northerly falloff at an incline of approximately 45° (Hahn, 2002). The predominant soils in the area are shallow and poorly developed sandy soils of an alluvial or colluvial origin, set on weathered rocky substrate (Breedlove and Fraser, 2000).

2.2.2 Climate

Given the complex interplay between topography, elevation, aspect, and vegetation cover it is very difficult to fit the aggregation of regional weather conditions meaningfully into any general climatological group. The considerable variation in orographic precipitation has been well documented (Hahn, 2002; Kabanda, 2003) and rainfall data from a historical weather station at the Lajuma Research Centre (covering a period of 25 years, from 1952-1976) were available. Conversely, temperature records were not at hand for any site within the Soutpansberg. These, therefore, were estimated from records generously made available by the South African Weather Service, Pretoria. Data from six regional weather stations (over a 5 year period, 1994-1998) were subjected to an elevation-corrected, inverse-distance-weighted, spatial interpolation procedure within a geographical information system in which the adiabatic lapse rate was preset at 0.65°C/100m (Mayes, 2003). Resulting values of climatic conditions at the study site are displayed alongside with recorded weather conditions (Section 2.4.1) over the observation period in Figure 2.3. On the basis of this, local climate could be classified as temperate/mesothermal, with cool dry winters (April-September) and warm to hot wet summers (October-March) which corresponds to the Cwb-group in Köppen's climate classification (Köppen, 1884). As with any broad scale categorisation, however, this characterisation merely offers a coarse indication of local climate. Ecologically notable perturbations in the general atmospheric scheme include severe periodic droughts due to prevailing el Niño and la Niña effects and a high incidence of mist precipitation in the Soutpansberg mist-belt zone.

2.2.3 Flora

Three different biomes are generally recognized within the Soutpansberg geographical range: Forest, Savanna and Grassland. Within each of these, several distinct vegetation types are described, although little consensus exists about the appropriate classification and nomenclature or indeed spatial distribution of these (White, 1983; Acocks, 1988; Low and Rebelo, 1996; von Maltitz, 2003). This is mainly due to the complexity and relatively poorly studied status of the Soutpansberg flora, which was recently exemplified by the description of a fourth biome in the region, Thicket (Gaigher, 2005). All four biomes are represented in the Lajuma study area.

Despite a general want for more knowledge, the Soutpansberg floral region is considered a centre of plant endemism (van Wyk and van Wyk, 1997). Somewhere between 2,500 and 3,000 vascular plant species, comprising 1,066 genera and 240 families have been recorded in the mountain range, 33 of which are endemic (Hahn, 2002; 2003). The percentage of succulents (10 % of all taxa) and the relatively high dependence on mist precipitation for survival are two of the more striking characteristics of the Soutpansberg flora.

2.2.4 Fauna

Although the fauna of the Soutpansberg is most remarkable in terms of its high biodiversity and level of endemism within invertebrate and herpetological taxa (Berger *et al.*, 2003; van de Wiel and Gaigher, 2005), this section puts most emphasis on potential competitor and predator species of the vervet monkey. Hence, the focus here lies on the mammalian and avian fauna at the Lajuma Research Centre. In addition, potentially dangerous snakes are mentioned.

Within the entire mountain range around 380-400 species of bird and 145 species of mammal have been recorded (Berger *et al.*, 2003). Even though most large mammals have effectively been purged from the area, all five southern-African representatives of the primate taxon still occur (chacma baboon: *Papio cynocephalus ursinus*; Sykes's monkey: *Cercopithecus mitis alboguralis*; vervet monkey: *Cercopithecus aethiops pygerythrus*; thick-tailed galago: *Galago crassicaudatus*; South African lesser bushbaby: *Galago moholi*). Details on dietary overlap between these species are non-existing for the region, but at least the three diurnal taxa are known to exploit an array of shared resources (*pers. obs.*). Vervet monkeys and Sykes's monkeys, moreover, occasionally form highly unstable polyspecific associations in which the latter have priority of access to food. In addition to the other primate taxa, various species of antelope are potential competitors of the vervets. The most notable in this context are bushbuck (*Tragelaphus scriptus*) and the highly endangered, but locally common, red duiker (*Cephalophus* *natalensis*). Both species were observed to associate with the main study group and agonistic interactions ensued whereby the monkeys appeared dominant. A last significant group of potential food competitors is represented by numerous frugi-gramivorous avian species, which are not treated in detail here.

Mammalian predators of vervet monkeys are well represented on site. Apart from baboons (2 confirmed and 2 suspected kills, see Section 2.3.1), a number of carnivores are known (leopard: *Panthera pardus*; caracal: *Felis caracal*; serval: *Leptailurus serval*; African wild cat: *Felis syvestris*) or potentially able (brown hyena: *Hyaena brunnea*; honey badger *Mellivora capensis*; representatives of the Viverridae) to pose a predation threat to at least some age-sex classes of vervet monkey. Leopard density was particularly high, with marked seasonal fluctuations and a maximum of 4 animals present on site at one point during the observation period. Estimates from scat analyses suggest that an adult leopard at Lajuma preys on approximately 20 vervets per annum (Gaigher, unpublished data), thereby posing a serious risk factor.

Predatory species of bird include crowned eagle (*Stephanoaetus coronatus*), verreaux's eagle (*Aquila verreauxii*) and, possibly, verreaux's eagle owl (*Bubo lacteus*). In addition, various smaller species of birds of prey are present at Lajuma, most of which elicit alarm responses from the monkeys. Of all potential avian predators, however, the crowned eagle poses the most severe threat. Numerous attacks were witnessed and one kill was observed. Moreover, a breeding pair held residence within the home range of the study group and successfully raised a chick to independence during the observation period.

Snakes, finally, were also encountered by the study group. The most venomous species included black mamba (*Dendroaspis polylepis*), Mozambican spitting cobra (*Naja mossambica*), puff adder (*Bitis arietans*) and boomslang (*Dispholidus typus*). In addition, one constrictor, the African rock python (*Python sebae*), is habitant at Lajuma but this species was never observed in the vicinity of the study group. Most encounters elicited alarm responses and some of the snakes present at Lajuma are reported to have killed primates (Isbell, 2006). With the likely exception of full-grown *P. sebae* and despite posing a potential cause of mortality, it remains questionable though whether most species of snake at Lajuma should be considered predators of vervet monkey *sensu stricto.*

2.3 Study Population

A brief survey of the vervet population at Lajuma yielded a number of potential study groups. It was clear from the outset, however, that due to the rugged geomorphology of the terrain, the inaccessibility of the vegetation and the -rather untypical- shyness of the monkeys, habituation and population monitoring potential were low. Nevertheless, attempts to habituate free-ranging monkeys were undertaken on four groups, albeit with limited success. Only individuals in one group (FH) reached a level of habituation that allowed meaningful data collection on behavioural patterns. Despite the assistance in the habituation of two additional groups by Susanne Back and Ilana Conradie (on the OM-group) and Annette Schneider (on the BP-group), most individuals in these groups never ceased to show distinct behavioural responses towards observer presence. These groups were, therefore, deemed unsuitable for data collection nor were complete estimates of group size and composition acquired. Habituation of a fourth group (WC) had reached a very promising stage towards the end of the field work period, although even on this group complete counts were not obtained.

2.3.1 Study group

Habituation of the FH-group commenced in August 2004 with animal tolerance towards observer presence reaching a level at which complete and consecutive follow days were feasible by October 2004. At this stage the emphasis of habituation efforts was shifted towards two neighbouring groups (OM and WC), while FH was being monitored during at least two complete follow days a week. At the onset of December 2004 all animals within the group were individually recognised and allowed meaningful data collection through focal animal and group scan sampling (Section 2.6). All results and analyses presented in this thesis, however, are restricted to behavioural observations made between May 2005 and April 2006 to guarantee internal consistency and quality of data and to enable comparisons to concurrent atmospheric and phenological records (Sections 2.4 and 2.5, respectively)

Table 2.2 Group size and composition of the main study group (FH) over the observation period. Underlined numbers indicate the age-sex class in which a demographic change occurred, whereas bold numbers signify changes due to the maturation of individuals.

Date	Event	AF	AM	SAF	SAM	JF	JM	IF	IM	n_{total}
	Habituation									
09-Oct-04	Birth	8+	2	0	1	1	5	1	2	20+
23-Oct-04	Birth	8+	2	0	1	1	5	1	3	21+
24-Oct-04	Birth	8+	2	0	1	1	5	1	4	22+
25-Oct-04	Predation baboon	7+	2	0	1	1	5	1	4	21+
??-Oct-04	Birth	7+	2	0	1	1	5	2	4	22+
02-Nov-04	Birth	7+	2	0	1	1	5	2	5	23+
16-Nov-04	Predation eagle	7+	2	0	1	0	5	2	5	22+
26-Nov-04	Complete group count	8	2	0	1	0	5	2	5	23
	Onset behavioural data collection									
13-Dec-04	Birth	8	2	0	1	0	5	2	6	24
31-Dec-04	Age-classes updated	8	2	0	**2**	**1**	**4**	**1**	6	24
15-Jan-05	Disappearance	8	2	0	2	1	4	1	4	22
01-Feb-05	Suspected predation eagle (AF) Disappearance (IM)	7	2	0	2	1	4	1	3	20
27-Apr-05	Emigration	7	1	0	2	1	4	1	3	19
	Observation period									
04-May-05	Immigration	7	2	0	2	1	4	1	3	20
08-May-05	Disappearance	7	1	0	2	1	4	1	3	19
19-May-05	Immigration	7	2	0	2	1	4	1	3	20
20-May-05	Disappearance	7	2	0	2	1	4	1	2	19
09-Jun-05	Disappearance	7	2	0	2	1	4	1	1	18
11-Aug-05	Suspected predation baboon	5	2	0	2	1	4	1	1	16
13-Oct-05	Birth	5	2	0	2	1	4	1	3	18
25-Oct-05	Disappearance	5	2	0	2	1	4	1	2	17
07-Nov-05	Predation baboon (IF) Disappearance (SAM)	5	2	0	1	1	4	0	2	15
31-Dec-05	Age-classes updated	5	2	0	**3**	1	**2**	0	2	15
19-Jan-06	Emigration	5	2	0	2	1	2	0	2	14
19-Feb-06	Immigration/Emigration	5	2	0	2	1	2	0	2	14
09-Mar-06	Emigration	5	2	0	1	1	2	0	2	13
04-Apr-06	Immigration (3 AM, 1 JM) Emigration (SAM)	5	5	0	0	1	3	0	2	16

AF= adult female; AM= adult male; SAF= semi-adult female; SAM= semi-adult male; JF= juvenile female; JM= juvenile male; IF= infant female; IM= infant male

Size and composition of the study group were extremely variable, both over the habituation and observation periods (Table 2.2). Effective mean group size (Jarman, 1974) over the data collection period (January 2005-April 2006) was calculated at 17.8. In total, 8 births (7 males, 1 female) were observed during two annual birth seasons and 6 animals (5 adult males, 1 juvenile male) immigrated into the group. In addition, 4 adult females, 1 semi-adult male and 1 juvenile female disappeared as a consequence of either confirmed (n= 3) or suspected (n= 3) predatory events. Disappearing infants (n= 6) were assumed to have died, although it was not always possible to distinguish between predation and other causes of mortality. Finally, 2 adult males were ousted by immigrant males and 3 semi-adult males emigrated from the group.

2.4 Atmospheric monitoring

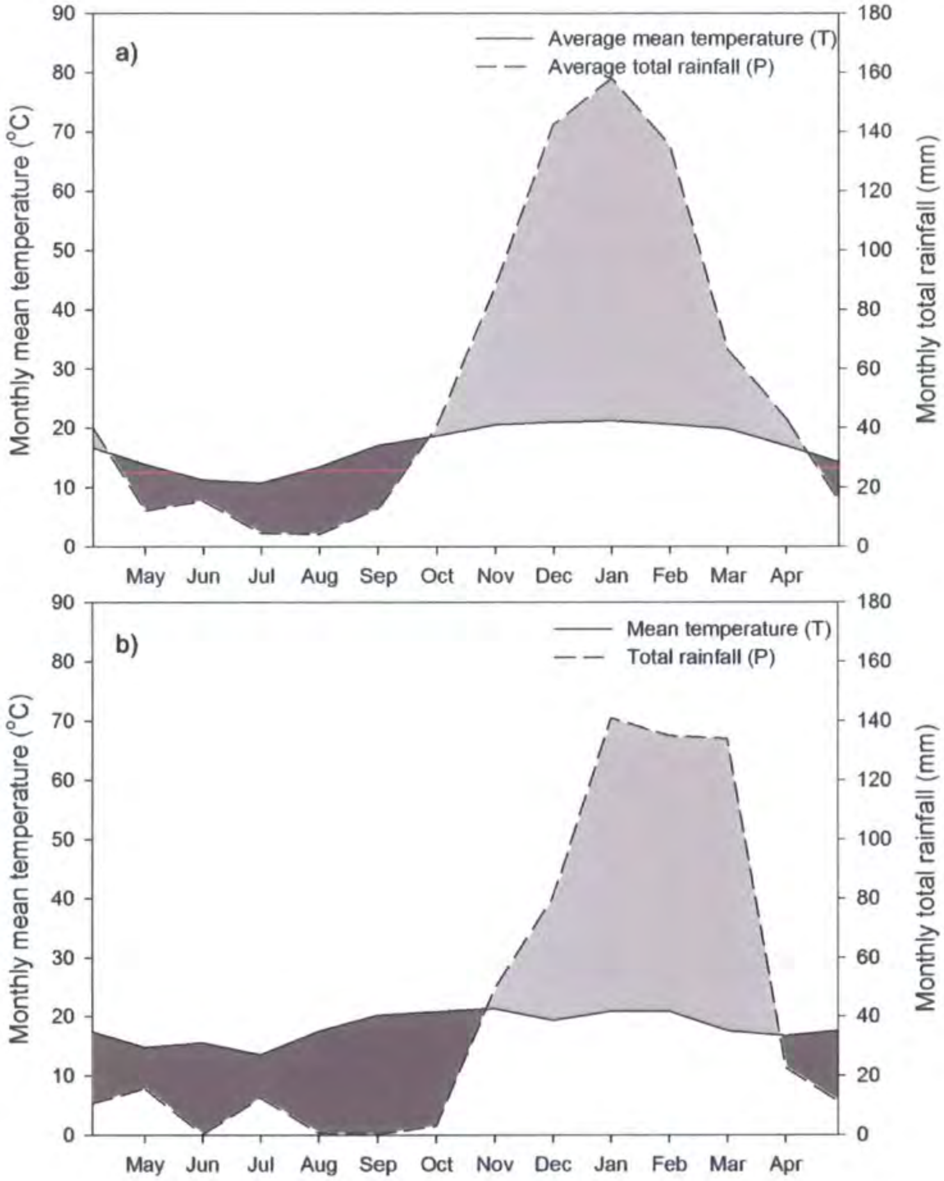
Weather and prevalent climatic conditions are principal determinants of important characteristics of a habitat that both directly (*e.g.* thermoregulatory adaptations and water requirements of the animals) and indirectly (*e.g.* seasonality, food availability and phenology of the vegetation) influence the distribution and activity of animals (Brower *et al.*, 1997; Mayes, 2003). While climate characterisations provide a good proxy for long-term selective pressures that shape the social organisation of a population, measurements on local weather conditions afford a more direct link to observed behavioural phenomena during a study period. It might, therefore, be important to distinguish between and compare the two disparate temporal scales at which atmospheric conditions articulate their effects. Hence, the characterisation of local climate from Section 2.2.2 is presented here alongside a brief summary of weather conditions recorded on site during the observation period.

2.4.1 Weather

Local atmospheric data were recorded at a 30 minute interval by a Davis Instruments Vantage Pro II Plus automated weather station. The station was erected within the home range of the study group during the first half of January 2005 and was situated at an elevation of 1340m. Unfortunately, data collection was severely delayed due to a faulty data logger and could only commence after the South African agent of Davis Instruments (C.W. Price (Pty) Ltd.) delivered a replacement unit in May 2005. To bridge this period, a standard rain gauge and minimum-maximum mercury thermometer were used to monitor key atmospheric conditions.

A suite of parameters encompassing the mean, minimum and maximum air temperature, air humidity, solar radiation, wind speed and direction, total precipitation, barometric pressure and intensity of UV radiation were recorded and a number of additional variables calculated. The latter included several apparent temperature indices (Steadman, 1979a; 1979b; Quayle and Steadman, 1998). All data were downloaded to a laptop on a monthly basis using the Davis Instruments WeatherLink® 5.5.1 software package. Monthly values were subsequently calculated from all available records (n= 15,751) and a graphical summary and accompanying table of key atmospheric conditions is presented in Figure 2.3. It should become clear from this figure that weather conditions during the observation period were warmer and considerably dryer than the long term average.

Finally, it is noted that the measurement of rainfall will have underestimated total local precipitation. Given that the Lajuma Research Centre is situated within the Soutpansberg mist-belt zone, and that in certain areas of the Soutpansberg mist precipitation accounts for more than 40% of the total annual meteorological precipitation (Department of Environmental Affairs, 1988), this inaccuracy may have been quite substantial.



Atmospheric variable	**Local climate (long term)**	**Local weather (May 2005-Apr 2006)**
$T_{\text{annual mean}}$ (°C)	17.1	18.3
$T_{\text{mean hottest month}}$ (°C)	21.2 (Jan)	21.3 (Nov)
$T_{\text{mean coldest month}}$ (°C)	10.7 (Jul)	13.4 (Jul)
P_{annual} (mm)	724	594.3
$P_{\text{wettest month}}$ (mm)	158 (Jan)	141.0 (Jan)
$P_{\text{driest month}}$ (mm)	4 (Aug)	0.2 (Jun/Sep)

Figure 2.3 Climatograph -a)- and weather graph over observation period -b)-. Light shades indicate months with a positive water balance (P>2T), whereas dark shades show months with a negative water balance (P<2T) (le Houérou and Popov, 1981). Key atmospheric variables are summarised in the table.

2.4.2 Photoperiod

An additional, and often overlooked, atmospheric variable that has a profound effect on the socio-ecology of primates is day length (Aujard *et al.*, 1998; Hill, 1999; Hill *et al.*, 2003). Intra-annual fluctuations in day length (or photoperiod) are most significant for sites at high latitudes and become more pronounced with increasing distance from the equator. The variation in photoperiod at the Lajuma Research Centre over the observation period is depicted conjointly with monthly averaged duration of animal activity in Figure 2.4. A strong and significant positive association between the two was apparent (Pearson's correlation test; r= .961, n= 12, p< .001).

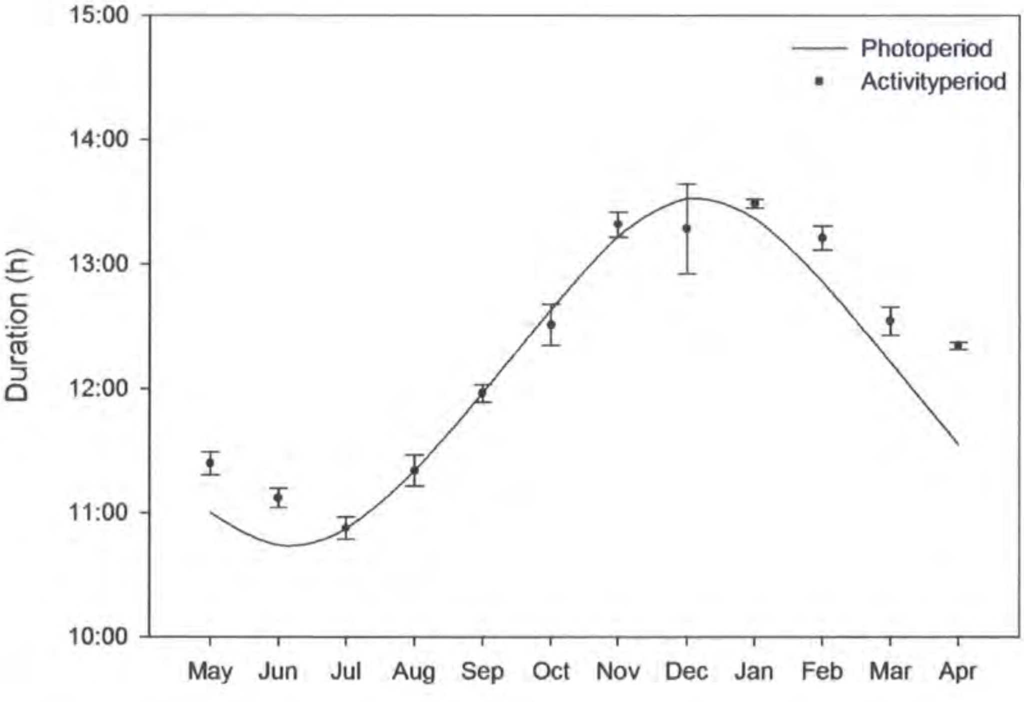


Figure 2.4 Photoperiod (day length) and monthly averaged activity period of the animals (determined over 7 successful follow days) as observed over the period May 2005-Apr 2006 (error bars represent ± 1se).

2.5 Vegetational sampling

Vegetation characteristics embody an important biotic component of a habitat and mould the evolution of life history traits and behavioural adaptations of animals (Ganzhorn, 2003). A detailed understanding of floristic and structural features, alongside with a firm grasp of spatio-temporal patterns within local phenology, thus allows a deep insight into the causal links between the phyto-matrix and behavioural phenomena of a study animal. Therefore, a number of complementary techniques were applied to achieve a multilateral understanding of the complex vegetation characteristics at the Lajuma Research Centre.

2.5.1 Remotely sensed and GIS data

Hyper-spatial panchromatic (local effective ground level resolution: 0.56m x 0.56m) and multispectral (local effective ground level resolution: 2.40m x 2.40m) Quickbird satellite imagery (acquisition date: 05-10-2004) served as base maps (Figure 2.5) and all information collected in the field (following subsections) was coupled to these maps within a Geographical Information System (GIS). Spatial accuracy of georeferenced satellite data was further enhanced by an orthorectification procedure relying on a 20m digital elevation model (DEM) of the study area and 54 additional ground control points. The 20m DEM product was created with ArcInfo's TOPOGRID function using 20 meter contours, spot heights and trigonometric beacons digitised from the South African National Topography map series (National Grid Cell 2329AB, scale 1:50,000). A graphical representation of the DEM is given in Figure 2.6.

In addition to satellite obtained information, a time-series of historical aerial photographs, stemming from routine land surveys by the South African government in 1957, 1965, 1972, 1983, 1993, 1997 and 2003, was kindly made available by Dr. I. Gaigher. These images were digitised, georeferenced, orthorectified and imported into the GIS, which offered a crucial insight into the historic and anthropogenic factors that shaped the complex floristic composition and patterning of the vegetation in the study area.

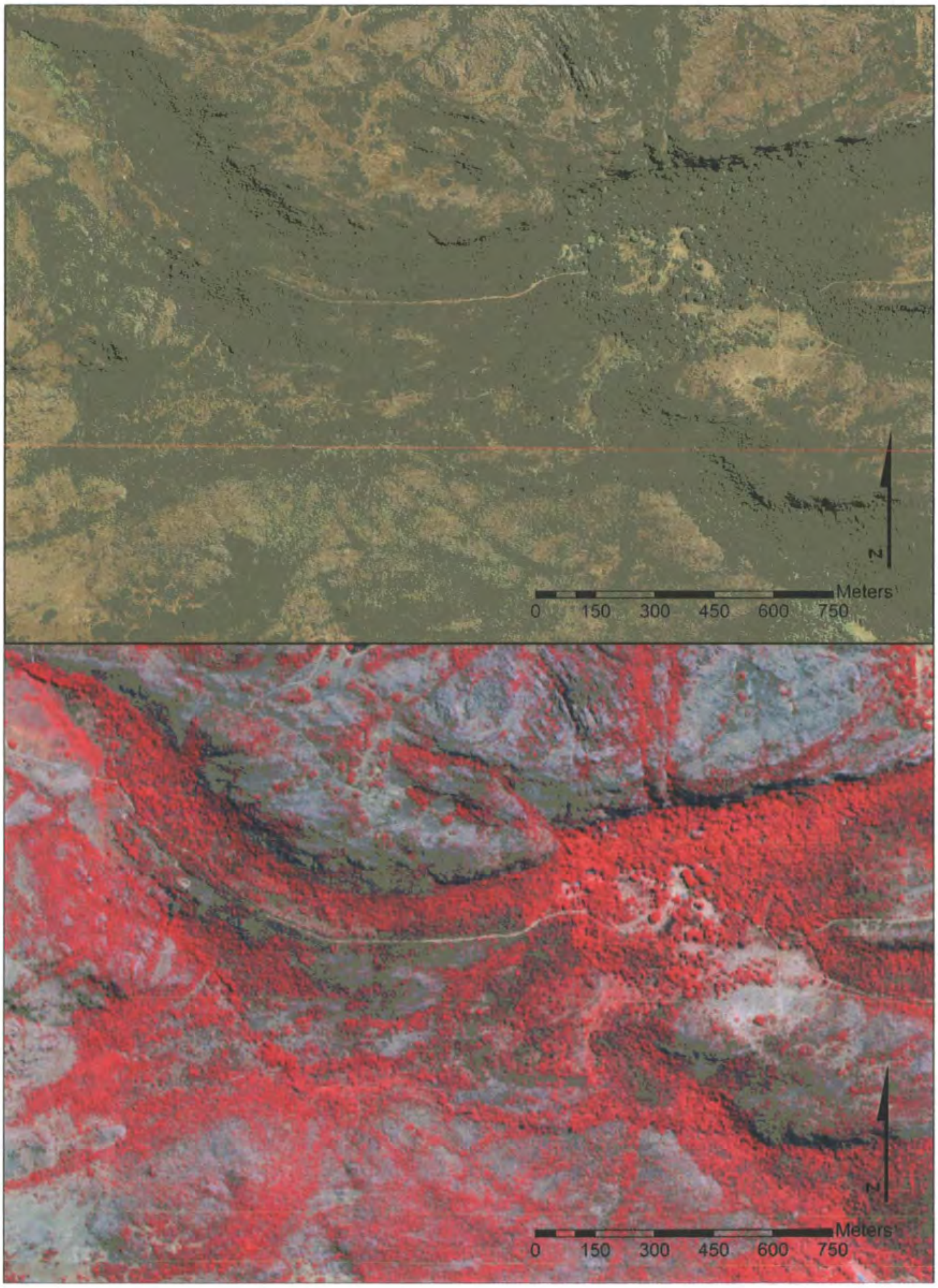


Figure 2.5 Natural and false (near infra-red) colour composites of Quickbird satellite data collected over the study area at the onset of the fieldwork (05-10-2004). The spatial extent of the images presented here, is such that it comprises the entire home range of the study group and is maintained in all home range maps throughout this thesis.

2.5.2 Initial field reconnaissance

Seven day-long field surveys were conducted in the company of two local specialists (Dr. I. Gaigher, in the capacity of botanist, and vegetation mapping expert Dr. P.J. Weisser) to identify and demarcate relevant mapping units in a study on vervet socio-ecology. Mapping units were defined as the largest unit of land containing a distinct vegetation type in terms of species composition, habitat structure, phenology, geomorphology, soil type and history of human utilisation. Initial mapping units were drawn up on a transparent overlay placed over the most recent hardcopy aerial photograph available at that time. Once more recent and more detailed satellite imagery became available a total of 172 mapping units were distinguished (Section 4.4.1).

2.5.3 Quadrat sampling

Given that distinct mapping units could be established during the initial field reconnaissance, the most adequate sampling method to quantitatively describe the floristic composition and structural characteristics of the plant community at Lajuma was quadrat sampling (Brower *et al.*, 1997; Ganzhorn, 2003). Potential sampling points were generated by overlaying a 5m x 5m grid over the estimated home range of the main study group within a GIS and randomly selecting 150 grid cells. Out of these, a subset was chosen to strive for even sampling of all provisional mapping units exploited by the monkeys. Geographical coordinates of the lower left corner of these semi-randomly selected grid cells were downloaded onto a Garmin® GPS 72 for field validation. Once located in the field, points were marked by a short wooden pole which served as the reference anchor point of a quadrat. To minimize any potentially confounding effects (*e.g.* due to possible zonation in the vegetation), the direction in which a quadrat was established, was randomly chosen from the four cardinal compass directions. A fifth direction was instituted for quadrats close to the main water stream. As these quadrats were to sample riverine vegetation they were put up parallel to the course of the stream. A total of 90 quadrats were sampled, but eventually data from the 75 quadrats within the

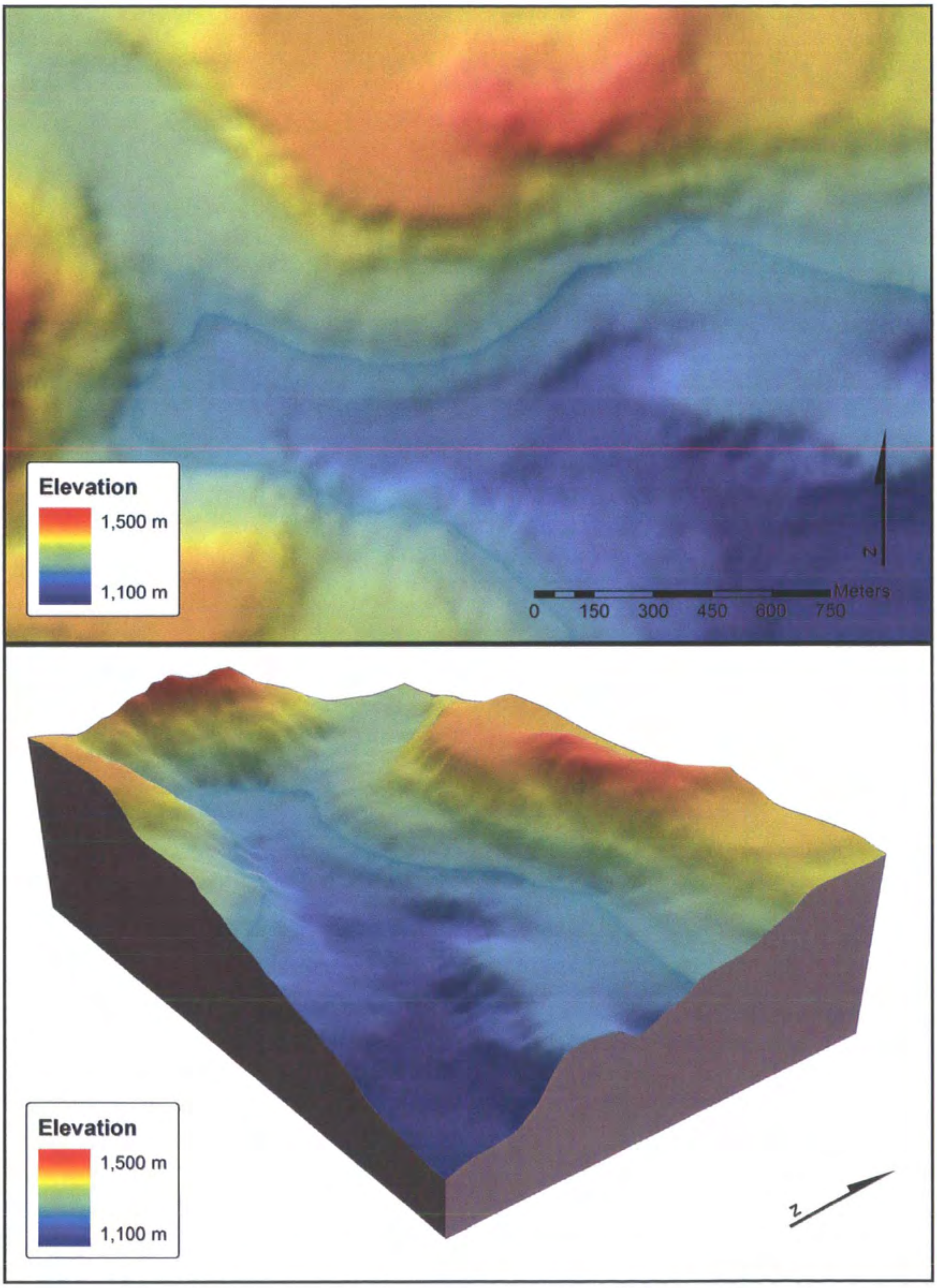


Figure 2.6 Two- and three-dimensional representations of the digital elevation model that was constructed of the study area.

annual home range were used in estimates of species density and food availability (Section 4.4). Since at the onset of sampling no definite vegetation types could be drawn up, species-area curve analyses to aid in the estimation of adequate quadrat size for the different plant communities were not feasible. Instead, a standard quadrat size of 100 m^2 (with sides in a 1:2-ratio) was chosen for all quadrats (Brower *et al.*, 1997; Ganzhorn, 2003). All woody plants with a trunk circumference at breast height greater than, or equal to, 10 cm were identified and measured. Structural variables acquired were circumference at breast height (for each trunk in the case of multi-stemmed individuals), maximum height, maximum crown diameter and crown diameter perpendicular to maximum crown diameter. From these, commonly used parameters related to plant productivity (Chapman *et al.*, 1992; Ganzhorn, 2002; Ganzhorn, 2003) were derived. In addition, data on local slope, aspect, percentage of herb-cover and rockiness were scored for each quadrat.

2.5.4 Point quarter sampling

The anchor points of quadrat sample plots, had also been intended for use in a habitat visibility analysis utilising point quarter sampling. On a monthly basis, a digital camera was to be set up at breast height at these anchor points to take a picture of a 1m x 1m red square, placed at breast height at a 10 m distance in the plane perpendicular to local directional slope. This procedure was to be performed for all four cardinal compass directions at each anchor point. The resulting digital photos could subsequently be imported into GIS-software to calculate the percentage of the surface of the red square not obscured by branches and leaves. The average value of these four directional visibility percentages would then be taken as an estimate of the mean horizontal habitat visibility at each point quarter sample. A similar technique was to be employed in determining vertical habitat visibility which would effectively result in an estimate of the percentage vegetational cover. However, due to the time-demanding nature and practical limitations of this technique in an extremely densely vegetated study area, this approach had to be abandoned at an early stage in the project.

2.5.5 Phenological sampling

Habitat wide productivity and food availability were monitored in the field on a monthly basis by assessment of the developmental stage of and counts of different plant parts on selected food species. This was done by walking phenological transects which were established in a way to achieve even sampling throughout the monkeys' home range. Along transects, 10 individuals of each of 9 selected tree species (Section 4.3.2) were labelled for monthly monitoring. Species were selected on the basis of their supposed importance to the monkey's diet at the time phenological sampling commenced in May 2005. Structural parameters were collected at this time as well. Data on the percentage of leaf cover, number of flowers and number of fruits were scored. The latter two were estimated on a logarithmic scale and, when direct counts were unfeasible, assessed by counting all items in a selected area of the tree and subsequently multiplying the obtained value by the number of times the sampled area would fit into the entire tree. Developmental stages that were discerned, varied from 'not applicable' (when the item was absent) to 'mature' (leaves and flowers) and 'overripe' (fruits).

2.6 Behavioural measurements

Behavioural data were collected from dawn till dusk on several successive days each month from January 2005 till the end of April 2006. Only behavioural observations obtained during the first seven complete follow days (*i.e.* days upon which the animals were observed travelling from sleeping tree to sleeping tree, without losing audiovisual contact over a continuous period exceeding 60 minutes) of each month within the May 2005-April 2006 period are used in the analyses presented in this thesis. A handheld computer (Palmtop™ Zire™ 21, equipped with the Pendragon Forms® 4.0 software package), GPS (Garmin® GPS 72) and paper notebook served as recording media. The three adopted recording methodologies are discussed in more detail below.

2.6.1 Focal animal sampling

To ensure that each focal animal was sampled evenly throughout a follow day, daily photoperiod was divided into four time zones of equal duration. Data collection was scheduled in a way to warrant that each individual was sampled during three successful 10 minute focal periods in each daily time zone per month, with instantaneous point samples (Altmann, 1974; Martin and Bateson, 1993) of the animal's activity at 60 second intervals. This approach yielded 10 point samples for each individual per complete focal session, which was equivalent to 120 point samples per individual per month (30 samples per individual in each of the four time zones). The same individual was, moreover, never sampled during successive time zones on the same day to warrant independence of measurements. This meant that a theoretical minimum of six complete follow days was required to obtain three successful focal samples per animal per time zone. All adults within the group were sampled from the outset of data collection, or, in the case of adults immigrating into the group during the study period, from the month following the

Table 2.3 Behavioural state and associated parameters collected at instantaneous point samples during focal animal sampling -continued on next page-.

	Main focal form	
Field	*Description*	*Input*
General		
Time	Time of day	hh:mm
Counter	Number of sample point	1-10
Time Zone	Number of time zone	1- 4
Weather	Brief characterisation of weather	*e.g.* sunny, misty
Focal		
Individual	Identity of individual	ID code of animal
Infant (when relevant)	Distance of dependent offspring to mother	1, 2, 3, 4, 5, 5< m
Activity	Behavioural state of individual at sample point	F, M, S, R, Out of sight
Position		
Sun	At least half of body surface in direct sunlight	yes, no
Position	Position of individual in relation to others in group	front, centre, side, back
Height	Height of individual above ground	0, 2, 5, 10, 15, 20, 25
Refuge (if Height =0)	Distance to refuge	0, 2, 5, 10, 15
Neighbour		
Neighbour	Identity of closest adult individual ≤ 5m	ID code of animal
Distance to neighbour	Distance to closest adult individual	0, 1, 2, 3, 4, 5 m
Continuous		
Interrupt	Individual breaks continuity of activity for ≥ 5 s	yes, no*
Remarks	Any noteworthy observation	Text

	Focal sub-forms	
Field	*Description*	*Input*
Feeding (F)		
Action	Mode of manipulation of food item	*e.g.* search, reach, bite
Item	Classification of food item	*e.g.* inanimate, fungi
Part	Part of food item being manipulated	*e.g.* seed, leaf, gum, egg
State	Developmental state of food item	*e.g.* ripe, unripe, adult
Species	Scientific name (plant food items only)	*e.g. Acacia karroo*
Moving (M)		
Gait	Mode of locomotion	*e.g.* walk, trot, climb
Speed	Velocity of locomotion	slow, normal, fast
Direction	Line, course or aim of locomotion	*e.g.* food patch in
Interpretation	Functional reading of behaviour	locomotion, foraging
Social (S)		
Affiliative	Benevolent interaction	allogroom, play, sex
Agonistic	Aggressive or defensive interaction	*e.g.* chase, hit, flee
Partner	Other individual involved in the interaction	ID code of animal
Resting (R)		
Autogrooming	Individual grooming part of own body	yes, no
Eyes	State of eyes	open, closed, unknown
Stance	Position of the body	*e.g.* sit, lie, quadrupedal
Posture (if Stance= sit)	Bearing or pose of the body	open, normal, closed
Interpretation	Functional reading of behaviour	*e.g.* pause, vigilance

* Strictly speaking the 'Interrupt' field qualifies as 1/0-sampling (Altmann, 1974; Martin and Bateson, 1993) rather than focal animal point sampling.

animal's first appearance (by which time a level of habituation was achieved that allowed focal sampling of the immigrant).

Due to the ruggedness of the terrain and dense nature of the vegetation throughout the study area, observation conditions were challenging. As a consequence, it was often impossible to stay in constant visual contact with the focal animal during a 10 minute sample period. To obviate this intricacy, a minimum of seven sample points at which the animal had to be in sight was set for a sample period to be considered successful. If this criterion was not met, the collected data were discarded and a new sample attempt was undertaken. This could usually be accomplished within the same time zone on the same follow day. On the relatively rare occasion, however, that this was not achieved, the lacking data were collected in the corresponding time zone on the seventh follow day of the month. In this respect the seventh follow day effectively served as a safety margin to assure equal data collection on all focal animals.

In addition to recording the behavioural state of the focal individual at each sample point, a number of other parameters were scored. A tabular overview is presented in Table 2.3. The use of the Pendragon Forms® 4.0 software package allowed highly automated and, therefore, fast data collection. Data were mostly fed into the system through pop-up menus and look-up lists from which the appropriate input could be selected. Back at base camp, data were then transferred to a laptop for storage and further processing.

2.6.2 Instantaneous group scan sampling

Instantaneous scan samples (Altmann, 1974; Martin and Bateson, 1993) with a duration of 5 minutes were collected at 30 minute intervals throughout a follow day to gather data on individual activity and behavioural synchronisation at the group level. The forms used for instantaneous group scan sampling were based on those used for focal animal sampling but, in addition, included an estimate of total group spread. Moreover, all individuals (adults and immatures alike) were scored. The number of individuals monitored during these sample periods varied from 0 to 13, with a median value of 4 individuals per scan.

Geographical coordinates for the centre of mass of the group were collected on all seven complete follow days each month; at the onset of first activity in the morning, the cessation of all activities in the evening -thus capturing the locations of sleeping sites- and throughout the day directly following instantaneous group scan samples. For this, a Garmin® GPS 72 was used which, for 5 minutes, was allowed to obtain a stable satellite signal. To enhance satellite reception it was often necessary to climb trees or cliffs, especially when the animals were close to the base of steep cliffs. Accuracy of satellite measurements averaged well below 10m (mean ± sd= 6.9m ± 2.3), thereby yielding very accurate input for estimates on day journey length and home range size (Section 5.2). At the end of each month, all coordinates were imported into a dBase-file using the DNR Garmin 4.4 software package for further processing and analyses.

2.6.3 Ad libitum sampling

Besides focal and scan sampling, supplemental observations were made on an ad libitum basis (Altmann, 1974; Martin and Bateson, 1993), both within and between focal and scan sampling periods. A paper notebook was used to write down information on alarm responses, agonistic and dominance interactions within the group, between group encounters and encounters/associations with other animals. Copulations and demographic changes in group composition were scored in the same way. A concise overview of the respective parameters scored for these collateral observations is provided in Table 2.4.

Table 2.4 Supplemental observations made on an ad libitum basis

Observation	Parameters
alarm responses	Date, Time, Individual, Presence/Absence Loud Calls, Predator, Group Response, Remarks
agonistic/dominance interactions	Date, Time, Actor, Behaviour, Reactor, Behaviour, Remarks/Context
between group encounters	Date, Time, Duration, ID other group, Chases (inter- intragroup), Physical Contact, Remarks
encounters with non-specifics	Date, Time, Species, Response, Remarks
copulations	Date, Time, Male, Female, Successful, Remarks
demography	Date, Individual, Birth, Immigration, Death, Emigration, Disappearance

2.7 Data analysis

Statistical analyses were conducted using a suite of software packages including SPSS 11.0 (SPSS Inc, 2001), IDRISI Andes (Eastmann, 2006) and SAM 2.0 (Rangel *et al.*, 2006). In addition, two analytical add-ins for ArcGIS 9.0 (ESRI, 2004) were employed: Hawth's Analysis Tools 3.26 (Beyer, 2004) and a currently unreleased version of Home Range Tools (Rodgers *et al.*, 2005), kindly made available by Dr. H.L. Beyer. An add-in for Microsoft Excel was used in analyses of spatial autocorrelation (ROOKCASE Sawada, 1999). Details on the followed statistical procedures are presented where relevant, but as a general rule assumptions of parametric and non-parametric techniques were assessed prior to analysis. Results are reported to be significant if two-tailed α-

values are below .05 (in the absence of Bonferroni corrections). To aid interpretation of the numerous tables throughout this script, statistically significant results are presented in a ***bold italic*** font, whereas statistical trends ($.05 < p \leq .10$) are printed in *italics*.

3 Climate and primary productivity

3.1 Introduction

One of the fundamental challenges within behavioural ecology lies in the identification of the proximate mechanisms that link environmental parameters to behavioural phenomena of one's study organism. Despite the inherently complex nature of ecological systems, characterised by both direct and indirect causal relationships and intricate feedback loops, a natural cascade among constituent variables can often be established. In models of primate socio-ecology, climate and primary productivity are generally thought to be key environmental factors at the top of the causal cascade underpinning primate societies (see Figure 1.3). Unfortunately, information on primary productivity has traditionally been far less straightforward to collect than information on climatic conditions. This situation has led quantitative modelling efforts to characterise primate habitats in terms of direct climatic factors (*e.g.* thermoregulatory stress; Hill, 2005), and indirect, climatic, proxies for primary productivity (usually indexed by rainfall (van Schaik *et al.*, 1993; 2005; Williamson and Dunbar, 1999)). Given the extensive literature on the well established causal relationship between climate and primary productivity (Rosenzweig, 1968; le Houérou and Hoste, 1977; 1981; 1984; Tuhkanen, 1980), this approach seems entirely justified. Nevertheless, the indirect assessment of primary productivity through its association with rainfall, may introduce undesirable noise in socio-ecological models of primate societies.

The last couple of decades have seen an exponential rise in the ecological application of remotely sensed data. Remote sensing (Lillesand *et al.*, 2004) has opened up a whole new realm of research perspectives and continues to prove an invaluable data source for biologists from varying fields (Kerr and Ostrovsky, 2003; Turner *et al.*, 2003). It has facilitated unprecedented insights into the relationship between climate and vegetation (biomass: (Tucker *et al.*, 1985b), net primary productivity: (Chong *et al.*, 1993), dynamics: (Anyamba and Tucker, 2005); biodiversity: (Waring *et al.*, 2006)). More recently this success in the ecological and plant sciences has been extended to explorations of the causal links between climate, vegetation and animal characteristics (biomass: (Evans *et al.*, 2006); body mass: (Pettorelli *et al.*, 2006); demography: (Rasmussen *et al.*, 2006); migration: (Hurlbert and Haskell, 2003); biodiversity: (Bailey *et al.*, 2004)). Despite these exciting developments and innovations in diverse ecological fields, fully integrative applications of remotely sensed data and Geographical Information Systems (GIS) within primatology have been few (Hughes, 2003).

This chapter, then, will explore sources of information that, up to this point, may have been underexploited by the primatological community. Extensive and accurate spatial datasets for climatic variables and primary productivity are developed for the whole of sub-Saharan Africa. These spatial datasets stem from GIS and remote sensing sources and are compiled in a format suitable for direct implementation into the systems model of vervet monkey socio-ecology that will be developed in Chapter 7. Here, these data are mainly used to assess the robustness of the annual association between climate and primary productivity at different spatial resolutions over sub-Saharan Africa. In addition, similar relationships are established more locally over the Soutpansberg area on a monthly basis. Current analyses mainly serve to illustrate the validity and potential pitfalls of the sole use of climatic data in models of primate socio-ecology and, in addition, draw attention to the inherently spatial nature of ecological data.

3.2 Sources of spatial information

Ideally, detailed climatic data and weather records should be readily available for each primate field site. In reality however, on site monitoring of atmospheric conditions is rarely the norm and data are often taken from a 'nearest' weather station, which may be far away and experiencing an accordingly different micro-climatic regime. The consequent inaccuracy of climatic input variables will leave ensuing modelling efforts flawed, a situation likely to be aggravated by utilising faulty climatic data to approximate primary productivity. Models of primate socio-ecology, therefore, stand a lot to gain from the use of spatially more accurate climatic data and by the implementation of a direct measure of local primary productivity. In this section, two such datasets are compiled to cover the natural distribution of vervet monkeys. Since different ecological communities within this geographical extent are likely to display different dynamics that, if pooled together, may confound interpretation, an additional dataset is implemented to allow investigations of the association between climate and primary productivity at different, biologically meaningful, spatial units.

3.2.1 Climate

Climatic data for Africa were extracted from the spatially interpolated climate dataset for global land areas developed by Hijmans *et al.* (2005). Although numerous datasets of climatic conditions over global land areas are available (*e.g.* Willmott and Matsuura, 2006; New *et al.*, 1999; New.*et al.*, 2002) this dataset was considered superior to others because of its: a) continuous surface format, directly suitable for GIS analysis; b) very high spatial resolution (the principal product has a 30 arc seconds resolution, which is equivalent to an area of 0.86 km^2 at the equator); c) the quantity of weather stations providing the input-data (global total numbers for precipitation: 47,553; mean temperature: 24,542; maximum or minimum temperature: 14,930) and; d) the use of a well-performing interpolation algorithm, incorporating high quality elevation data from the Shuttle Radar Topography Mission project (SRTM; for details see www2.jpl.nasa.gov.srtm).

Monthly averages of climatic variables measured at all weather stations were compiled, mostly for the period 1950-2000, and spatially interpolated to create global climate surfaces for mean monthly precipitation, minimum and maximum temperature. In addition, 19 variables were calculated to generate biologically more meaningful climate surfaces. These bioclimatic variables mainly represent annual trends (*e.g.* mean annual temperature), seasonality (*e.g.* the coefficient of variation for precipitation) and extreme or potentially limiting climatic factors (*e.g.* mean maximum temperature of the warmest month). For the purposes of this chapter, the 2.5 arc minutes ESRI-grid product (version 1.4) was downloaded from www.worldclim.org and Figure 3.1 shows a graphical representation of two example datasets.

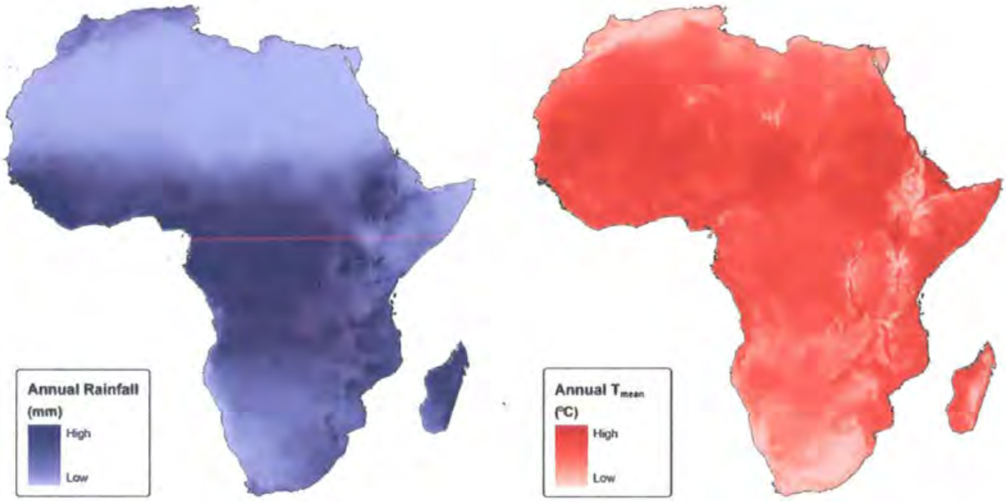


Figure 3.1 Graphical representation of two key variables in the climatic dataset composed for Africa. The intensity of colour corresponds to quantitative data stored in a geographically associated table.

3.2.2 Primary productivity

Numerous vegetation indices have been developed within the remote sensing community to monitor spatio-temporal patterns in terrestrial green vegetation, (Rouse Jr *et al.*, 1974; Tucker, 1979; Huete, 1988; 2002; Myneni *et al.*, 1995; Verstraete and Pinty, 1996; Thiam and Eastman, 2006). A vegetation index is essentially an arithmetic transformation of the information captured by two or more spectral bands of a remote sensing device that enhances the contribution of vegetation properties in the output imagery. Thereby, these indices facilitate a more reliable quantitative assessment of terrestrial photosynthetic activity and structural variation in vegetation canopy (Huete *et al.*, 2002).

One of the first and still most widely applied vegetation indices (despite its shortcomings; Huete *et al.*, 2002) is the Normalised Difference Vegetation Index (NDVI; for an overview of the scope of ecological applications for this index, see: Pettorelli *et al.*, 2005). The NDVI is a slope-based index (Jackson and Huete, 1991) and is defined as:

$$\mathrm{NDVI} = \frac{\rho_{NIR} - \rho_{red}}{\rho_{NIR} + \rho_{red}}$$

, where ρ_{NIR} and ρ_{red} are the bidirectional surface reflectance factors (*i.e.* the amount of sunlight reflected by the earth surface and captured by the sensor) for the near infra-red and visible red regions of the electromagnetic spectrum. This formula, as is true for most vegetation indices, exploits the distinctively differential interaction between green vegetation and energy in the visible and near infra-red regions of the spectrum (Tucker, 1979).

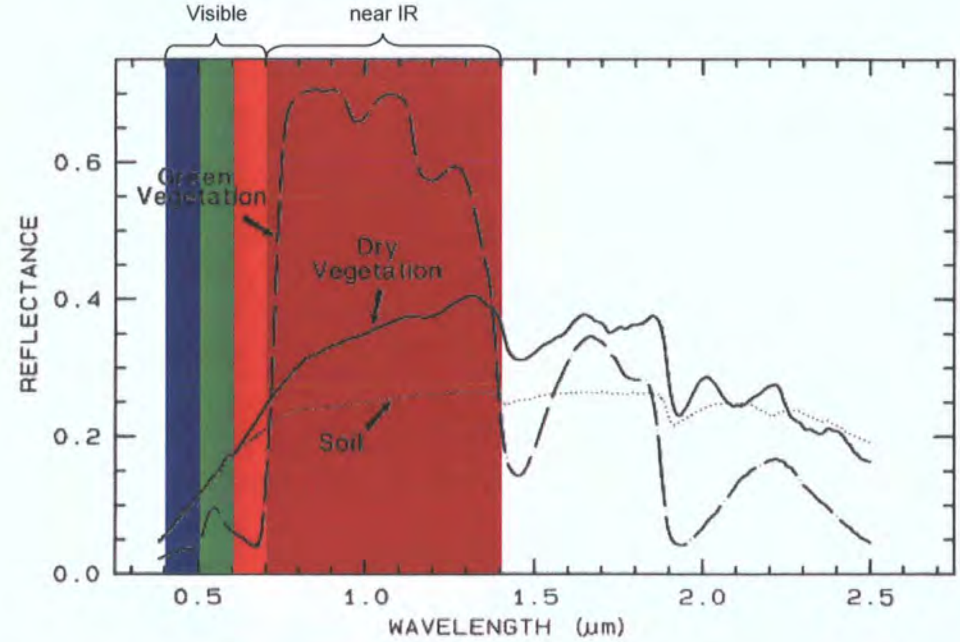


Figure 3.2 Illustration of the reflectance pattern of healthy green vegetation in comparison to other substrates typically scanned by land surveying satellites. The strong disparity in the amount of energy reflected in the visible red and near infra-red regions of the spectrum is exploited by the NDVI to obtain accurate quantitative assessment of photosynthetic activity on the planet's surface (figure adapted from Clark, 1999).

Plant pigments (most notably chlorophyll) strongly absorb energy for photosynthetic activity in the visible part of the spectrum (Figure 3.2).This is most pronounced for the blue and, in particular, red wavelengths which leads to the characteristic green colour of healthy leaves. The energy of near infra-red wavelengths, however, is not used in photosynthesis but is instead strongly scattered by the internal leaf structure. This results in a very high apparent reflectance of near infra-red spectral energy.

As follows from its formula, the NDVI is a dimensionless index which can adopt values that range from -1 to 1. Negative values correspond to an absence of vegetation and higher positive values signify more photosynthetically active vegetation. The NDVI has successfully been applied to appraise direct effects of climatic conditions on vegetation at various spatial and temporal resolutions (Schultz and Halpert, 1993; Nicholson and Farrar, 1994; Kawabata *et al.*, 2001; Lucht *et al.*, 2002; Nemani *et al.*, 2003; Wang *et al.*, 2003; Herrmann *et al.*, 2005; Vicente-Serrano *et al.*, 2006).

Numerous NDVI datasets from different sources are available, each with their specific spatio-temporal resolution and coverage. The dataset chosen here is derived from data collected by the Advanced Very High Resolution Radiometer (AVHRR) meteorological satellites (Cracknell, 2001) operated by the United States' National Oceanic and Atmospheric Administration (NOAA). AVHRR daily daytime 4 km global area coverage data were processed into an 8 km spatial resolution dekadal (10 day) composite NDVI time-series for the African continent by the Global Inventory Modelling and Mapping Studies (GIMMS) group at the National Aeronautics and Space Administration's (NASA) Goddard Space Flight Centre (Tucker *et al.*, 2005). The temporal coverage of this dataset extends from July 1981 to December 2004. The main innovations in this dataset include corrections for: a) residual sensor degradation and sensor intercalibration differences; b) effects of changing solar zenith and viewing angles; c) volcanic stratospheric aerosols; d) atmospheric water vapour and cloud cover using non-linear empirical mode decomposition methods (Pinzon *et al.*, 2004) and; e) maximum value compositing to minimize cloud contamination (Holben, 1986). A final advantage of the dataset is its dynamic range, which is similar to that of NDVI data from more advanced satellite sensors such as the Moderate Resolution Imaging Spectrometer (MODIS; see Chapter 4), thereby allowing direct comparisons. The African dekadal NDVI product was downloaded from the Africa Data Dissemination Service (ADDS) website of the United States Agency for International Development's (USAID) Famine Early Warning System (FEWS) at http://earlywarnings.usgs.gov/adds.

3.2.3 Spatial units of analysis

Data to define the spatial units at which the association between climate and primary productivity was examined, were retrieved from the digital global map of terrestrial ecoregions, described in (Olson *et al.*, 2001). This dataset was downloaded from the Global Environment Outlook (GEO) database on the United Nations Environment Programme's website (UNEP: http://geodata.grid.unep.ch/).

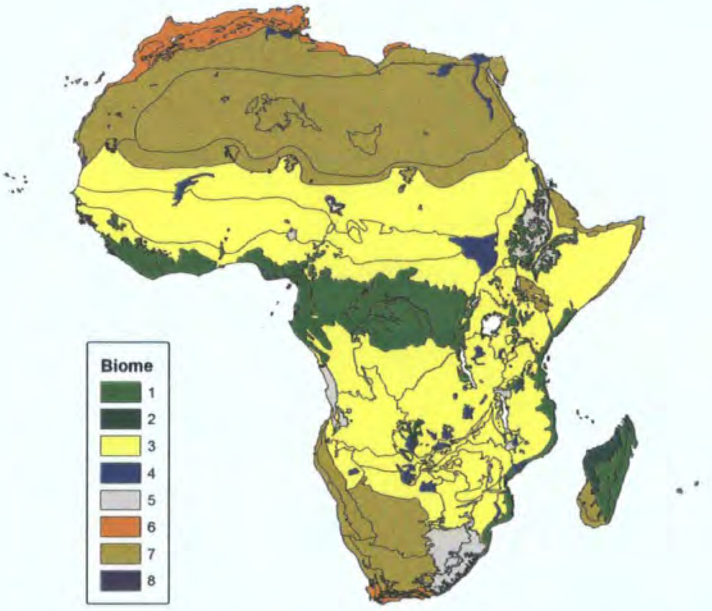


Figure 3.3 Map of the different terrestrial biomes and ecoregions that are distinguished within Africa. Biomes are indicated by colours whereas ecoregions are demarcated by black polygons (Legend key: 1 Tropical & Subtropical Moist Broadleaf Forests; 2 Tropical & Subtropical Dry Broadleaf Forests; 3 Tropical & Subtropical Grasslands, Savannas & Shrublands; 4 Flooded Grasslands & Savannas; 5 Montane Grasslands & Shrublands; 6 Mediterranean Forests, Woodlands & Scrub; 7 Deserts & Xeric Shrublands; 8 Mangroves).

The map recognizes 90 ecoregions within 8 biomes in sub-Saharan Africa (Figure 3.3) and was originally designed for conservation planning on global and regional scales. It represents a very high resolution biogeographical resource and is the result of an extensive collaboration between over a 1,000 biogeographers, taxonomists, conservation biologists and ecologists from around the world (Olson *et al.*, 2001). In the demarcation process, the authors defined an ecoregion as 'a relatively large unit of land containing a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of those natural communities prior to major land-use change'. A biome was subsequently defined as 'an aggregation of ecoregions that: a) experience comparable climatic regimes; b) have similar vegetation structure; c) display similar spatial patterns of biodiversity; d) contain flora and fauna with similar guild structures and life histories; e) have similar minimum requirements and thresholds for maintaining certain biodiversity features; and f) have similar sensitivities to human disturbance'. Ecoregions and biomes, consequently, reflect the distribution of species and communities more accurately than other conceivable geospatial units, based on, for example, gross biophysical features such as rainfall and temperature (Köppen, 1884), vegetation structure (*e.g.* for Africa; White, 1983) or spectral signatures from remote sensing data (Tucker *et al.*, 1985a; DeFries *et al.*, 1995; Loveland and Belward, 1997a; 1997b; 2000). Ecoregions are, moreover, thought to approximate the dynamic arena within which ecological processes interact most strongly (Orians, 1993).

3.3 Compilation of datasets

The raw data described in the previous section required careful manipulation and examination to ensure inter-consistency and conformity before they could serve as auxiliary datasets in the construction of a primate systems model. Moreover, to investigate the association between climate and primary productivity, independence within and between variables had to be assessed.

3.3.1 Pre-processing

The combined raw datasets consisted of 55 climate surface grid files (12 for mean monthly precipitation, 24 for mean monthly maximum and minimum temperature and 19 for the aforementioned bioclimatic variables), 36 dekadal NDVI Band-Interleaved by Line (BIL) files and 1 vector file representing the global map of terrestrial ecoregions. The map of terrestrial ecoregions was firstly converted to three grid files; one to demarcate sub-Saharan Africa ecoregions, one to demarcate sub-Saharan Africa biomes and one to demarcate the Soutpansberg area. These three files, along with the 55 climate surface files, were subsequently reprojected in Albers Equal Area Conic projection to match the coordinate system of the NDVI dataset[†]. To avoid pseudo-replication and spurious associations within the data, a nearest neighbour resampling algorithm was concurrently applied and output files were clipped to match pixel size (64 km^2) and spatial extent of the NDVI dataset. Then, all 94 grids were converted to ArcInfo raster ASCII format and imported into the IDRISI Andes software package for further pre-processing and analyses.

A number of additional climate surfaces were constructed for specific variables that have been found to be of particular relevance to the socio-ecology of primates (Bronikowski and Webb, 1996; Williamson, 1997; 1999; Hill, 1999; 2002). These included surfaces for mean monthly temperature and two additional indices of seasonality (Shannon's index of rainfall evenness and the number of months in which rainfall, expressed in mm, exceeds twice the mean monthly temperature, expressed in °C -*i.e.* the length of the growing season, (le Houérou and Popov, 1981)-). Climate surfaces for time-lagged variables (rainfall and mean temperature of the previous month) and a cumulative variable (rainfall over the current and preceding two months) were also calculated, given their reported relationship to monthly primary productivity (Schultz and Halpert, 1993; Nicholson and Farrar, 1994; Farrar *et al.*, 1994; Wang *et al.*, 2003; Herrmann *et al.*, 2005).

[†] A new projected coordinate system file had to be written for this. Based on the Albers equal area conic projection provided in the ESRI database, the following parameters were modified: the central meridian was reset to 20.0, the 1st and 2nd standard parallels were changed to -19.0 and 21.0 respectively, and latitude of origin was changed to 1.0. Lastly, the geographic coordinate system was altered to Clarke 1866.

Monthly maximum value composites were calculated from dekadal NDVI data (Figure 3.4). This served to minimize signal degradation due to atmospheric, zenith angle, cloud cover and topographical contaminations (Holben, 1986) while at the same time matched the temporal resolution of NDVI data to that of all climatic variables. From these monthly maximum value composites, a quadratic mean annual composite was created to approximate mean annual productivity. All byte binary NDVI values were then converted to real NDVI values by an arithmetic scalar transformation.

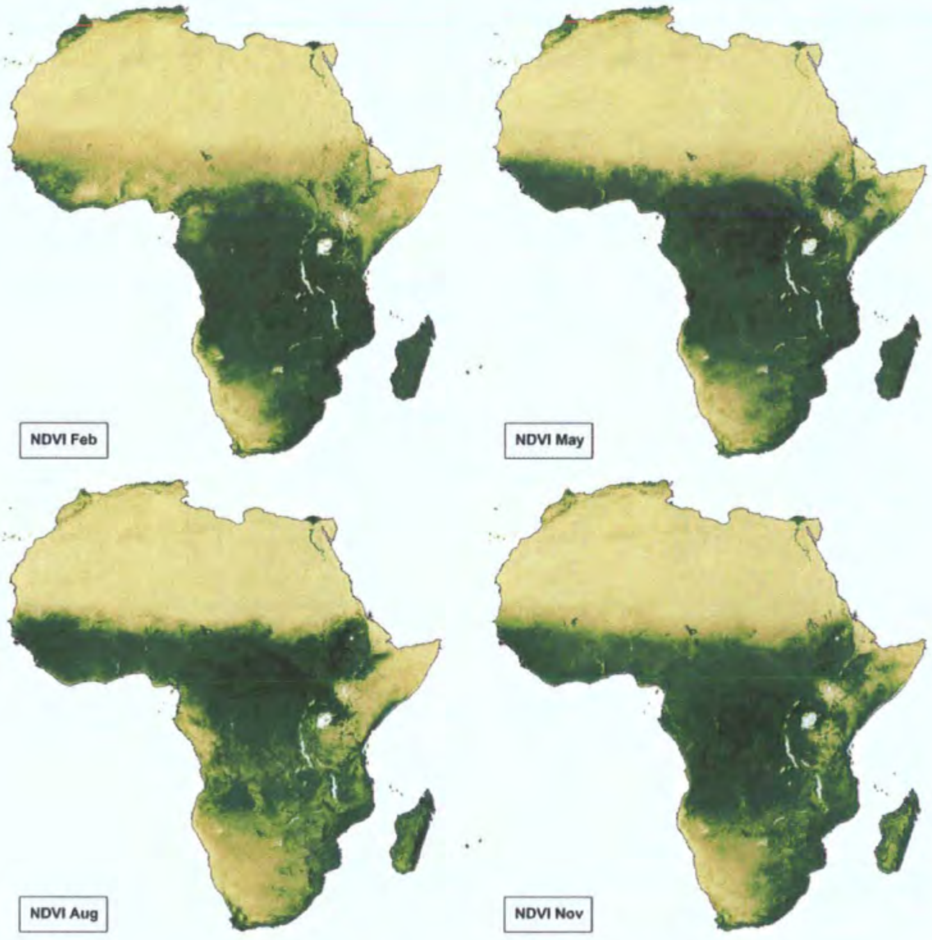


Figure 3.4 Four monthly maximum value composites of the AVHRR NDVI data illustrating seasonality in plant productivity over Africa. Dark green colours indicate high photosynthetic activity, light brown areas correspond to low photosynthetic activity.

Finally, mask images were composed for the different spatial units of analysis (ecoregions and biomes of sub-Saharan Africa and the Soutpansberg area). Care had to be taken in defining the masks to exclude all redundant pixels introduced by the resampling and reprojection procedures on input data from different sources.

3.3.2 Spatial autocorrelation

Given the inherently spatial nature of the datasets used in this chapter, it is important to control for the presence of spatial autocorrelation prior to analyses. Spatial autocorrelation may seriously complicate the analysis and interpretation of spatial data in ecology and, if unaccounted for, will result in an overestimation of effective sample size (Clifford *et al.*, 1989), incorrect significance levels (Legendre, 1993) and potentially even a systematic bias towards certain explanatory variables (Lennon, 2000); but see: (Diniz *et al.*, 2003). Surprisingly, it is still regularly ignored or not even identified as a confounding factor in numerous studies in spatial ecology (Lennon, 2000).

Levels of autocorrelation within the compiled datasets were exceptionally high (typically: Rook's case 1st lag Moran's $I > .90$, $p < .001$). This implied that findings from spatially non-explicit analyses on a pixel by pixel basis would be misleading and difficult to interpret. A crude, yet statistically valid way around this complication has been suggested by running spatially non-explicit analyses on a subset of data in which the level of autocorrelation is not significant (Legendre, 1993; Lennon, 2000). Two different sub-sampling routines were adopted here: 1) a random, spatially non-autocorrelated subset of 1,000 pixels (Rook's case 1st lag $z_{\text{Moran's } I} < 1.96$, for all datasets) was selected over the whole of sub-Saharan Africa and; 2) average values were extracted for each ecoregion and biome. The latter procedure, although suffering from the disadvantages of dramatically decreasing sample size and removing spatial information from the data, has the biological advantage of focussing on ecologically meaningful units of analysis. As an extra precaution to inflated Type I errors, correlations between climate and primary productivity within the random subset of 1,000 pixels were assessed using both standard and spatial procedures (Dutilleul, 1993). Similarly, standard and spatial associations between monthly climate and primary productivity were investigated over the Soutpansberg area on a random, spatially independent (Rook's case 1st lag $z_{\text{Moran's } I} < 1.96$ for all parameters) subset of 25 pixels.

3.3.3 Independence of variables

The inter-relatedness between climatic variables is a well-known phenomenon (le Houérou and Hoste, 1977) and to avoid complications in terms of strong collinearity between predictor variables in the eventual regression analyses of Chapter 7, analyses are confined to three principal components of sub-Saharan African climate (Williamson, 1997). These key variables are total annual rainfall, a measure of rainfall seasonality (indexed by three different variables) and mean annual temperature. Independency was evaluated using the 1,000 pixel subset described above (Table 3.1).

Table 3.1 The outcome of exploratory Pearson correlation analyses to assess the degree of interrelatedness between three principal components of sub-Saharan African climate. Results from standard correlation analyses are given above the diagonal, those from spatial analyses (Dutilleul, 1993) below.

		P	P>2T	$P_{Shannon}$	P_{CoV}	T_{mean}
P	r		***.840***	***.555***	***-.567***	-.027
	df		998	998	998	998
	Sig. (2-tailed)		<.001	<.001	<.001	.392
P>2T	r	***.840***		***.704***	***-.726***	***-.258***
	df	18.22		998	998	998
	Sig. (2-tailed)	<.001		<.001	<.001	<.001
$P_{Shannon}$	r	***.555***	***.704***		***-.989***	***-.453***
	df	28.43	30.41		998	998
	Sig. (2-tailed)	<.001	<.001		<.001	<.001
P_{CoV}	r	***-.567***	***-.726***	***-.989***		***.451***
	df	26.81	28.59	16.26		998
	Sig. (2-tailed)	<.001	<.001	<.001		<.001
T_{mean}	r	-.027	-.258	***-.453***	***.451***	
	df	31.89	39.40	22.36	22.31	
	Sig. (2-tailed)	.880	.101	<.050	<.050	

P = total annual rainfall (mm); P>2T = length of growing season (n months); $P_{Shannon}$ = Shannon's index of rainfall evenness; P_{CoV} = rainfall coefficient of variation; T_{mean} = mean annual temperature (°C)

Before interpreting these results, it is interesting to note that, although no significant spatial autocorrelation was present in the dataset, significance levels of the spatial correlation analyses were more conservative than those of the standard technique. In one instance, the correlation between one of the rainfall seasonality indices (P>2T) and mean annual temperature even lost significance. This strongly underlines the importance of explicitly accounting for the spatial nature of ecological data and the outcome of the spatial procedure should be given precedence over that of the standard correlation.

It is clear from Table 3.1 that the principal components of sub-Saharan African climate are not independent. Despite this, these variables have commonly been applied simultaneously in previous modelling efforts in primate socio-ecology. Some justification for this may lie in the intuitive differential biological significance of the parameters and as long as levels of multicollinearity are not too high, no statistical complications should arise. However, since the three indices of rainfall seasonality investigated here represent different measures of the same climatic parameter, only one of these should be entered in a single regression equation at a time.

3.4 Associations between climate and primary productivity

Now that spatial datasets for climate and primary productivity have been developed, the association between the two can be investigated. This is first done on an annual basis over the whole extent of the potential natural range of vervet monkeys. Subsequently, it will be assessed whether the established associations also hold on a monthly basis over the ecogeographical unit in which the field site of this study was located, the Soutpansberg mountain range in South Africa.

3.4.1 Annual associations over sub-Saharan Africa

The strength of annual linear associations between key climatic variables and primary productivity was assessed at three spatial resolutions through the computation of standard and, where appropriate, spatial correlation coefficients (Table 3.2).

Table 3.2 Summary of standard and spatial (Dutilleul, 1993) correlation analyses between key climatic variables (columns) and primary productivity (rows) at three different spatial resolutions over sub-Saharan Africa.

		P	**P>2T**	**P_{Shannon}**	**P_{CoV}**	**T_{mean}**
NDVI $_{\text{pixel}}$	r	***.749***	***.823***	***.578***	***-.596***	***-.216***
(standard)	df	998	998	998	998	998
	Sig. (2-tailed)	<.001	<.001	<.001	<.001	<.001
NDVI $_{\text{pixel}}$	r	***.749***	***.823***	***.578***	***-.596***	-.216
(spatial)	df	16.46	17.26	39.16	16.00	32.03
	Sig. (2-tailed)	<.001	<.001	<.001	<.001	.219
NDVI $_{\text{ecoregion}}$	r	***.561***	*.770*	***.408***	***-.407***	-.119
(standard)	df	88	88	88	88	88
	Sig. (2-tailed)	<.001	<.001	<.001	<.001	.265
NDVI $_{\text{biome}}$	r	.391	*.720*	.049	-.100	.063
(standard)	df	6	6	6	6	6
	Sig. (2-tailed)	.338	.044	.909	.814	.883

NDVI= Normalised Difference Vegetation Index; P = total annual rainfall (mm); P>2T = length of growing season (n months); P_{Shannon} = Shannon's index of rainfall evenness; P_{CoV} = rainfall coefficient of variation; T_{mean} = mean annual temperature (°C)

Standard and spatial analyses were undertaken on the spatially non-autocorrelated subset of 1,000 pixels. Both approaches illustrated highly significant and strong associations between primary productivity and all rainfall variables under investigation. Interestingly, the standard correlation in addition suggested an association between productivity and mean annual temperature, whereas this relationship was reported as non-significant in the spatial analysis. It thus appears that, despite the level of autocorrelation within the data being not significant, the spatial structure of the data still inflates the significance values of standard analyses. This was unexpected, so precedence of interpretation is given to the outcome of the spatially explicit approach.

Standard correlation coefficients of the linear association between climate and primary productivity at the level of ecoregions, showed similar signs, magnitudes and significance levels to those of the spatial analyses on a pixel by pixel basis. As ecoregions arguably represent the biologically most sound unit of analyses (Orians, 1993), this finding adds greatly to the biological plausibility of the associations established at pixel resolution.

A further decrease in the resolution of analyses resulted in the loss of all but one significant association. At the biome level, only the length of the growing season (P>2T) accounted for a significant proportion of annual primary productivity. The standard correlation coefficient of this association was similar to those in the analyses at the ecoregion and pixel level.

After inspections of scatter plots and given the biological plausibility (Kay *et al.*, 1997), the existence of quadratic associations between total annual rainfall and primary productivity was assessed using regression techniques (Figure 3.5). Again, analyses at pixel resolution took both a standard and spatially explicit approach. In the latter, significant terms of a 3rd order polynomial Trend Surface Analysis (TSA) were incorporated into a partial regression (Borcard *et al.*, 1992; Legendre, 1993; Rangel *et al.*, 2006). This allowed the variation in NDVI values to be partitioned over four components (Table 3.3).

Table 3.3 Overview of the amount of variation within NDVI values of the 1,000 pixel sub-sample explained by the standard and spatial regression model (OLS= ordinary least square estimation).

Regression model	**Component**	**(partial) R^2**		
Standard OLS	Environment (P, P^2)	.788		
	Unexplained	.212		
Spatial Partial OLS	Non-spatial environment (local P, P^2)	.105	.788	.859
	Spatially structured environment (regional P, P^2)	.683		
	Spatial (significant terms of 3rd order TSA)	.071		
	Unexplained	.141		

Note that the spatial model not only explained a larger overall proportion of variation by incorporating the implicit spatial structure of the data, but also differentiated between a non-spatial ('local'; Ruggiero and Kitzberger, 2004) environmental and spatially structured ('regional'; Ruggiero and Kitzberger, 2004)) environmental component.

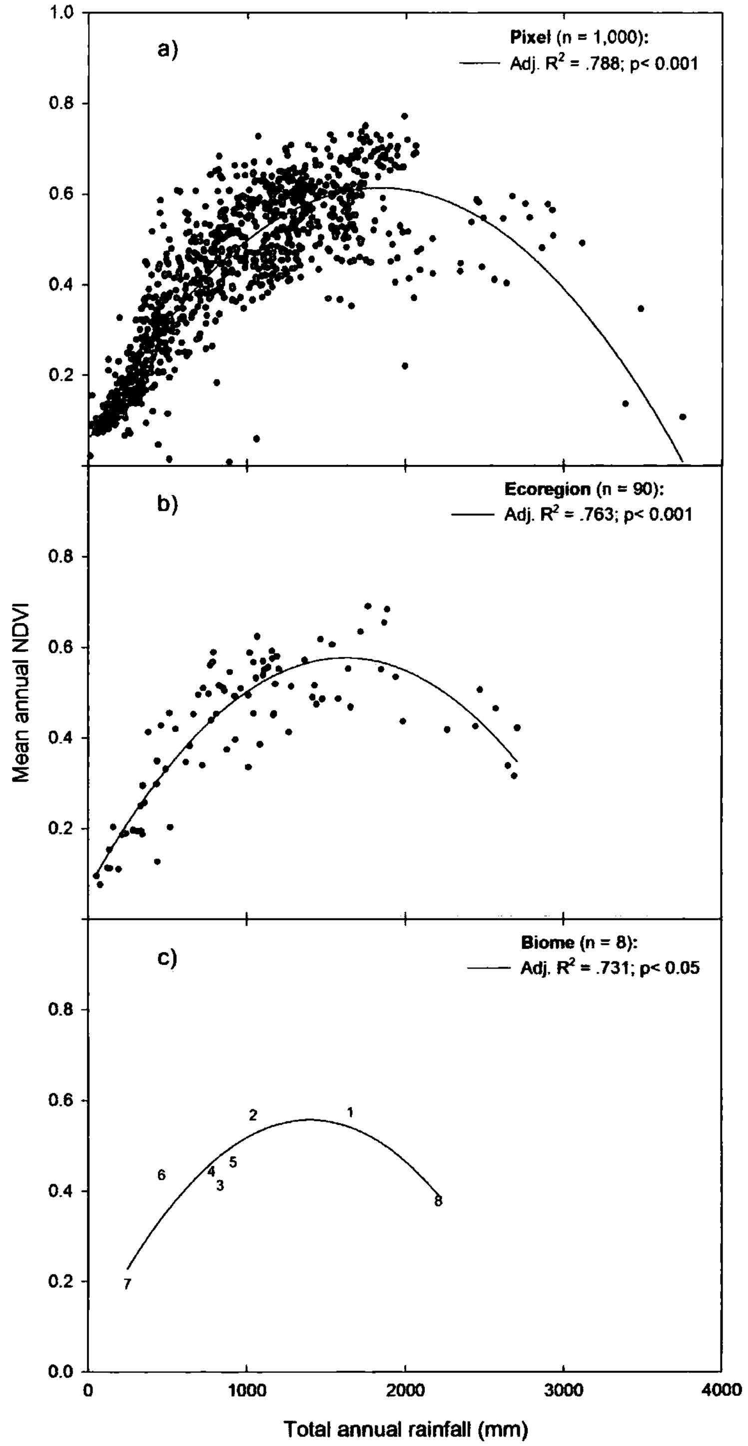


Figure 3.5 Scatter plots and plotted quadratic regression models for total annual rainfall and mean annual primary productivity (NDVI). Quadratic associations were significant at; a) pixel, b) ecoregion and c) biome resolution (see Figure 3.3 for key to biome names). Regression coefficients and significance levels of non-spatial analyses are given for all three units of analyses to allow direct comparison.

All quadratic regressions based on total annual rainfall explained more variance in NDVI values than linear models. At biome resolution this implied that a significant quadratic association was revealed where a linear association had been absent. It should be noted that the sign and magnitude of regression coefficients were similar for all three spatial units of analysis.

To summarize the findings of this section it can be concluded that primary productivity over sub-Saharan Africa showed strong significant quadratic relationships to total annual rainfall, regardless of the spatial resolution of analysis. Out of three rainfall seasonality measures (P>2T, $P_{Shannon}$ and P_{CoV}), the length of growing season (P>2T) displayed both the strongest and spatially most consistent linear relationship to primary productivity. Mean annual temperature was not found to be related to productivity.

3.4.2 Monthly associations over the Soutpansberg mountain range

Intra-annual variability in the significance and strength of association between climatic variables and primary productivity was assessed for the Soutpansberg ecogeographical region. Initially, concurrent, cumulative and lag correlation coefficients were calculated to gauge the strength of linear associations between monthly variables of rainfall, temperature and primary productivity. Significance values of standard and spatial techniques led to different conclusions in 4 out of 72 analyses and, as in the previous section, precedence of interpretation was given to the spatially explicit approach. Results are summarised in Table 3.3.

Rainfall-related explanatory variables showed significant and moderately strong positive associations to primary productivity throughout the year, whereas the best performing temperature-related variable displayed significant negative associations in 4 months only. Out of all rainfall-related variables, total monthly rainfall had the strongest linear association with mean monthly primary productivity over the greatest number of months. Mean monthly temperature was the temperature-related variable most often and most strongly correlated to mean monthly primary productivity.

Table 3.3 Summary of monthly spatial correlation analyses (Dutilleul, 1993) between climatic variables (columns) and primary productivity (rows) over the Soutpansberg area.

		P	**P-1m**	P_{cum3}	T_{min}	T_{mean}	T_{max}
$\mathbf{NDVI}_{\mathbf{January}}$	r	***.626***	***.638***	***.616***	*-.414**	*-.382*	*-.355*
	df	17.69	16.45	17.31	18.84	20.46	20.84
	Sig. (2-tailed)	.003	.004	.004	.063	.075	.097
$\mathbf{NDVI}_{\mathbf{February}}$	r	***.605***	***.627***	***.621***	-.301	-.316	-.324
	df	17.20	18.14	17.53	21.39	21.90	21.91
	Sig. (2-tailed)	.006	.003	.003	.159	.134	.123
$\mathbf{NDVI}_{\mathbf{March}}$	r	***.598***	***.592***	***.601***	-.305	-.302	-.293
	df	18.14	17.35	1.87	19.77	21.31	21.76
	Sig. (2-tailed)	.005	.007	.004	.170	.158	.166
$\mathbf{NDVI}_{\mathbf{April}}$	r	***.584***	***.573***	***.580***	-.215	-.215	-.214
	df	18.36	17.85	17.60	19.94	19.94	20.30
	Sig. (2-tailed)	.006	.008	.008	.337	.337	.335
$\mathbf{NDVI}_{\mathbf{May}}$	r	***.671***	***.589***	***.596***	-.225	-.271	-.303
	df	16.63	17.72	17.29	16.32	17.86	18.83
	Sig. (2-tailed)	.002	.007	.006	.365	.249	.183
$\mathbf{NDVI}_{\mathbf{June}}$	r	***.475***	***.644***	***.575***	-.137	-.181	-.212
	df	15.43	17.30	17.46	15.29	17.19	18.52
	Sig. (2-tailed)	.050	.003	.009	.597	.456	.362
$\mathbf{NDVI}_{\mathbf{July}}$	r	***.567***	***.558***	***.621***	-.201	-.248	-.273
	df	17.74	16.63	17.36	16.81	21.00	23.43
	Sig. (2-tailed)	.001	.014	.004	.413	.253	.182
$\mathbf{NDVI}_{\mathbf{August}}$	r	***.656***	***.601***	***.623***	-.257	-.298	*-.317*
	df	16.50	19.17	18.08	20.26	24.92	27.02
	Sig. (2-tailed)	.003	.004	.003	.245	.132	.094
$\mathbf{NDVI}_{\mathbf{September}}$	r	***.759***	***.738***	***.760***	*-.401**	***-.427***	***-.432***
	df	18.56	15.77	17.44	19.74	22.69	23.56
	Sig. (2-tailed)	<.001	<.001	<.001	.066	.034	.029
$\mathbf{NDVI}_{\mathbf{October}}$	r	***.560***	***.759***	***.655***	***-.456***	***-.432***	*-.405**
	df	16.45	17.97	16.04	20.00	21.19	20.82
	Sig. (2-tailed)	.014	<.001	.003	.033	.039	.056
$\mathbf{NDVI}_{\mathbf{November}}$	r	***.662***	***.536***	***.635***	***-.525***	***-.500***	***-.475***
	df	18.72	17.02	17.78	20.17	21.14	21.20
	Sig. (2-tailed)	.001	.018	.003	.012	.015	.021
$\mathbf{NDVI}_{\mathbf{December}}$	r	***.721***	***.643***	***.661***	***-.540***	***-.517***	*-.493**
	df	13.90	14.41	13.29	12.89	13.59	13.68
	Sig. (2-tailed)	.002	.006	.006	.038	.043	.055

NDVI= Normalised Difference Vegetation Index; P = total monthly rainfall (mm); P-1m = total rainfall previous month (mm); P_{cum3} = cumulative rainfall over the current and two previous months (mm); T_{min} = mean monthly minimum temperature (°C); T_{mean} = mean monthly temperature (°C); T_{max} = mean monthly maximum temperature (°C)

* correlation coefficients that were significant using standard correlation analyses

The observed intra-annual variation in the relative strength of association between climatic variables and primary productivity implied that, in different months different factors may have been constraining photosynthetic activity. This was most pronounced for the effect of temperature, which was only significantly associated to productivity over the last four months of the calendar year. Interestingly, this period roughly coincides with the first half of the warm-wet season in the Soutpansberg.

Inspections of scatter plots were ambiguous about the desirability of investigating potential quadratic relationships between monthly rainfall and primary productivity. Nevertheless, linear and quadratic spatial regression models (see previous section) were constructed. To compare these models, adjusted coefficients of determination and the difference between corrected Akaike's Information Criteria (AICc) were calculated on a monthly basis and subsequently plotted in Figure 3.6.

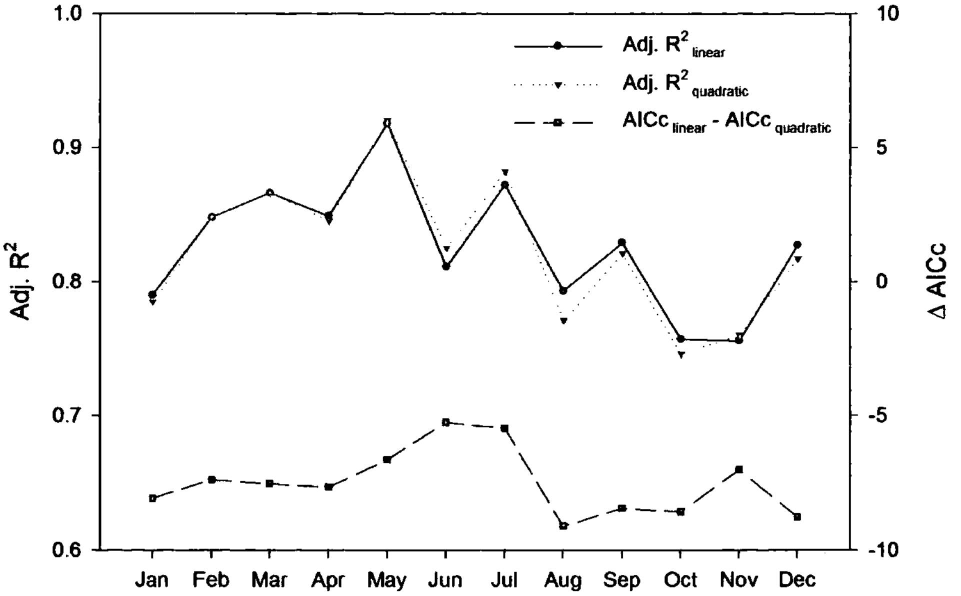


Figure 3.6 Annual profile of the coefficient of determination and Δ AICc of the linear and quadratic regression models that express monthly primary productivity in terms of total monthly rainfall.

The first thing to note from this figure is that coefficients of determination of the linear model are much higher than would be expected on the basis of Table 3.3. This increase in goodness of fit was effectuated by the incorporation of a 3rd order TSA term (see previous section) into the regression model to account for the implicit spatial structure of the data. The figure further illustrates that, on the basis of the values of the coefficients of determination alone, it is impossible to opt for a 'best' model to relate monthly rainfall to primary productivity: during six months of the year the linear model marginally outperforms the quadratic one, whereas the reverse is true for four other months. In two months the coefficients of determination of the models were identical up to four decimals. In contrast, the difference in the information theory based selection criterion employed here (Akaike, 1974; Burham and Anderson, 2002; Johnson and Omland, 2004) gave unequivocal support to the linear model: AICc values of the linear model were consistently smaller than those of the quadratic model, reflected by the consistently negative Δ AICc values in Figure 3.6.

For the Soutpansberg ecogeographical region then, monthly primary productivity was positively correlated to a number of monthly rainfall variables year round. Monthly temperature on the other hand, only exerted a significant negative effect on primary productivity during the first half of the warm-wet season. Subsequent spatial regression analyses revealed that the relationship between monthly rainfall and primary productivity was best expressed by a linear term. Incorporating the spatial structure of the data by a 3rd order polynomial equation moreover, greatly increased the total amount of variation explained by the regression models.

3.5 Discussion

Quantitative approaches to modelling primate socio-ecology have traditionally relied on climatic variables to factor both a direct climatic constraint into the models (thermoregulatory stress), as well as an indirect, climate related, parameter (primary productivity) (Dunbar, 1992; Bronikowski and Altmann, 1996; Srivastava and Dunbar, 1996; Williamson, 1997; Hill, 1999). This indirect assessment of a key input parameter can be imputed to an initial lack of awareness of alternative, more direct measures of primary productivity and, later -perhaps-, the rather specialist knowledge required to extract information from remotely sensed data sources. Another unfortunate confounding factor in the construction of socio-ecological models has been a lack of on site climatic data from primate field studies. This problem has habitually been overcome by direct extrapolation of measurements from a nearby weather station, yet more recent models have shifted to more appropriate interpolation techniques from long term climatic datasets (Korstjens *et al.*, 2006).

This chapter sought to provide a way to overcome these inaccuracies in previous models of primate socio-ecology by compiling long term spatial datasets for both key climatic variables and primary productivity. The climatic dataset presented here, was extracted from spatially interpolated climate surfaces based on extensive field observations, mostly over the period 1950-2000 (Hijmans *et al.*, 2005). Quantitative information on primary productivity on the other hand, was amassed from a well-established spectral correlate of photosynthetic activity (NDVI). The remotely sensed archive from which data were extracted spans the period between July 1981-December 2004 and was produced by the GIMMS group at NASA's Goddard Space Flight Centre (Pinzon *et al.*, 2004; Tucker *et al.*, 2005). Both datasets were tailored for direct implementation into the systems model of vervet socio-ecology that will be developed in Chapter 7. Their respective potential scope, however, is far from limited to the applications within this thesis.

A secondary mainspring of this chapter was to demonstrate the usefulness of the compiled datasets through investigations of the relationship between climate and primary productivity throughout the natural range of vervet monkeys. This was done on an annual basis for the whole of sub-Saharan Africa and on a monthly basis for the biogeographical region in which the field site of this study was situated.

Total annual rainfall was found to be quadratically associated to annual primary productivity, whereas indices of rainfall seasonality were linearly related to annual sub-

Saharan African productivity. Mean annual temperature in contrast, did not correlate significantly with primary productivity. Since the same pattern was found at three spatial units of analysis (pixel, ecoregion and biome), and current findings are in line with previous, more traditional (Rosenzweig, 1968; le Houérou and Hoste, 1977; 1981; 1984; Tuhkanen, 1980) and contemporary (Chong *et al.*, 1993; Nemani *et al.*, 2003; Wang *et al.*, 2003) research, results obtained from annual analyses of the compiled spatial datasets seem both trustworthy and robust.

In a further test of the potential of the developed datasets, the relationship between regional climate and productivity over the Soutpansberg mountain range was assessed on a monthly basis. Monthly primary productivity exhibited a year round positive linear association to monthly rainfall whereas monthly mean temperature was a significantly negative correlate only during the first half of the warm-wet season. Interestingly, this period coincides with the onset of the growing season which may suggest that during this time of the year water loss due to evaporation and evapotranspiration is particularly inhibiting productivity of the Soutpansberg flora.

As stated before, instead of offering an in depth discussion of the underlying mechanisms relating climate to primary productivity, the main aim of the presented analyses was to illustrate the analytical power and usefulness of the compiled datasets. This was done on two, spatial (continental and regional) and temporal (long term averaged annual and monthly) resolutions, relevant to primatologists. In passing, the importance of incorporating the implicit spatial structure of ecological data into statistical analyses and the usefulness of an information theory based model selection criterion have been exemplified. The lessons learned in this chapter then may not only improve the quality of input data, but also the methodological procedures of systems models in primate socio-ecology.

The next chapter will go one step further down the causal cascade underpinning primate behavioural ecology and consider the relationship between primary productivity and food availability. This will be done on a regional and local scale and will integrate detailed field observations on weather conditions and local phenology with concurrently collected remotely sensed data in a GIS environment.

4 Primary productivity, phenology and food availability

4.1 Introduction

The great potential of GIS and remotely sensed data as input for inter-populational models of primate socio-ecology has been alluded to in the previous chapter. Information stemming from spatially interpolated long-term field measurements and satellite monitoring was shown to offer reliable estimates of two key environmental parameters of the models -climate and primary productivity-. Here, additional facets of the potential usefulness of remotely sensed data within ecological primatology are explored.

Vegetation indices, such as the NDVI, not only provide a quantitative measure of primary productivity but also offer valuable information on plant phenology. This information has successfully been exploited in empirical and modelling studies on seasonal habitat productivity and ranging behaviour of herbivorous ungulates (Boone *et al.*, 2006; Ito *et al.*, 2006; Ryan *et al.*, 2006; van Bommel *et al.*, 2006). Unfortunately the relationship between primary productivity and phenology on the one hand and food availability on the other, is less straightforward for opportunistic omnivores such as vervet monkeys. Interestingly though, strong correlations have been found between the NDVI and migration patterns of non-herbivorous birds (Ruegg *et al.*, 2006). Of even greater significance here, are studies that have associated the NDVI to the distribution of non-folivorous primates (including vervet monkeys) in eastern and central Eritrea (Zinner *et al.*, 2001; 2002). It may thus be worthwhile to further explore the usefulness of remotely sensed data to, not only to assess temporal patterns of productivity within the home range area of the study group, but also to relate it to local food availability.

In the first section of this chapter, the association between weather conditions and primary productivity over the home range area of the study group is established by linking field measurements of the former to concurrently remotely sensed information on the latter. Subsequently, primary productivity of the home range area during the observation period is compared to the long-term average and mean annual productivity of its direct surroundings. The second section moves on to investigate whether remotely sensed data can be used to faithfully measure patterns in local phenology. The third section develops estimates of availability and spatio-temporal distribution of key food resources within the home range of the animals. A hybrid approach, in which field observations and remotely sensed data are integrated into a simple model, is developed for later implementation into a GIS.

4.2 Local primary productivity

In a way this section can be viewed as a logical extension of section 3.4 in which the grain of analysis has decreased dramatically. The initial goal is to establish an association between atmospheric conditions and primary productivity, yet the spatio-temporal resolution of enquiry has shifted from a near-continental level, to that of the home range of a single vervet monkey group, and from average field measurements of climatic conditions over several decades, to direct observations of the weather over 12 months. Subsequent tests on the sensitivity of the NDVI, further endorse its usefulness for primatologists.

4.2.1 Association between weather and local NDVI

Most studies that have linked atmospheric conditions to remotely sensed vegetation indices such as the NDVI, have done so by using long-term datasets (Schultz and Halpert, 1993; Kawabata *et al.*, 2001; Nemani *et al.*, 2003; Wang *et al.*, 2003; Anyamba and Tucker, 2005; Herrmann *et al.*, 2005; Vicente-Serrano *et al.*, 2006). This is also true for the previous chapter. Here, a variation on this general theme is introduced to ascertain whether the relationship between atmospheric seasonality and phenological seasonality can also be established at the spatio-temporal resolution of a primate home range during a

12 months observation period. Field measurements from the weather station at the Lajuma Research Centre and concurrently collected NDVI data are correlated on a monthly basis over the period May 2005 - April 2006.

To monitor patterns in the vegetation at the Lajuma Research Centre, data from the Moderate Resolution Imaging Spectrometer (MODIS) were collated for the entire Soutpansberg mountain range. This sensor, operated by NASA as part of its Earth Observing System (EOS) mission, maintains the same high temporal resolution as the AVHRR at a far superior spatial resolution (respective effective pixel sizes at the area of interest: 231m x 231m and 4,000m x 4,000m). It thus allows more meaningful sampling at the scale of a vervet monkey home range. The MODIS NDVI dataset, moreover, had two particularly compelling advantages over alternative datasets from other satellite sensors, namely: 1) a consistent availability of data covering the area of interest over the desired period; and 2) a similar dynamic range as the AVHRR NDVI dataset which allows direct comparisons between the output of two sensors (Tucker *et al.*, 2005; Brown *et al.*, 2006). Monthly maximum value composites (Holben, 1986) were composed from the MODIS/TERRA VI 16 day L3 Global 250m ISIN grid (MOD 13Q) dataset, which was retrieved from the United States Governmental Earth Resources Observation System (EROS) website at http://eros.usgs.gov/products/satellite.html. A suspiciously high monthly composite value for January 2006 was discarded after examinations of the associated data quality assessment data sets (QA SDS). Instead, the mean of December 2005 and February 2006 was taken as a more accurate estimate of the true value.

Monthly linear associations between key weather variables and primary productivity within the home range were assessed through the computation of Spearman correlation coefficients (Table 4.1). The analyses illuminated significant and strongly positive correlations between monthly primary productivity and mean air humidity and total rainfall. Total solar radiation and total evapotranspiration on the other hand, displayed strongly negative correlation coefficients, whereas temperature had no association to productivity levels. Significance levels increased when lag correlations (up to 2 months) and cumulative values (up to 3 months) were considered.

Table 4.1 Summary of the Spearman correlation analyses on the monthly association between weather conditions and remotely sensed primary productivity over the home range of the study group during the period May 2005-April 2006.

		T_{min}	T_{mean}	T_{max}	**Photo**	**Hum**	**P**	**Sol**	**ET**
NDVI $_{\text{home range}}$	r_s	-.077	-.084	-.063	.168	***.811***	***.722***	***-.643***	***-.839***
	Sig. (2-tailed)	.812	.795	.846	.602	<.001	.008	.024	<.001
	n	12	12	12	12	12	12	12	12

		Hum_{-1m}	P_{cum3}	ET_{cum2}
NDVI $_{\text{home range}}$	r_s	***.855***	***.946***	***-.873***
	Sig. (2-tailed)	<.001	<.001	<.001
	n	11	12	11

NDVI= Normalised Difference Vegetation Index; $T_{min/mean/max}$ = mean minimum/mean/maximum temperature (°C); Photo = mean length of photoperiod (h); Hum = mean air humidity (%); P = total rainfall (mm); Sol = total solar radiation (Wm^{-2}); ET = total evapotranspiration (mm)
The subscripts '-1m' and 'cum2/3' in b) respectively mean: 'value of the previous month' and 'cumulative value of the current and previous/previous two month/s'

These findings corroborate results from the previous chapter in that atmospheric variables denoting water availability appear to be the most important correlates of primary productivity. In addition, the negative association with solar radiation and evapotranspiration further exemplified the degree of water-stress experienced by the vegetation at Lajuma.

4.2.2 Annual NDVI over study period and the long-term average

After having established that primary productivity of the home range indeed correlates with concurrent weather conditions, it is only a small logical step to evaluate NDVI values over the study period against the long-term average. Adverse effects of the unfavourable weather conditions during the observation period (recall from Chapter 2 that the study period was considerably warmer and dryer than the norm) on local vegetation might be reflected by a lower annual NDVI value. To test this supposition, monthly values were extracted from the MODIS dataset and compared to the AVHRR long-term average (Figure 4.1). The area for which this was assessed, covered 64 km^2

(equivalent to the surface area of the pixel in the AVHRR archive containing the Lajuma Research Centre) and is referred to below as Greater Lajuma.

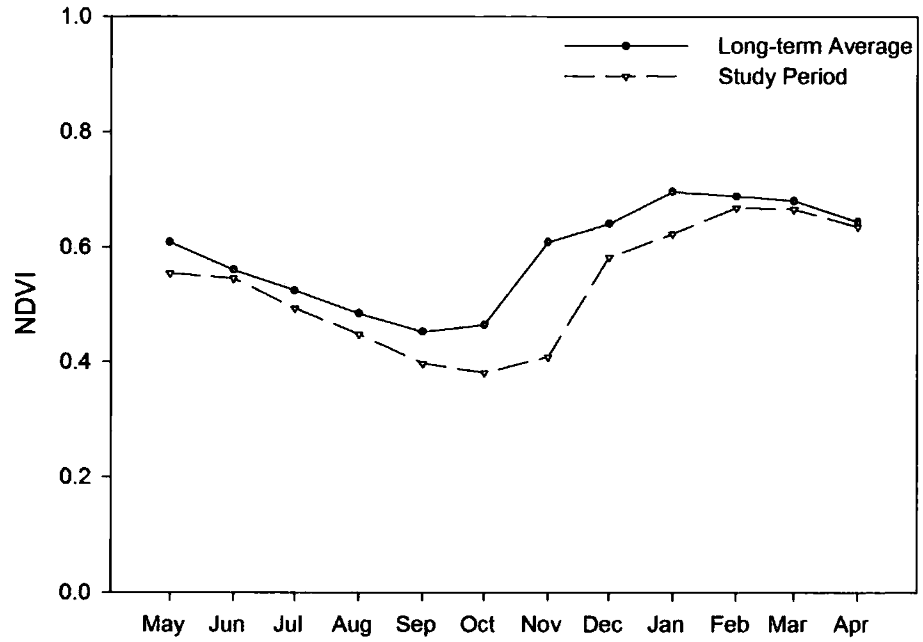


Figure 4.1 Monthly NDVI values of Greater Lajuma during May 2005 - April 2006 compared to the long-term monthly average over July 1981 - December 2004. Although data stem from different satellite sensors, they are inter-calibrated to allow direct comparison (Tucker *et al.*, 2005; Brown *et al.*, 2006).

A paired-samples t-test revealed that the vegetation of Greater Lajuma had a significantly lower annual NDVI value during the study period (mean ± se= 0.533 ± 0.031) than on average (mean ± se = 0.587 ± 0.089; $t_{(11)} = 3.62$, $p < 0.005$). The negative effect of adverse weather conditions on local vegetation during the observation period thus appears to be reflected by the NDVI.

4.2.3 Monthly NDVI of home range and surrounding areas

Estimated home ranges of vervet monkeys in eastern and central Eritrea have been reported to exhibit higher NDVI values than the average value of the complete area of survey (Zinner *et al.*, 2002). This was taken to suggest that, in selecting the location of home ranges, vervet monkeys prefer areas of elevated productivity relative to the surrounding habitat. To ascertain whether the animals in the study group pursued a similar strategy, monthly NDVI values over the home range area were evaluated against those of two directly surrounding regions. The areas chosen for comparison were Greater Lajuma and the entire Soutpansberg mountain range. A graphical representation of the NDVI time-series of these areas is given in Figure 4.2.

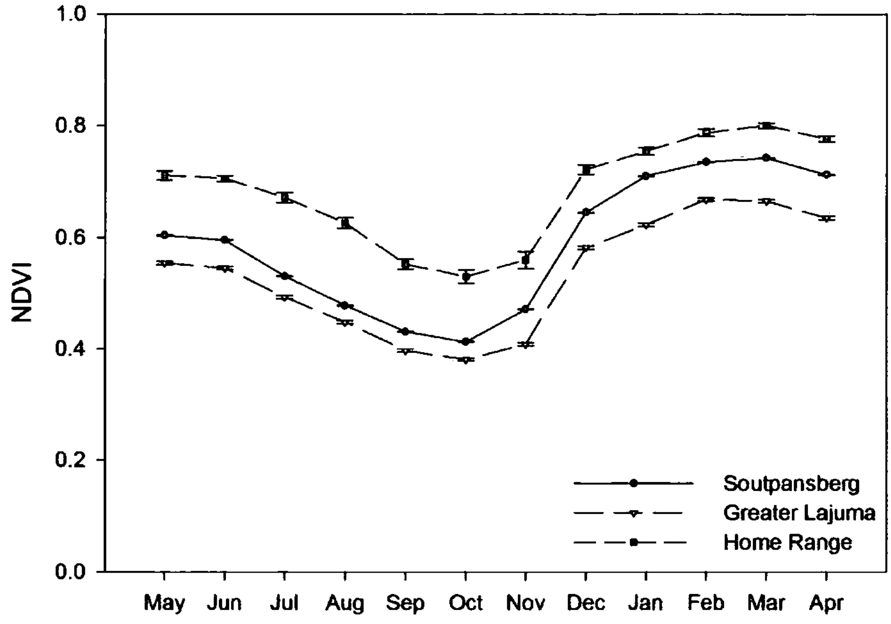


Figure 4.2 NDVI time-series of the Soutpansberg, Greater Lajuma and the home range of the study group over the observation period (May 2005 - April 2006; error bars represent ± 1 se).

To assess the effects of month and area on primary productivity, a two-way mixed analysis of variance was conducted. Mauchly's test pointed out that the assumption of sphericity was violated ($\chi^2_{(65)}$= 5.5 x 10^5, p< .001), which implied that all degrees of freedom had to be corrected using lower-bound estimates (ε= .09). Results indicated that monthly NDVI values differed (F $_{(1,\ 61307)}$= 690.54, p< .001) and planned contrasts moreover revealed a significant cubic trend in this difference (F $_{(1,61307)}$= 700.85, p<.001). This finding reflects the annual seasonality in productivity. In addition, a difference between NDVI values of the three areas under investigation was detected (F $_{(2,61307)}$=

141.52, $p < .001$). Subsequent Bonferroni corrected pair-wise comparisons illuminated that the NDVI over the home range was higher than over either the Greater Lajuma area or the entire Soutpansberg mountain range ($p < .001$ in both comparisons). The same post-hoc procedure also showed that NDVI values of the Soutpansberg as a whole were significantly higher than those of Greater Lajuma ($p < .001$). Finally, a significant interaction effect between month and area was found ($F_{(2, 61307)} = 72.22$, $p < .001$). To summarise these findings, it may be concluded that the study group exploited a home range area with higher monthly NDVI values than the overall average of the Soutpansberg mountain range, despite inhabiting a region with a value slightly below this average. This provides strong support for the observations on NDVI and vervet home range areas in Eritrea (Zinner *et al.*, 2002) and suggests that vervets indeed prefer areas with elevated productivity. If this is a general behavioural strategy of the species, it may enable vervet monkeys to utilise seemingly inauspicious habitats and, in addition, could account for the frequent association with water courses throughout their natural geographic range (Fedigan and Fedigan, 1988; Enstam and Isbell, 2007). Proximately, however, rather than maximising primary productivity vervet monkeys are maximising access to essential resources, such as food and shelter. These may be positively associated with habitat productivity and the NDVI may therefore prove to be an invaluable tool for primatologists.

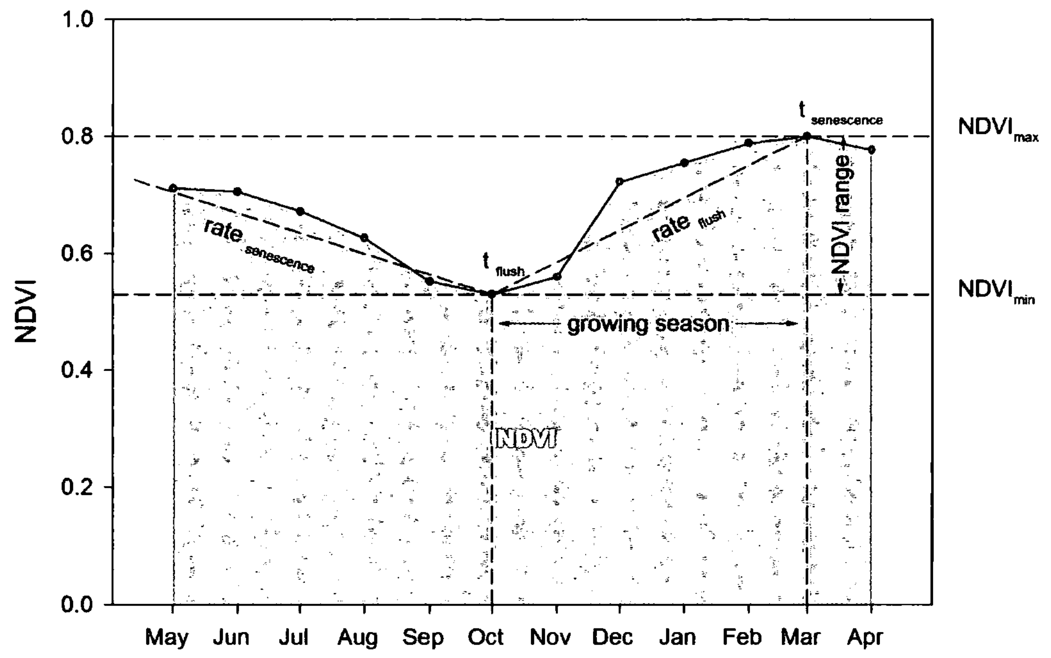
4.3 Local phenology

Phenological records are routinely collected within primatology to characterise seasonal changes in habitat productivity and, often more importantly, seasonal variation in local food availability. Whereas information on the former is relatively easily collected in the field by random or stratified sampling, the latter requires a detailed knowledge of the diet of the study animals prior to measurement (Ganzhorn, 2003). Paradoxically, dietary composition will often only become apparent during the field work period. Monitoring food availability, moreover, offers less obvious promise for remote sensing at its current technological state than the monitoring of community wide productivity. A potential role within the assessment of both, however, can not be ruled out in advance. Here, some remotely sensed phenological metrics are introduced and the relation between NDVI time-series and monthly field observations on the vegetative phenology of key species within the diet of the study group assessed.

4.3.1 Remote sensing of vegetative phenology

Bearing its underlying biophysical principles in mind (Section 3.2.2), it is clear that the NDVI will only be of direct use in monitoring phenological events in relation to habitat productivity. Monitoring food availability for non-folivorous primates requires screening of all three phenophases (flushing, flowering and fruiting) which is currently beyond sensor capabilities, although advances in hyper-spectral sensing (Lillesand *et al.*, 2004) may hold promise. Despite this limitation, numerous NDVI-derived metrics have successfully linked vegetative phenology (flushing) to species richness (Hurlbert and Haskell, 2003; Bailey *et al.*, 2004; Evans *et al.*, 2006), distribution (Boone *et al.*, 2006; Ito *et al.*, 2006; Marshal *et al.*, 2006; Ryan *et al.*, 2006), body mass (Pettorelli *et al.*, 2005a) and timing of demographic events (Pettorelli *et al.*, 2006; Rasmussen *et al.*, 2006). Key measures that have been used in these studies (DeFries *et al.*, 1995; Pettorelli *et al.*, 2005b) are presented in Figure 4.3.

This overview, being far from exhaustive, is mainly presented to illustrate how indices of phenological seasonality can be computed from NDVI time-series. Because they characterise temporal patterns in habitat productivity, these metrics quantify an important intermediate level through which climatic periodicity asserts its influence on animal behaviour. A proximate understanding of primate socio-ecology, therefore, may greatly benefit from the implementation of these remotely sensed indices.



Metric	Definition
NDVI$_{\text{max}}$	maximum annual photosynthetic activity, evergreen and deciduous vegetation
NDVI$_{\text{min}}$	minimum annual photosynthetic activity, evergreen vegetation only
NDVI$_{\text{range}}$	indicator of annual seasonality (NDVI$_{\text{max}}$ - NDVI$_{\text{min}}$)
NDVI$_{\text{mean}}$	mean annual productivity ((NDVI$_{\text{max}}$ + NDVI$_{\text{min}}$)/2) -not depicted in figure-
INDVI	total annual productivity, integrated NDVI value -shaded area in figure-
t$_{\text{flush}}$	month in which leaf flushing of deciduous vegetation commences
t$_{\text{senescence}}$	month in which leaf senescence of deciduous vegetation commences
growing season	time-span between t$_{\text{flush}}$ and t$_{\text{senescence}}$
rate$_{\text{flush}}$	degree of increase in productivity due to leaf flushing of deciduous vegetation
rate$_{\text{senescence}}$	degree of decrease in productivity due to leaf senescence of deciduous vegetation

Figure 4.3 Graphical illustrations and definitions of some phenological metrics that can be derived from the NDVI time-series over the home range of the study group during the observation period (May 2005 - April 2006).

4.3.2 Field observations on phenology

While satellite sensors can detect patterns in vegetative phenology (flushing), detailed knowledge on variation in food availability requires additional and extensive monitoring of the reproductive phenologies (flowering and fruiting). This can currently only be achieved on the ground. What is more, meaningful assessment of food availability critically hinges on a comprehensive knowledge of the composition of the local diet of the study animals. Data stemming from focal animal sampling on adult individuals revealed that the study group spent 75.9 % of its total feeding time on consuming plant matter (Figure 4.4).

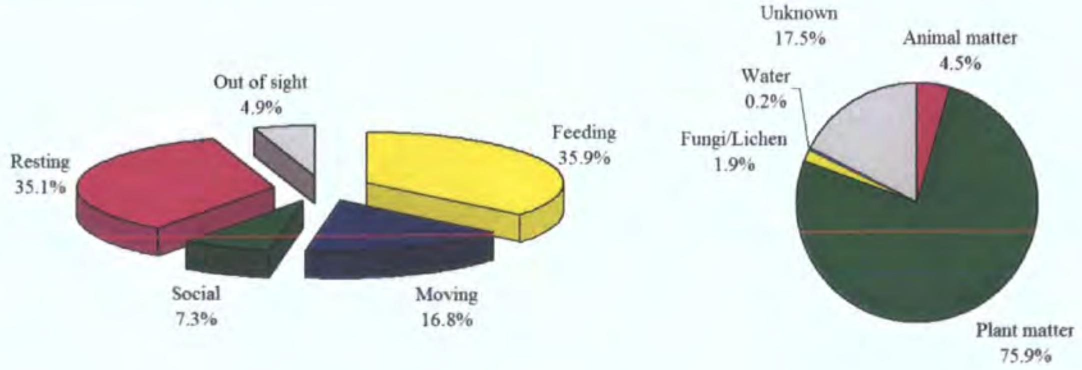


Figure 4.4 Overview of overall time allocation by the study group (left) and the proportion of total feeding time spent on plant matter (right). Pie-charts are based on focal animal observations on adult animals over the period May 2005-April 2006 and percentages are rounded to 1 decimal.

If correction is allowed for the large proportion of time the animals spent feeding on food items that could not be identified at the moment of sampling, this figure increases to an even more substantial 92.0 %. Overall food availability then, seems adequately measured by sampling key plant species within the animals' diet.

Out of an estimated more than 100 plant species on which the monkeys fed, 84 could be identified. The vast majority of these merely accounted for marginal proportions of the diet: 68 species each constituted less than 1.0% of total feeding time on plant matter. Nine species were selected for monitoring at the onset of phenological sampling, based on their perceived importance to the overall diet (see section 2.5.4). These species, the parts on which the monkeys fed and the respective percentages of time they accounted for in total feeding time on identified plant matter, are given in Table 4.2.

Table 4.2 The nine tree-species initially selected to monitor food availability. The parts eaten by the monkeys are presented as are the percentages of time the animals spent feeding on them. Figures are based on focal animal observations on adult individuals and percentages are rounded to 1 decimal.

Scientific name	**English name**	**Leaf**	**Flower**	**Fruit/Seed**	**Gum**	**?**	**Total**
Acacia ataxacantha	Flame acacia	0.3	-	5.1	0.2	0.6	6.2
Acacia karroo	Sweet thorn	3.9	-	20.8	6.4	0.4	31.5
Englerophytum magalismontanum	Transvaal milkplum	-	-	-	-	-	0.0
Ficus spp.	Fig *spp.*	-	-	5.0	-	-	5.0
Hyperacanthus amoenus	Thorny gardenia	<0.1	<0.1	2.9	-	<0.1	3.0
Rhus chirindensis	Red current	<0.1	0.1	9.8	0.1	<0.1	10.0
Syzygium cordatum	Water berry	-	-	6.6	-	<0.1	6.7
Syzygium legatii	Mountain waterberry	-	-	1.5	-	-	1.5
Ziziphus mucronata	Buffalo thorn	-	-	2.7	-	-	2.7
Total		**4.3**	**0.1**	**54.4**	**6.7**	**1.1**	**66.6**

It deserves notice that a number of known food species were not recorded in focal samples over the study period. The most striking example of this was the Transvaal milkplum (*Englerophytum magalismontanum*). Mast fruiting (Kelly and Sork, 2002) during the pre-observation season made this species a major resource for the monkeys. Yet over the following season, coinciding with the study period, virtually no fruit was produced which explains the absence from the reported diet. For this reason, *E. magalismontanum* was omitted from further analysis, despite its substantial importance to the monkeys. It thus appears that inter-annual variation in food availability may pose an important factor shaping the behavioural ecology of the study group, but unfortunately this is beyond the scope of this thesis.

Qualitative representations of the three phenophases of the remaining eight species are presented in Figure 4.5. Note that seasonality in flushing of the deciduous species (*A. ataxacantha, A. karroo, R. chirindensis* and *Z. mucronata*) was highly synchronised (Table 4.3), whereas community wide synchrony in flowering and fruiting was not apparent.

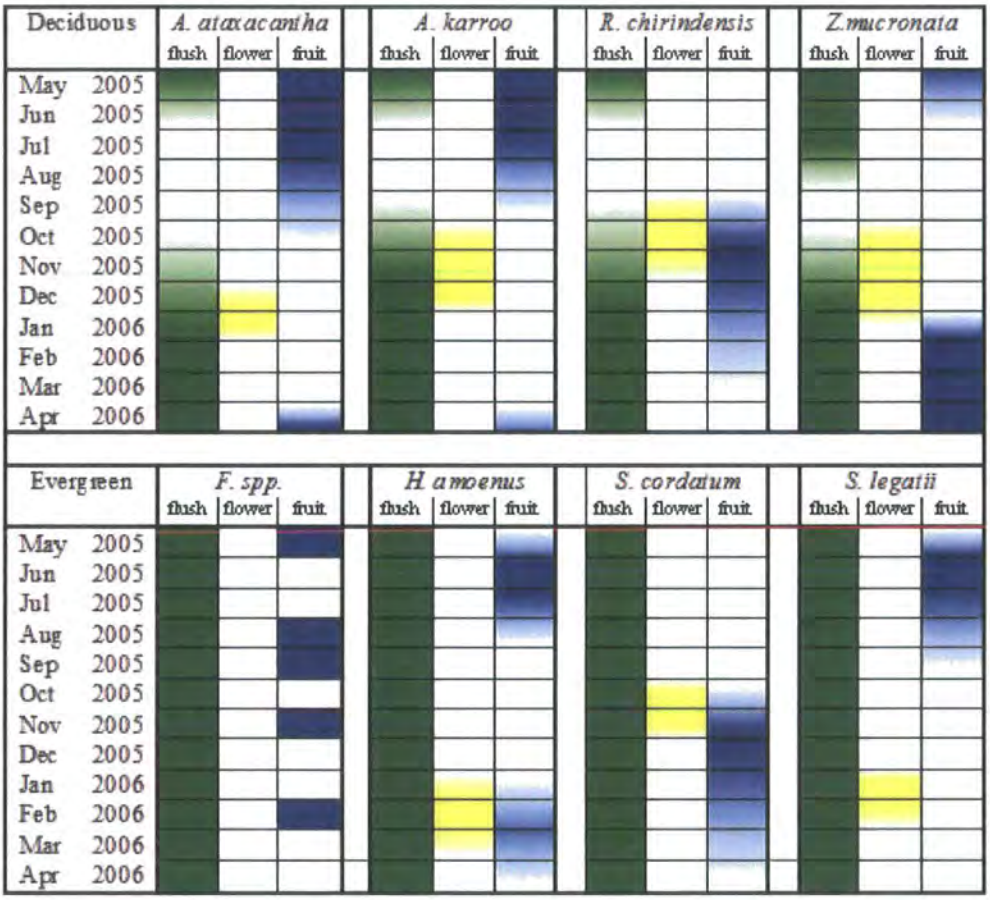


Figure 4.5 Graphical representation of the three phenophases of the eight monitored species, based on quantitative and qualitative field observations. Intensity of colour is approximately proportionate to the number and developmental stage of the different plant parts (note that colours for July 2005 are interpolated from previous and subsequent months as data were lost in a corrupt transfer between Palmtop and laptop).

Table 4.3 Significant correlation coefficients between monthly field estimates of leaf cover on the four deciduous species in the diet of the study group that were monitored. This result is taken to indicate the level of synchrony in leaf production and abscission (vegetative phenology).

		A. karroo	*R. chirendensis*	*Z. mucronata*
A. ataxacantha	r_s	***.868***	***.924***	***.793***
	Sig. (2-tailed)	.001	.000	.004
	n	11*	11*	11*
A. karroo	r_s		***.981***	***.732***
	Sig. (2-tailed)		.000	.011
	n		11*	11*
R. chirindensis	r_s			***.820***
	Sig. (2-tailed)			.002
	n			11*

* July 2005 data were lost due to a corrupt transfer between Palmtop and laptop

Overall, these observations are in line with phenological patterns at a number of other primatological field sites (van Schaik *et al.*, 1993; van Schaik and Pfannes, 2005) and are representative of the complex matrix of abiotic and biotic factors that has given rise to different plant strategies in the timing of the respective phenophases (Borchert *et al.*, 2002; Hamann, 2004; Bendix *et al.*, 2006).

Lastly, to investigate whether community-wide assessment of food availability was feasible, three structural parameters were measured on each monitored tree. These parameters (height, crown area and trunk diameter at breast height -DBH-) have previously been reported to be good proxies for the amount of flowers and fruit produced (Chapman *et al.*, 1992; Chapman *et al.*, 1994). As these measures were strongly interrelated (Table 4.4 a), the most accurately measurable parameter in the field (DBH, or average DBH for multi-stemmed trees) was associated to estimated maximum number of flowers and fruits (Table 4.4 b).

Table 4.4 Correlation analyses between structural characteristics of the monitored trees revealed a high inter-relatedness between these measures (a). Trunk diameter at breast height (DBH) subsequently showed significant associations to the median maximum values of estimated number of flowers and fruits (b).

a)

		crown area	**(average) DBH**
height	r	***.500***	***.564***
	Sig. (2-tailed)	.000	.000
	n	79*	69**
crown area	r		***.640***
	Sig. (2-tailed)		.000
	n		69**

b)

		max. n flower	**max. n fruit**
(average) DBH	r_s	***.400***	***.358***
	Sig. (2-tailed)	.002	.002
	n	59***	69**
max. n flower	r_s		***.287***
	Sig. (2-tailed)		.017
	n		69**

* one of the trees died over the observation period and was excluded

** DBH's of *H. amoenus* were below minimum measurement threshold

*** *F. spp.* receptacles were scored as fruit

The significant relationships were again in line with previous findings (Chapman *et al.*, 1992; Chapman *et al.*, 1994; Sterck, 1995; Ganzhorn, 2003) and suggested that community-wide assessment of overall food availability at Lajuma was possible through a coupling of phenological observations to species specific density data stemming from quadratic plot samples.

4.3.3 Association between satellite and field phenology

To conclude this section on local phenology, the level of agreement between remote sensing and field estimates was ascertained for observations on vegetative phenology. Leaf flushing and senescence as measured by the NDVI was highly correlated with estimates of leaf cover from the field (Spearman's rank correlation test; r_s= .837, n= 11[†], p< .005). This relationship was even more significant when monthly NDVI values were evaluated against field observations on deciduous species only (Spearman's rank correlation test; r_s= .887, n= 11, p< .001). This strong congruency between remotely sensed data and field observations on seasonality in leaf production was encouraging in that it may warrant extrapolation to the quantitative assessment of the reproductive phenophases using remotely sensed information.

Given the recognised inter-dependence between the vegetative and reproductive phenologies (Singh and Kushwaha, 2006), leaf cover may be used as a proxy for the number of reproductive structures (flowers and fruits). The reasoning behind this supposition is that the quantity of leaves determines the amount of solar energy that can be metabolised and thereby preordains the amount of energy available to the production of flowers and fruits. Extending this logic, NDVI values on vegetative phenology may be quantitatively proportionate to reproductive phenology. Data on the timing of species specific flower and fruit production, however, can only be determined from local phenological records or field observations. By establishing the respective times of onset, peak and end of reproductive phenologies, remotely sensed information on primary

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[†] Since field data on phenology from July 2005 were lost due to a corrupt transfer from Palmtop to laptop, sample size was reduced to 11 months.

productivity may help to estimate food availability for secondary consumers in a truly quantitative way. Given the inherently spatio-temporal properties of remotely sensed data this might be a powerful synergistic approach to the analyses of food availability for non-folivorous primates such as vervet monkeys. This exciting possibility will be explored in the following section.

4.4 Local food availability

Food availability is perhaps the single most important bottom-up selective force on primate biology, acting upon facets as diverse as physiology (Kemnitz *et al.*, 2002; Knott, 2005; Schmid and Kappeler, 2005), life history variables (Schmid and Kappeler, 2005), social organisation (Wrangham, 1980; van Schaik, 1983; 1989; 1996; Sterck *et al.*, 1997), community structure (van Schaik *et al.*, 2005), range use (Barton *et al.*, 1992; Doran, 1997; Hemingway and Bynum, 2005) and time budgets (Dunbar, 1993; 1996; Doran, 1997; Williamson and Dunbar, 1999). It is also difficult to ascertain. Section 4.3 identified the main food resources of the study group and described their phenologies. This information is used here to generate spatio-temporal estimates of food availability within the home range area of the study group over the observation period.

4.4.1 Demarcation of vegetation types

The first step to estimate food availability in a spatio-temporal way is the categorisation of the annual home range into distinct habitats or vegetation types. Unfortunately, the Lajuma Research Centre houses a notoriously complex mosaic of plant communities (Dr. N. Hahn, *pers. comm.*) which leaves routine classification and ordination procedures (*e.g.* Geldenhuys and Venter, 2002) of limited use. This intricacy was overcome by delineating distinct units within a GIS on the basis of three main sources of information: 1) GPS fixes and field knowledge from extensive surveys; 2) visual interpretation of high resolution multi-spectral satellite imagery and time-series of aerial photographs and; 3) structural and floristic data from quadrat plot samples (section 2.5.5). In addition, spectral classification (Lillesand *et al.*, 2004; Eastmann, 2006) of high resolution multi-spectral satellite imagery was attempted. Results from spectral analyses, however, were not incorporated in the eventual demarcation. This was not due to an inherent inapplicability of these techniques, but rather to the lack of frequent coverage of the study site by high resolution satellite sensors.

Classification of the vegetation within the study group's home range produced 172 mapping units (Section 2.5.2) divided over 8 broad plant communities, totalling 19 putative vegetation types. Polygon overlays representing the mapping units and habitat types eventually recognised (Section 4.4.3) are given in Figure 4.6.

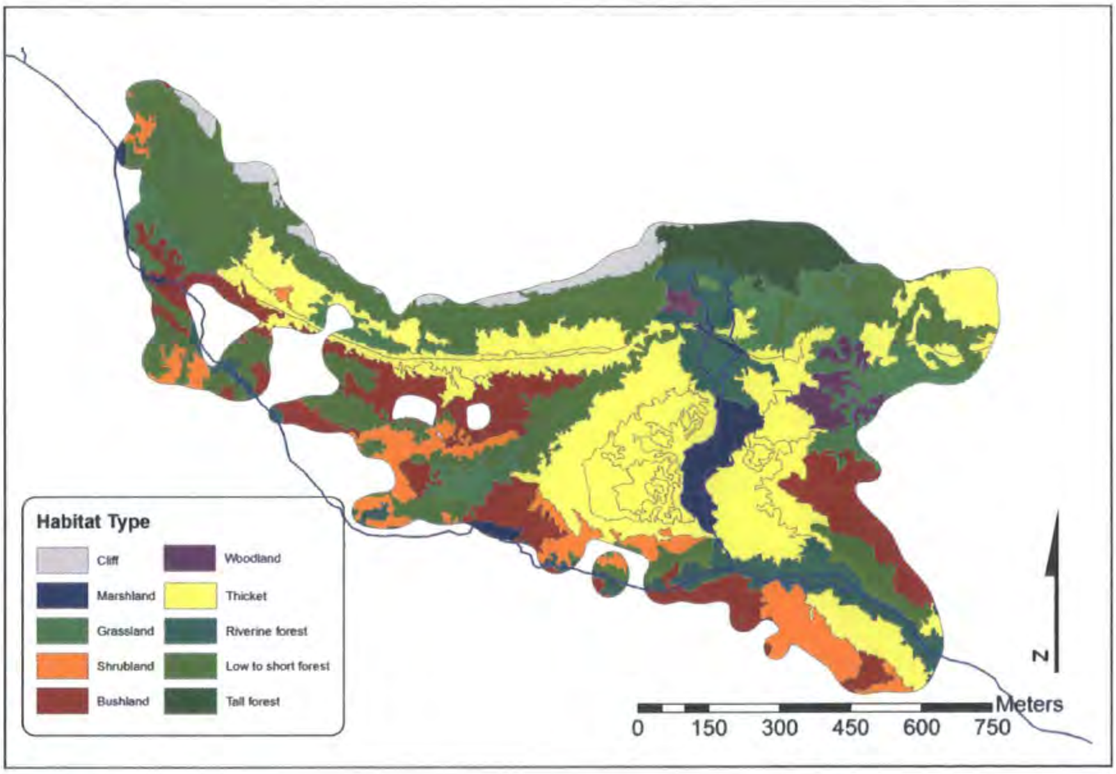


Figure 4.6 Demarcation lines of the 172 mapping units (grey outlined polygons) distinguished within the home range area of the study group over the period May 2005 - April 2006. Main habitat types are indicated by different colours and permanent water systems are depicted by blue lines.

4.4.2 Structural and floristic description of vegetation types

Recently the flora of the Soutpansberg has been described as the Northern Mistbelt Forest Group (von Maltitz, 2003) whereas previous authors had placed it under either North-Eastern Mountain Sourveld and Sourish mixed Bushveld (Acocks, 1988), or Soutpansberg Arid Mountain Bushveld and Afromontane Forest (Low and Rebelo, 1996). All classification schemes acknowledge elements of the Forest and Savanna biomes yet ignore the presence of Grassland and Thicket. For current purposes, therefore, descriptions of different communities and vegetation types were based on a practical field classification scheme (Edwards, 1983) that does justice to all biomes present within the animals' home range.

Overall, the home range area (Section 5.2.1) consisted of mostly low to tall evergreen forest generally at the base of cliffs, associated with drainage lines in rocky substrate (kloof forest) or along the main stream system. Semi-deciduous thicket was also well represented. Although referred to elsewhere as scrub or regrowth forest (von Maltitz, 2003), the label thicket was preferred here to emphasize the near impenetrable and thorny nature of this community type. The study area further comprised a mosaic of marshlands and a mixture of grasslands, shrublands, and bushlands on predominantly steep and south facing rocky slopes. Woodland elements were also present. The high incidence of mist has had a profound influence on the vegetation and sustains an abundant and varied community of mosses and lichens. Lastly, a strong historical anthropogenic factor has contributed to the heterogeneity and patchiness of the local vegetation.

Below, a brief description of the different plant communities and their respective vegetation types is given.

1. Cliff

The northern border of the home range consisted of a steep tall cliff onto which the monkeys rarely ventured. It made up 2.9 % (3.3 ha) of the total home range area and could be described as sparse herb- and shrubland. It was not studied in any detail since vegetation density was very low.

2. Marshland

This community covered approximately 2.4 % (2.8 ha) of the home range area and was exclusively found in flat regions along permanent water streams on peat. No quantitative studies were conducted since woody elements are generally absent. Vegetational components included reeds, sedges and grasses (hydric, mesic and xeric). *Amarantaceae* and *Polygonaceae* were abundant and occasional *Cyperaceae* occur. Towards the west and south, these communities acted as boundaries to the home range. Two types were distinguished; *primary reed marsh* and *secondary transitional marsh* in which recolonisation by trees, most notably *Syzygium cordatum*, was advancing.

3. Grassland

Grassland comprised 8.6 % (9.8 ha) of the study area and two seral stages were recognised. *Primary grassland* was confined to poor soils (either exposed sand or weathered rocky outcrops) whereas *secondary grassland* displayed various stages of succession with recolonisation by shrubs. *Frimbistylus spp.* and *Heliochrysum spp.* were common in primary areas, whereas *Acacia ataxacantha*, *Acacia karroo, Dichrostachys cinerea* and *Lypia javanica* were the main invading shrubs of secondary grasslands.

4. Shrubland

Three different vegetation types were documented within this community, which together covered 6.5 % (7.5 ha) of the animals' home range. *Southeast to southwest facing shrubland* on generally rocky slopes (< 10°) was confined to areas north of the Kutetsha river. South of the river, *northeast to east facing shrubland* occurred on steep rocky slopes (>15°). *Secondary shrubland* finally, represented a successional transition from abandoned fields to the natural potential vegetation on sandy soils. *Aloe arborescens, Kalanchoe spp.* and *Rhus pentheri* were observed and average height of the vegetation was below 2 m.

5. Bushland

Bushland constituted 12.8 % (14.6 ha) of the home range and was divided into *southeast to southwest facing bushland* north of the Kutetsha river, and *northeast facing bushland* associated with drainage lines in the slopes south of the river. All but one of the mapping units represented the maximum natural potential vegetation on rocky and often steep inclines (up to 45°). *Combretum kraussii*, *Englerophytum magalismontanum*, *Euclea linearis* and *Olinea rochetiana* were represented, although vegetation density was low. Height of these vegetation types averaged around 5 m.

6. Woodland

Woodland elements within the home range area represented remnants of tall forest and accounted for 1.7 % (2.0 ha) of the study area. No species composition data are available and no sub-categorisation was made.

7. Thicket

This community comprised 28.4 % (32.5 ha) of the home range. A considerable degree of variation in successional stages was observed and led to a variable structural and floristic composition. Three broad vegetation types could be discerned. In the far southeast of the home range, a patch of semi-deciduous *primary thicket*, or scrub forest, was found. *Low secondary transitional thicket* and *short secondary transitional thicket*, or regrowth scrub forest, formed semi-deciduous vegetation types that were strongly associated with areas of intense human use at various times in the past. They occupied areas that would naturally have harboured either evergreen forest or primary thicket. Whereas certain mapping units consisted mainly of young plants, others showed signs of over-maturity and decomposition indicating the reversion to a more primary community. Common species of particular relevance to the monkeys included *Acacia ataxacantha*, *Acacia karroo*, *Brachylaena discolor (transvaalensis)*, *Catha edulis*, *Celtis africana*, *Mimusops zeyheri*, *Rhus chirindensis* and *Ziziphus mucronata*. The high occurrence of succulents (*Aloe spp.* and *Kalanchoe spp.*) in the ground layer was also relevant in this respect.

8. Forest

Low to tall forest covered 36.5 % (41.7 ha) of the study area and showed the greatest biodiversity in woody species of all communities. The term forest was reserved for primary evergreen mapping units in which stratification of different vegetation layers was pronounced. Lianas and climbers (most notably *Rhoicissus tomentosa* and *Keetia gueinzii*) were locally abundant. A distinction was made between five forest types. *Riverine forest* was well established along the main water streams and was characterised by the occurrence of *Syzygium cordatum*. Forests exploiting seepage water at the base of cliffs were divided into *cliff base low forest*, *cliff base short forest* and *cliff base tall forest*. Whereas the first two of these cliff base forests were rich in food species for the vervet monkeys (*Canthium mundianum*, *Englerophytum magalismontanum*, *Hyperacanthus amoenus*, *Olea capensis macrocarpa*, *Rhus chirindensis*, *Syzygium legatii* and *Tarenna zimbabwensis*), the latter was relatively poor. Remaining forest stands were grouped as *sandy loam forest* and occurred in fragmented patches forming impoverished remnants of more extensive historic forest stands.

4.4.3 Estimates of food availability

Standard methodologies to assess food availability within primatology tend to be ordinal estimates and, although informative, may not always represent phenological patterns with a high level of accuracy (Chapman *et al.*, 1992; Chapman *et al.*, 1994; Ganzhorn, 2003). Complications with precision of repeated measures further confound the analytical power and sensitivity of these parameters (Brower *et al.*, 1997). Because of these reasons, the potential use of NDVI data as a proxy for primate food availability is investigated here through its integration into a simple model that depends on a minimum input of field data whilst maintaining a faithful correspondence to observed phenological patterns. The outcome of this model is similar to that of a model based on phenological field observations alone. Results of both models can be implemented into a GIS to aid an in depth spatio-temporal investigation of the distribution and abundance of food for the vervet monkeys at the study site.

To meaningfully quantify food availability, the level of detail and scope of the estimates of overall food availability were restricted considerably. Firstly, food species density data were judged too few and too unevenly distributed over the vegetation types to warrant validity at this resolution. As a consequence, food availability had to be assessed on a plant community level, though a distinction between three broad forest types was preserved. For ease of discussion, these different vegetation units are referred to as habitat types. Secondly, only food species accounting for more than 5% of the animals' time spent feeding on plant matter (*Acacia ataxacantha*, *Acacia karroo*, *Rhus chirindensis* and *Syzygium cordatum*) were included and only the fruit/seed category was considered. Justification for this comes from the observation that, between them, the fruits and seeds of these four species represent a year-round food supply, compose over 40% of total time spent feeding on plant matter and, moreover, are present in sufficiently different densities to distinguish between habitats. In addition, previous studies have argued that the local diet of vervet monkeys is commonly restricted to a relatively small number of staple foods (Harrison, 1984; Whitten, 1988; Lee and Hauser, 1998; Alberts *et al.*, 2005). Lastly, each food item is assumed to be of roughly equal nutritional value to the animals, which means that estimates on abundance are taken to be directly commensurable. Food items were either pods (typically containing up to 10 seeds) for the two *Acacia* species, a cluster of drupes on a bunch for *R. chirindensis* and individual berries for *S. cordatum*. Food availability as assessed in the field is expressed as the median monthly value of the estimated number of food items per unit of DBH (Figure 4.7).

Some problems pertaining to the biological validity and analytical power of this estimate are immediately apparent. Firstly, the number of food items is a continuous variable yet was assessed on a categorical scale in the field. This seriously compromised accuracy and sensitivity of the resulting pattern and may moreover have introduced artefacts due to a lack of precision (*e.g.* the drop in numbers of food items for *A. ataxacantha* over August 2005 and the subsequent recovery to the previous level).

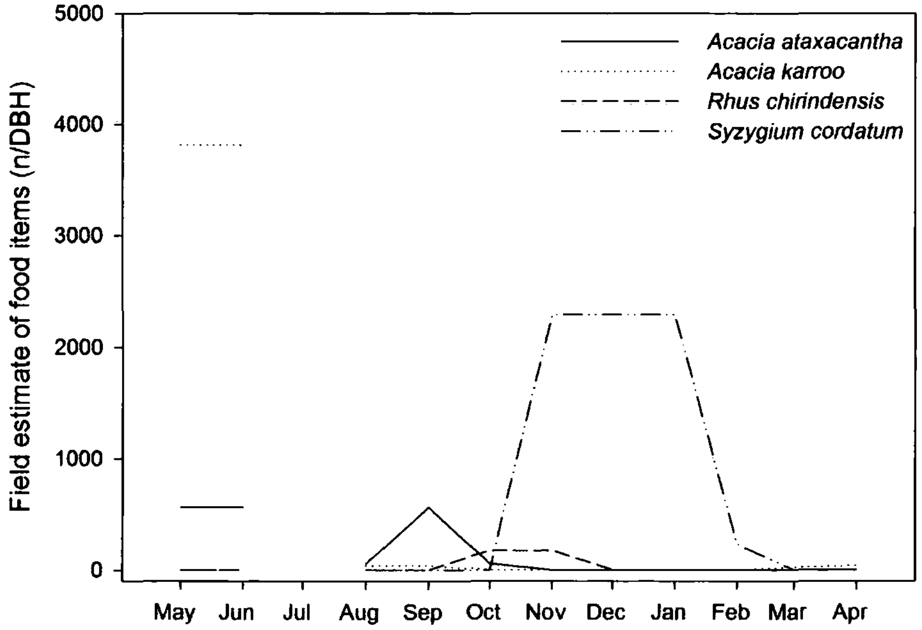
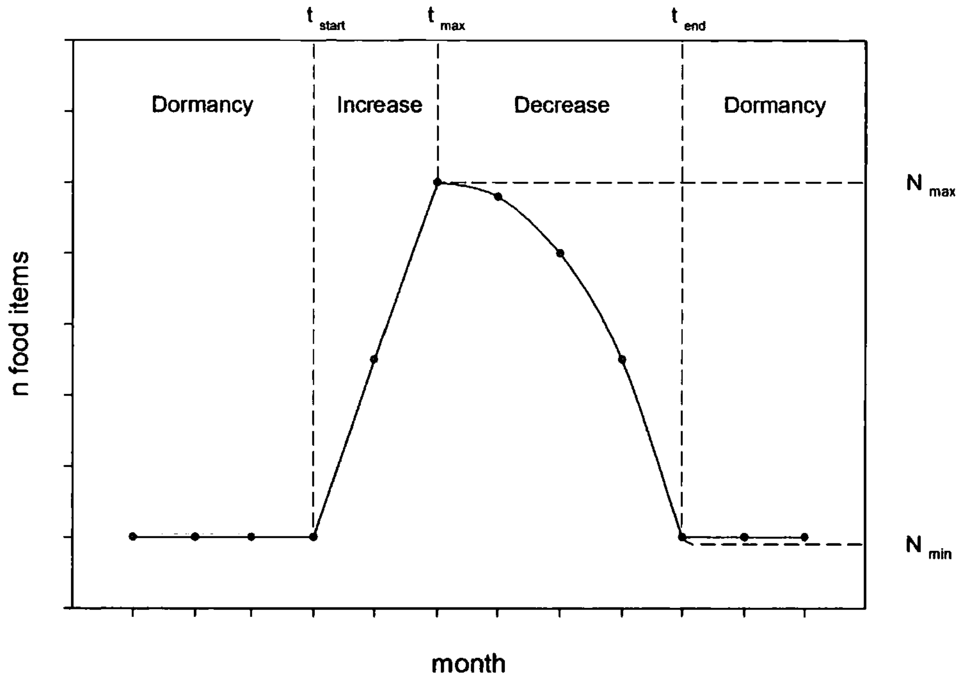


Figure 4.7 Field estimate of food availability over the observation period based on monthly median values for the four main food species. Data for July 2005 are missing due to a corrupt transfer between Palmtop and laptop.

For statistical reasons ordinal variables moreover have to resort to the use of median values, which resulted in an underestimation of the number of months during which food items were available: individual trees of a species may still carry food items in months for which the median value indicates an absence of food. Secondly, since sample size (n= 10 per species) is small, estimated food availability may not be truly representative and median values were furthermore found to systematically underestimate observed numbers of food items (*e.g.* for *R. chirindensis* over December 2006: mean observed value = 12,011; median value = 0).

In order to acquire a more accurate, biologically more valid and statistically more powerful estimate of food availability a simple model is proposed (Figure 4.8).



$$n_{food\ items}(t) = \begin{cases} (N_{max} - N_{min}) \cdot \dfrac{t - t_{start}}{t_{max} - t_{start}} & t_{start} \leq t < t_{max} \quad \text{(Increase)} \\ \dfrac{N_{max} - N_{min}}{2\,t_{max}t_{end} - t_{max}^2 - t_{end}^2} \cdot (t^2 - 2t_{max}t + t_{max}^2) + (N_{max} - N_{min}) & t_{max} \leq t < t_{end} \quad \text{(Decrease)} \\ N_{min} & t_{end} \leq t < t_{start} \quad \text{(Dormancy)} \end{cases}$$

Figure 4.8 Graphical representation and equations of the three-spline function employed to model the phenology of food items. Five parameters determine the overall pattern: three temporal measures (time of start, maximum and end of presence of food items), and two quantities (N_{min} and N_{max}). Algorithm and Figure are based on a function originally developed to model global vegetative phenology (Lüdeke *et al.*, 1996).

This model approximates the observed phenology of food items for each species by the use of an algorithm consisting of three distinct intervals. The first interval (Increase) commences with the onset of production of food items and proceeds over a relatively brief period at a linearly increasing rate. When the maximum number of food items is reached, food availability is modelled to decline following a parabolic function (Decrease). Finally, a dormancy interval is reached when food items are no longer present (Dormancy). This phased pattern was derived from a three-spline function originally employed to model global patterns in vegetative phenology (Lüdeke *et al.*, 1996). The elegance of the model lies in its minimal requirements of five, relatively easily collected, parameters from the field and its biological intuitivity. Resulting estimates of species specific food availability are presented in Figure 4.9.

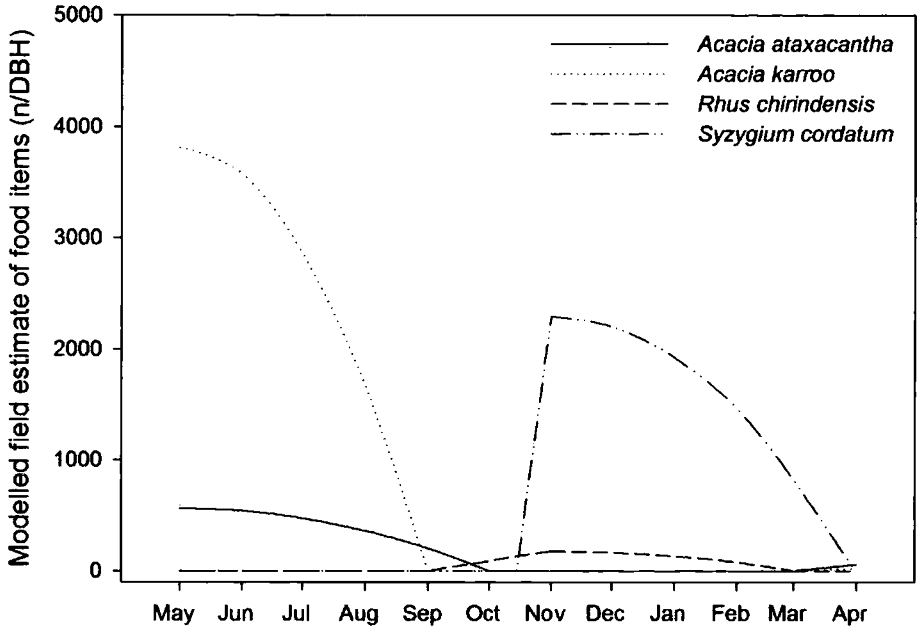


Figure 4.9 Modelled field estimate of the number of food items of the four main food species over the observation period.

The three most notable improvements of the modelled field estimate in comparison to the initial approximation of food availability are: 1) a more gradual (and hence more realistic) change over time; 2) a more accurate appraisal of the period during which food items are available for each species, and; 3) complete data coverage over the observation period. Note that, since the maximum number of food items in the model is parameterised by observed monthly median values, the magnitude of the peaks in the modelled estimate is the same as in the initial estimate.

To investigate the degree of agreement between these two estimates of food availability, a correlation analysis was performed (Table 4.5).

Table 4.5 Spearman's rank correlation tests conducted to establish the degree of association between two estimates of food availability (observed and modelled).

	A. ataxacantha	*A. karroo*	*R. chirindensis*	*S. cordatum*
r_s	***.806***	***.856***	*.569*	***.930***
Sig. (2-tailed)	.003	.001	.068	.000
n	11	11	11	11

For three out of the four species a significant and strongly positive relationship was revealed. In the case of *R. chirindensis* the association just failed to reach statistical significance, most likely due to the considerably longer period over which food items were scored to be present in the modelled estimate. Recall however that the model here is more truthful to the field situation due to the systematic underestimation of the period over which food items are available caused by the use of monthly median values. It is thus concluded that food availability is not only approximated biologically more valid by the model, but also more accurately.

Because of the biological and analytical attractiveness of the modelled estimate of food availability, a second model was developed. Conceptually, the only difference between the two modelling approaches lay in the source of information used to estimate the quantity of food items. Where the first model utilised maximum monthly median values to approximate the species specific N_{max} in the spline functions, the second model substituted these by the difference between maximum and minimum observed NDVI values (see Section 4.3.3 for the justification of this). This entailed two implicit assumptions; firstly, all species were assumed to convert metabolised solar energy (as indexed by the difference between maximum and minimum NDVI values) into an equal amount of food items and, secondly, this 'conversion efficiency' was taken to be independent of the habitat in which a specimen of a certain food species is located. Both assumptions are disputable, although the second assumption is shared with the previous model and indeed with the more traditional approach of estimating food availability from monthly median values. Theoretically, however, the second model need not make this assumption although limitations on the grain of analysis posed by the spatial resolution of available NDVI data, dictated it here. The more debatable first assumption on the other hand, is unique to the second model and may have compromised biological validity. No information on species specific ‘conversion efficiency’ is available but the inaccuracy introduced by this assumption, may be less severe than the inherent error associated to the use of median values based on small sample sizes from which the first model suffers. The two models thus only differed in the magnitude of their peaks, which meant that correlation coefficients and significance levels of the association between the second model and the traditional approach were the same as those found for the first model (Table 4.5).

Finally, to assess food availability on a monthly basis per habitat type, density data (Σ DBH/ha) obtained from quadrat plots were multiplied by the total area of each habitat (ha) in order to obtain food species specific abundance indices per habitat (Σ DBH). These values were subsequently multiplied by the monthly outcomes of the two models. Since all food items were considered to be of equal value to the animals, the sum of estimated number of food items of all four species was taken to signify overall monthly food availability. The resulting two estimates of monthly food availability per sampled habitat are presented in Figure 4.10. The proportional differences between the two models in relative food availability are entirely caused by the use of median values for estimated number of food items in the first model and the use of annual home range wide NDVI values in the second.

A priori there is no compelling argument as to which of the two models most accurately reflects true food availability. Unfortunately, monthly food availability within the four habitat types for which no quadrat sample data were available, could not be computed but was likely to be low.

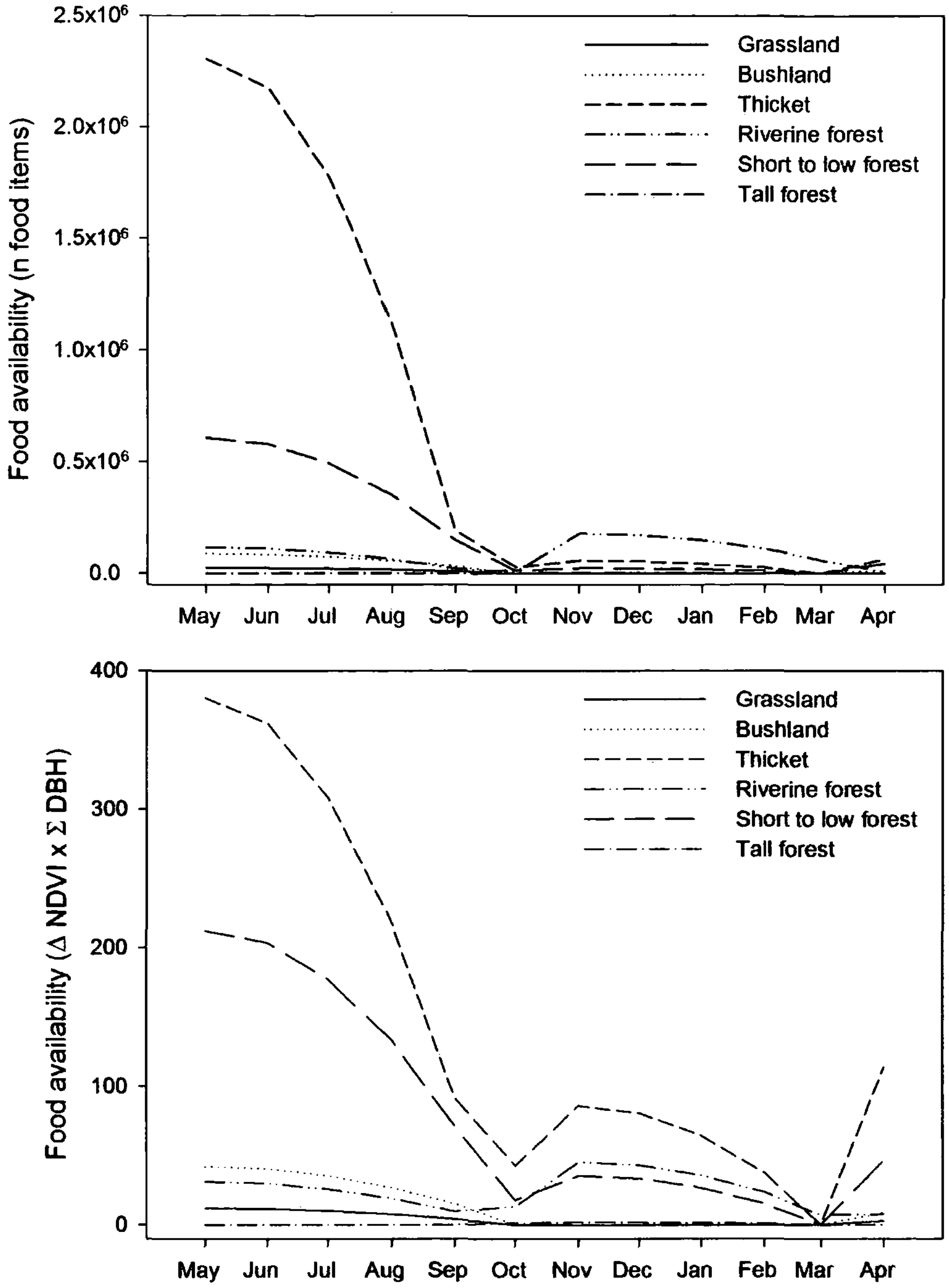


Figure 4.10 Two modelled estimates of food availability per sampled habitat type. The top graph is strictly derived from field observations, whereas the bottom graph incorporates remotely sensed information on the community wide vegetative phenology.

4.4.4 NDVI and monthly food availability

Now that estimates of food availability are in place, the potential association between local food availability and primary productivity can be assessed. All three estimates of food availability deviated from normality ($p_{K\text{-}S} < .005$) but this complication was resolved by log-transforming the data. Subsequent regression analyses revealed significant quadratic and cubic relationships between monthly NDVI and all estimates of food availability, yet biological interpretation and model selection criteria (AICc) suggested that quadratic models should be preferred. Scatter plots and best-fit quadratic regression lines are presented in Figure 4.11.

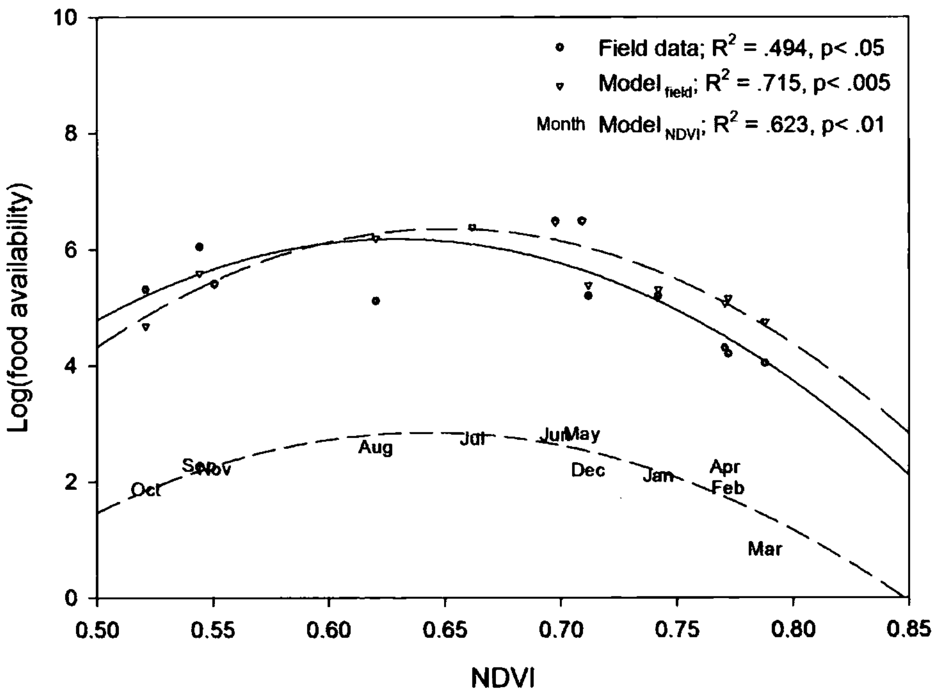


Figure 4.11 Scatter plots and quadratic regression lines that relate monthly primary productivity over the observation period to concurrent estimates of food availability.

To visualise annual progression over the months, data points of the NDVI-derived model were labelled (Figure 4.11). This helped reveal that at the onset and end of the cool dry winter at Lajuma (March and October, respectively) food availability started to increase. These two months correspond with maximum and minimum monthly productivity and, consequently, food availability was at its highest during months with intermediate NDVI values, resulting in the demonstrated significant quadratic association. Two annual peaks in food availability may thus be distinguished, a large peak shortly after maximum productivity (May) and a smaller peak following minimum primary productivity, which coincides with the arrival of the first rains (November). These two peaks in food availability reflect the two main fruiting strategies of different key food species in the vervet monkeys' diet that ensure a year round food supply. The main finding here, however, is that local NDVI could indeed be used to estimate monthly food availability.

4.5 Discussion

Building on from the well-established association between primary productivity and long-term climatic conditions at a global and continental scale (Lucht *et al.*, 2002; Nemani *et al.*, 2003), this chapter started off by gauging whether this relationship also held at the much finer spatio-temporal resolution of a primate home range over a 12 months observation period. Monthly weather conditions as measured in the home range of the study group were indeed strongly associated to concurrently collected NDVI data. Subsequently, the NDVI was found to be sensitive enough to pick up reduced productivity over the observation period due to adverse weather conditions. Additional support for the value of remote sensing in primate socio-ecology came from the corroboration of the suggestion that vervet monkey home ranges have higher NDVI values than the contiguous environment (Zinner *et al.*, 2002).

Encouraged by these findings, temporal patterns of NDVI data were then tested for their informative content on phenological events. Strong relationships between field and remotely sensed data on the vegetative phenology within the study group's home range were found and metrics to express phenological seasonality were presented. In conjunction with commonly used climatic indices of seasonality, these NDVI derived metrics may aid a more proximate understanding of the causal cascade underpinning primate socio-ecology.

The final section of this chapter integrated all previous findings in the assessment of habitat specific monthly food availability within the home range of the study group. It was argued that the traditional approach, depending on monthly median values of field estimates suffered more severely from complications in terms of biological validity, analytical accuracy and precision than a simple model. The modelling approach was therefore subsequently used to produce two estimates of monthly food availability in the different habitat types of the animals' home range: the first model was based on field observations only, whereas the second took a hybrid approach, linking field observations on the timing of crucial phenological events to the quantitative information contained within NDVI time-series. The two models yielded similar patterns in food availability and, given the slightly different assumptions both models had to make, it was not possible to argue which one should be preferred over the other. Lastly, it was found that local food availability could be expressed as a quadratic function of monthly NDVI.

In summary, this chapter and the previous have suggested several potential uses and applications of the NDVI in ecological contexts that are of direct interest to primatologists. In doing so, the biological validity of this remotely sensed index has continuously been emphasised by detailed illustrations of its intermediate position linking two key environmental factors in primate socio-ecology (atmospheric conditions and food availability). The next chapters will therefore move on and routinely incorporate the NDVI into the matrix of environmental conditions investigated for its explanatory power to certain aspects of the behaviour of the study group (Chapter 5 and 6) and of vervet monkeys throughout their natural range of distribution (Chapter 7).

5 Range use

5.1 Introduction

Central to the study of animal ecology is an understanding of how animals utilise their environment over space and time. A detailed knowledge of this is not only fundamental to the study of the social organisation of a species but also, and ever increasingly more so, in directing conservation efforts to identify key areas and resources for management. In primatology, the vast majority of range use studies has focused on identifying the ecological and social factors that affect the ranging behaviour of the animals. In this respect the distribution and availability of resources such as food, water and sleeping sites have received most attention (Hamilton *et al.*, 1976; Wrangham, 1979; 1981; Rasmussen, 1979; 1983; Raemaekers, 1980; Harrison, 1983; Barton *et al.*, 1992). Effects of atmospheric seasonality (Hill *et al.*, 2003; Hill, 2005; Takemoto, 2004) and predation risk (Harrison, 1983; Isbell, 1991; Cowlishaw, 1997; Enstam and Isbell, 2002; Isbell and Enstam, 2002; Hill and Weingrill, 2006) are also well-documented and additional factors of importance include access to mates and conspecific competition (Struhsaker, 1974; Rasmussen, 1979), habitat structure (Gautier- Hion *et al.*, 1981; Whitten, 1982), disease control (Freeland, 1980) and human activity (Li *et al.*, 1999).

This vast body of research has generated strong support for inter- and intra-specific associations between range use and diet, physiology and group size within the primate taxon (Milton and May, 1976; Clutton-Brock and Harvey, 1977; Dunbar, 1988). Of particular interest here are inter-populational studies on baboons that have quantitatively linked annual home range size (Hill, 1999) and day journey length (Dunbar, 1992; Bronikowski and Altmann, 1996; Williamson, 1997; Hill, 1999) to group size and climatic conditions.

As a prelude to the systems model of vervet socio-ecology, this chapter looks at temporal and spatial variation in range use parameters of the study group. The aim is to relate the observed behaviour to some of the environmental factors mentioned above, both over time and space. To begin with, the parameters of range use considered throughout the chapter are introduced. Next, temporal relationships between monthly ranging behaviour and atmospheric conditions, primary productivity and food availability are examined. Subsequently, spatial associations between the intensity of range use and local environmental conditions such as habitat type, access to resources and predation risk are investigated. The chapter concludes by considering some implications of the current findings for the development of the inter-populational model in Chapter 7.

5.2 Parameters of range use

Often, studies on range use by semi-terrestrial primates such as vervet monkeys report home range size, day journey length and the level of terrestriality on both a monthly and annual basis (Harrison, 1983). In this respect, this study is no exception although the methodology was sometimes fundamentally different from most previous work on primates. The main advantages of the techniques applied here include an increased accuracy in the assessment of commonly used measures of range use by incorporating information on local topography and the introduction of a probabilistic range use measure that will allow quantitative spatial analyses on the internal structure of the home range in Section 5.4. This section then, briefly introduces the parameters of range use considered throughout this chapter and describes the observed temporal variation within them.

5.2.1 Monthly core areas, annual home range and the utilisation distribution

In explaining patterns of range use, two associated concepts are generally thought to be of particular relevance: the home range area and its underlying utilisation distribution

(Johnson, 1980; Anderson, 1982; Getz and Wilmers, 2004). For mammals, the home range has perhaps most intuitively been defined as 'that area traversed by the animal [social unit, group] in its normal activities of food gathering, mating and caring for young' (Burt, 1943). The utilisation distribution on the other hand, is an analytically more explicit concept and quantifies the intensity of space use within the home range (Hayne, 1949; Jennrich and Turner, 1969; van Winkle *et al.*, 1973; van Winkle, 1975). Since primate home ranges are typically estimated by non-statistical procedures such as minimum convex polygon and grid cell occupancy analyses (Herbinger *et al.*, 2001; Kaplin, 2001; Singleton and van Schaik, 2001; Lehmann and Boesch, 2003; Robbins and McNeilage, 2003; Ganas and Robbins, 2005), the utilisation distribution has received relatively little attention within the primatological literature. Moreover, given some biologically unsound assumptions and weaknesses of the more traditional procedures (Anderson, 1982; Ostro *et al.*, 1999; Burgman and Fox, 2003; Börger *et al.*, 2006), an alternative was sought here to estimate both the home range area and annual utilisation distribution of the study group.

One of the best known and currently most widely applied home range estimators in animal ecology (Strickland and McDonald, 2006) is kernel density estimation. This procedure relies on non-parametric algorithms to calculate a probability density landscape from a set of Cartesian points (Silverman, 1986; Worton, 1989; Seaman and Powell, 1996). In terms of animal ranging this translates into the estimation of a utilisation distribution, based on locational observations on the study animals (*e.g.* GPS-coordinates). Within this theoretical framework, a home range can be defined as the smallest area of the utilisation distribution that accounts for a certain percentage of the animal's total space use. The most established method to calculate this relies on the computation of percentage volume isopleths from the utilisation distribution of the animals (Jennrich and Turner, 1969; Anderson, 1982; Gitzen *et al.*, 2006; Millspaugh *et al.*, 2006). This study follows this approach and monthly core areas, annual home range and annual utilisation distribution were determined by kernel density estimation and the subsequent calculation of isopleths.

GPS-coordinates collected on the centre of mass of the group over complete follow days (Section 2.6.2; n= 2,208) were imported into a GIS. To ensure that monthly utilisation distributions were proportional to the amount of time the group spent at each location, only GPS-coordinates collected at constant time intervals were included in the kernel density estimation process (Anderson, 1982; Seaman and Powell, 1996). This meant that fixes at the onset and cessation of daily activity (n= 168) were discarded. In addition, stacked points (n= 27) were shifted randomly by 1 meter prior to analyses to most effectively parameterise the kernels' bandwidth through least squares cross-validation (Dr. H.L. Beyer, *pers. com.*). A fixed Gaussian kernel was applied and cell size of all output raster files was preset to 5m to match GPS accuracy in the field (mean ± sd= 6.9m ± 2.3). The annual utilisation distribution was subsequently calculated by adding monthly estimates together and dividing resulting cell values by the number of months (n= 12). Monthly core areas were delineated by 50% volume isopleths (Börger *et al.*, 2006), whereas total annual home range was determined by 99% volume isopleths[*]. The outline of the resulting estimate of annual home range is presented along with its underlying utilisation distribution in Figure 5.1.

Given the ruggedness of the topography at Lajuma, it was deemed necessary to incorporate altitudinal information into the eventual estimates of monthly core areas and annual home range. Elevation data, upon which these true surface estimates are based, were retrieved from a digital elevation model of the study area (Section 2.5.5) and resulted in an estimated home range over the 12 months observation period of 114 ha (Figure 5.2).

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[*] Since a Gaussian kernel yields an infinite distribution a 100% isopleth, strictly speaking, does not exist. A value of 99% was instead chosen to approximate the total annual home range area.

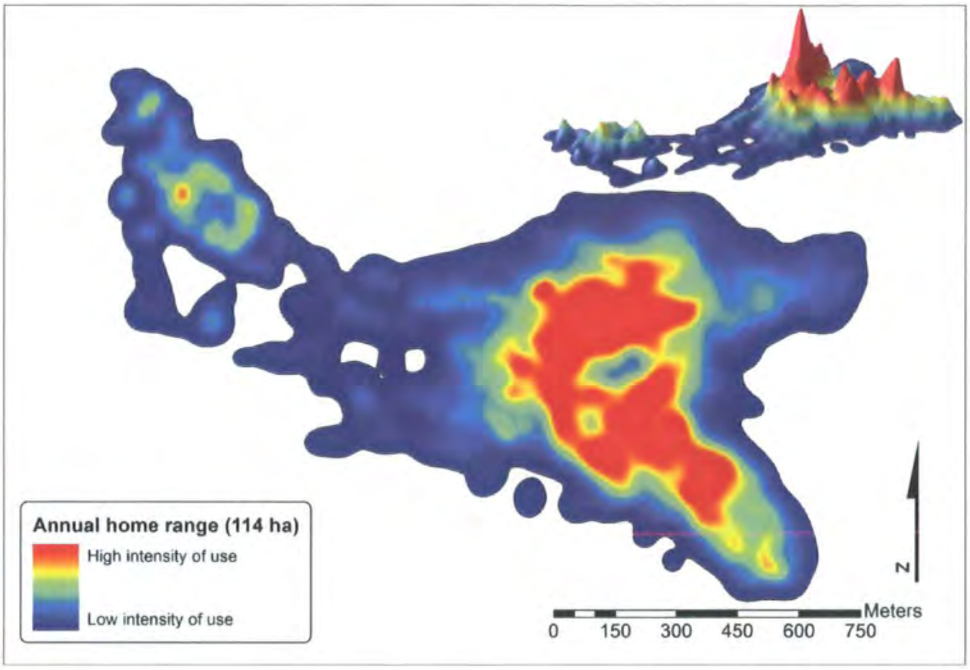

Figure 5.1 Estimated annual home range of the study group as obtained through kernel density estimation. The 3D inset shows the associated utilisation distribution as viewed from the south-west. The colour code and height of peaks are proportional to the percentage of time the group spent at each location within its home range.

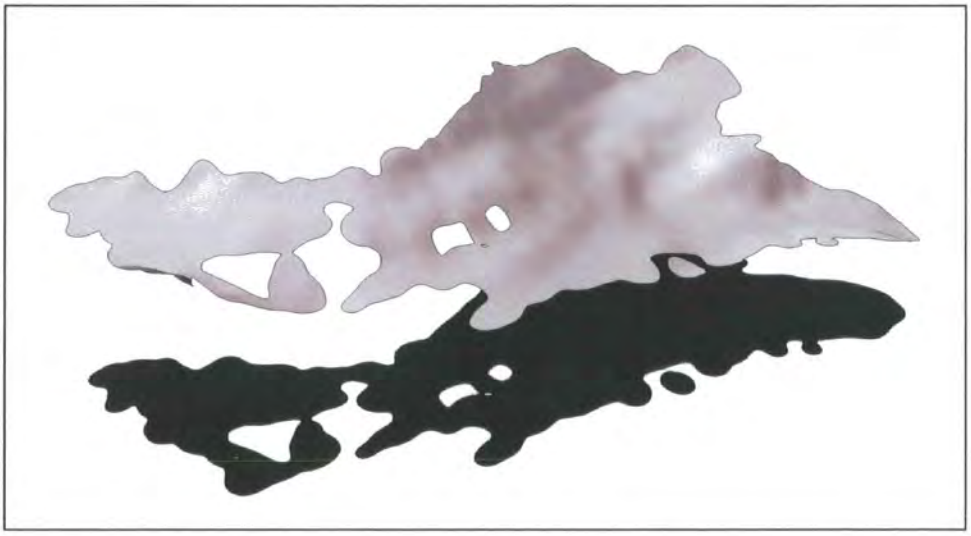

Figure 5.2 Illustration of the two dimensional annual home range viewed from the south-west (black polygon) and its three dimensional projection on the digital elevation model of the study site (grey-shaded polygon). The true surface area (three dimensional) was calculated within a GIS at 114 ha.

To assess whether the size of monthly core areas differed over the two seasons (Section 2.2.2), monthly true surface areas exploited by the animals during the warm wet summer (median= 8.2 ha) were compared to those of the cool dry winter (median= 11.4 ha). No significant difference was found (Mann-Whitney U-test: *U*= 9.0, p= .180; Figure 5.3).

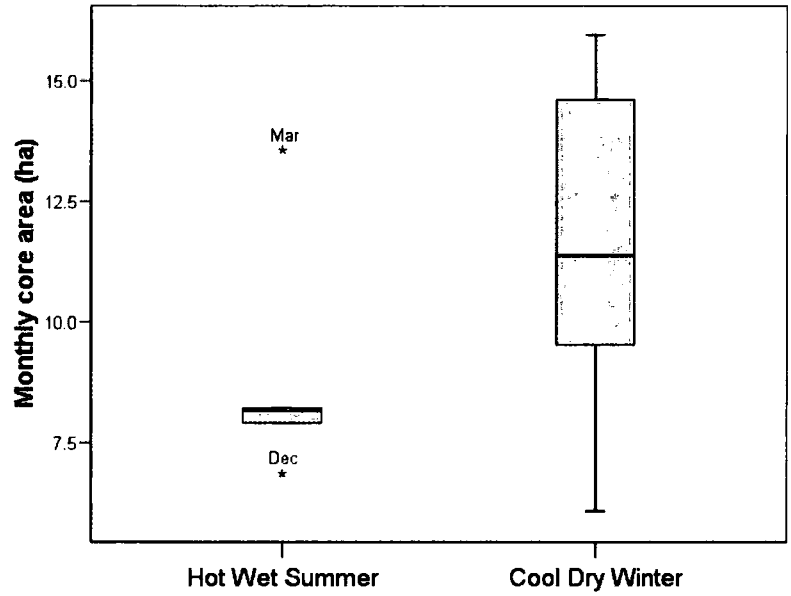

Figure 5.3 Box plots of monthly core areas over the warm wet summer and cool dry winter (asterisks indicate outliers).

5.2.2 Day journey length

Average day journey length was calculated within a GIS by summing daily straight line distances between sequential GPS-coordinates (n= 2,208). Although this measure inevitably underestimates the actual distance travelled by any individual, it provides an appropriate measure for broad-scale comparisons in inter- and intraspecific analyses (Isbell *et al.*, 1999). Analogous to the calculation of true surface ranging areas, altitudinal information from the digital elevation model was incorporated in the calculations of true surface (three dimensional) day journey lengths.

Seasonal differences in day journey length were detected as the group travelled further during the warm wet summer (mean ± se= 1651.0m ± 48.3) than during the cool dry winter (mean ± se= 1510.4m ± 44.3; independent samples t-test; $t_{(82)} = 2.15$, $p < .05$). Monthly differences were also significant (one-way independent ANOVA; $F_{(11,72)} = 4.21$, $p < .001$) and planned polynomial contrasts moreover revealed a cubic trend ($F_{(1,72)} = 7.71$, $p < .01$), indicative of the gradual seasonal change in the daily distance travelled by the study group (Figure 5.4).

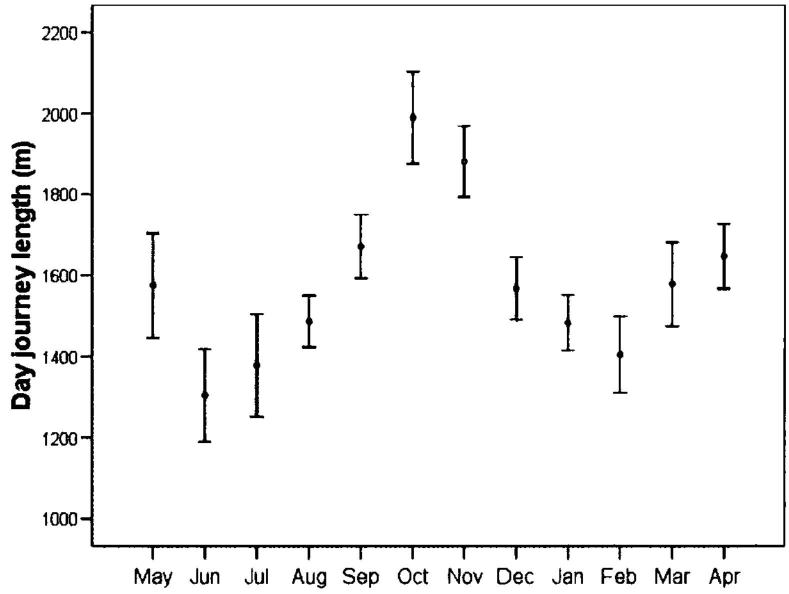

Figure 5.4 Mean monthly estimates of day journey length (error bars represent ± 1se).

5.2.3 Terrestriality

The final range use parameter considered in this chapter, was the amount of time the animals spent on the ground. Since vervet monkeys are generally classified as semi-terrestrial (Fedigan and Fedigan, 1988; Enstam and Isbell, 2007), temporal variation within ranging height of the study group was anticipated. To investigate this, daily percentages of terrestriality were calculated from instantaneous group scan samples on all age-sex classes (Section 2.6.2; n= 8,073).

The vervets spent less time on the ground during the warm wet summer (median= 26.6 %) than during the cool dry winter (median= 40.7 %; Mann-Whitney U test; U= 525.5, $p< .05$). Monthly differences in the level of terrestriality were also significant (Figure 5.5; Kruskal-Wallis test; $H_{(11)}$= 60.74, $p< .001$). Unfortunately, statistical significance of the non-linear trend in monthly mean levels of terrestriality, as suggested by Figure 5.5, could not be assessed since non-parametric equivalents of polynomial contrasts do not exist. Nevertheless, the pattern appears very similar to that observed for day journey length.

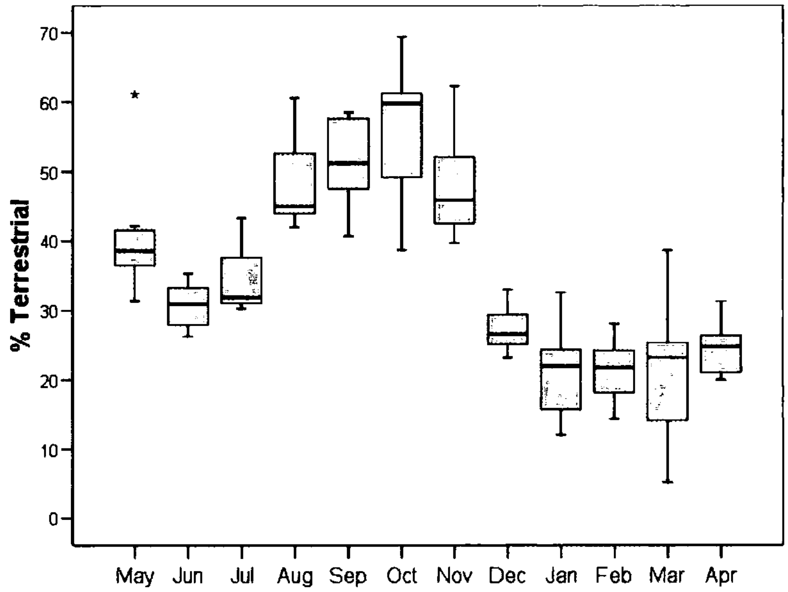

Figure 5.5 Box plots of the monthly percentage of time the animals spent on the ground (the asterisk indicates an outlier).

5.2.4 Range use, group size and interdependency of measures

Before looking at correlations between the temporal patterns observed in ranging behaviour and environmental conditions, two factors that may complicate biological interpretation of results need to be considered. Firstly, the substantial variation in group size over the observation period (Table 2.2) may have had an effect on the range use of the group. Secondly, a possible interdependency between monthly averaged range use parameters (note that monthly averaged values of all range use parameters were normally distributed) had to be assessed. These two confounding factors were investigated through Pearson correlation analyses (Table 5.1).

Table 5.1 Confounding associations between monthly group size and terrestriality and the interdependence between terrestriality and day journey length as revealed by correlation analyses.

		Core area	Day journey length	Terrestriality
Group size	r	.151	.156	***.589***
	Sig.(2-tailed)	.638	.628	.044
	n	12	12	12
Core area	r		-.294	.175
	Sig.(2-tailed)		.354	.587
	n		12	12
Day journey length	r			***.599***
	Sig.(2-tailed)			.040
	n			12

The level of terrestriality was positively related to both total group size and day journey length. This suggested that the decrease in group size over the observation period led to the animals spending less time on the ground. Moreover, through its association with terrestriality, group size may have indirectly affected day journey length, even though a direct correlation did not exist. Given these intricacies, temporal analyses of the association between environmental conditions and range use should control for the effect of group size on the latter. The need for this precaution is furthermore supported by ample evidence from the literature (Clutton-Brock and Harvey, 1977; van Schaik *et al.*, 1983; Wrangham *et al.*, 1993; Janson and Goldsmith, 1995; Chapman *et al.*, 1995; Chapman and Chapman, 2000a, b; Lehmann and Boesch, 2003). Environmental conditions that influence both day journey length and terrestriality at the same time, moreover, are perhaps best ascribed to the range use parameter that makes most biological sense.

5.3 Temporal associations between monthly range use and the environment

The previous section revealed marked monthly variation in range use parameters of the study group. To appraise this temporal variation for its adaptive significance, associations with monthly averaged atmospheric conditions, phenology and food availability were investigated. First-order semi-partial correlations (controlling for the effect of group size on range use, see Section 5.2.4) were employed throughout this section and significant results are taken to suggest a causal relationship that needs to be interpreted for its biological significance.

5.3.1 Atmospheric conditions

Seasonality and diurnal rhythms within atmospheric conditions have often been reported to assert a strong direct (chronobiology, thermoregulation) and indirect (phenological seasonality, food availability) influence on primate behaviour (Erkert, 2003; Mayes, 2003; Anselin, 2006). Here associations with monthly patterns in range use were examined.

A suite of atmospheric variables including several apparent temperature indices (Section 2.4.1) was calculated from the local weather station. In addition, a monthly mist-likelihood index was considered since mist was such an important and frequent phenomenon at the study site. Prior to semi-partial correlation analyses, a significant deviation from normality in monthly rainfall values (K-S test; $D_{(12)} = .263$, $p < .05$) was corrected by a square root transformation. Table 5.2 summarizes the results from linear analyses whereas investigations of scatter plots did not reveal the need to consider non-linear relationships.

A first inspection of this table shows that the size of monthly core areas was not related to any atmospheric variable and also that none of the range use parameters was correlated to rainfall.

Table 5.2 First-order semi-partial correlations between monthly atmospheric conditions and range use, controlling for the effect of group size on range use.

		Core	DJL	Terre			Core	DJL	Terre
T_{min}	r	-.320	***.678***	*.437*	**Photo**	r	*-.545*	***.629***	.232
	Sig.(2-tailed)	.331	.020	.086		Sig.(2-tailed)	.079	.035	.392
	n	12	12	12		n	12	12	12
T_{mean}	r	-.315	***.674***	*.438*	**WC**	r	-.334	***.654***	.416
	Sig.(2-tailed)	.340	.021	.085		Sig.(2-tailed)	.310	.027	.105
	n	12	12	12		n	12	12	12
T_{max}	r	-.309	***.671***	*.440*	**HI**	r	-.406	***.655***	.348
	Sig.(2-tailed)	.349	.021	.084		Sig.(2-tailed)	.210	.026	.186
	n	12	12	12		n	12	12	12
Hum	r	*-.555*	-.138	***-.627***	**THW**	r	-.427	***.615***	.309
	Sig.(2-tailed)	.072	.682	.005		Sig.(2-tailed)	.185	.041	.246
	n	12	12	12		n	12	12	12
SolRad	r	-.089	***.683***	***.617***	**THSW**	r	-.434	***.624***	.319
	Sig.(2-tailed)	.792	.018	.006		Sig.(2-tailed)	.177	.037	.229
	n	12	12	12		n	12	12	12
$\sqrt{P}$	r	-.411	.003	*.-435*	**Mist**	r	-.507	-.250	***-.673***
	Sig.(2-tailed)	.204	.993	.088		Sig.(2-tailed)	.106	.452	.001
	n	12	12	12		n	12	12	12

Core: monthly core area (ha); DJL: monthly mean day journey length (m); Terre: monthly mean % time the animals spent on the ground; $T_{min/mean/max}$: monthly mean minimum/mean/maximum temperature (°C); Hum: monthly mean air humidity (%); SolRad: monthly mean solar radiation (Wm^{-2}); $\sqrt{P}$: square root transformed monthly total rainfall (mm); Photoperiod: monthly mean day length (h); HI: Heat Index; monthly mean apparent temperature taking air temperature and relative humidity into account (°C); WC: Wind Chill; monthly mean apparent temperature taking air temperature and wind speed into account (°C); THW: Temperature-Humidity-Wind Chill index; monthly mean apparent temperature taking air temperature, relative humidity and wind speed into account (°C); THSW: Temperature-Humidity-Solar radiation-Wind Chill index; monthly mean apparent temperature taking air temperature, relative humidity, solar radiation and wind speed into account (°C); Mist: monthly mean mist-likelihood index (°C)

Monthly mean day journey length was positively associated to photoperiod, all investigated measures of temperature and solar radiation. The first finding is intuitively understood in that longer days allow the group to maintain longer activity periods (Section 2.4.2) which enables the animals to cover more distance. A feasible explanation for the positive relation between range use and all temperature indices lies in the relatively low ambient temperature at the Lajuma Research Centre. Low ambient temperatures impose high thermoregulatory demands (Scholander *et al.*, 1950a; 1950b; 1950c) which may have forced the group to minimise energy expenditure by reducing day journey length. As temperature rises, thermoregulatory demands decrease and higher levels of activity become energetically sustainable, resulting in an increase of day journey length. A similar association was observed between temperature and feeding activity of a group of vervet monkeys in Senegal, but only over the coldest month of the study period (Harrison, 1985). It thus appears that, at Lajuma, monthly mean air temperature was sub-optimal throughout the year.

An alternative interpretation of the relationship between temperature and day journey length, however, considers the strong association between the different temperature measures and photoperiod (Pearson correlations; $.856 \leq r \leq .921$, $n = 12$, $p < .001$). In this scenario, temperature and day journey length are only indirectly related through the association between photoperiod and day journey length (a third-variable association). A more conservative interpretation of current results therefore suggests that day journey length merely increased with day length. A conclusive inference on the extent to which the thermal environment and day length influence day journey length will therefore have to be postponed till Section 5.3.4, where a multiple regression analysis will consider all potential explanatory variables simultaneously.

The amount of time the animals spent on the ground was negatively related to air humidity and mist likelihood but positively so to solar radiation. Air humidity and mist likelihood were strongly interrelated (Pearson correlation; r: $.994$, $n=12$, $p < .001$) and, at Lajuma, it seemed reasonable to take both as indicative of mist precipitation. The negative relationship between mist incidence and the level of terrestriality exhibited by the study group may have come about by reduced habitat visibility which differentially affects perceived predation risk by different predator classes (Lima and Dill, 1990; Shultz *et al.*, 2004). Under conditions of reduced visibility, the risk of encounters with terrestrial ambush predators, such as leopards, increases (Enstam and Isbell, 2002), while at the same time the risk of attacks by aerial predators, such as eagles, decreases. Spending less time on the ground during periods of reduced visibility could therefore be an adaptive anti-predation response.

As mentioned, solar radiation was not only related to day journey length but also (and more strongly) to the amount of time the animals spent on the ground. The biologically most intuitive interpretation of this seems that the animals sought out shelter from intense solar radiation as a thermoregulatory response. The level of terrestriality would thereby increase since the most effective shelter and coolest shadow are found on the ground (Mayes, 2003). Subsequently, day journey length would increase through its positive association with terrestriality (Section 5.2.4).

A final point is made here. Table 5.2 revealed that, out of all investigated temperature indices mean ambient air temperatures were more strongly related to the behaviour of the monkeys than any of the apparent temperature indices. This seems in contrast to previous studies that have suggested apparent temperature indices ('perceived environmental temperatures'; Hill, 1999) were more suitable to assess the thermal environment of primates (Hill *et al.*, 2004; Hill, 2005). These previous studies, however, were conducted in relatively open and exposed terrain in which the thermal environment of the animals was far more prone to the modulating effects of air humidity, solar radiation and wind speed. The advocated use of apparent temperature indices in these studies then, seems particularly fit to the study of primates in relatively open and exposed habitats, whereas current findings suggest that ambient air temperatures may be more informative in densely vegetated or otherwise more sheltered environments.

5.3.2 Primary productivity

The influence of monthly variation in home range productivity on the ranging behaviour of the study group was investigated. Unfortunately, and despite the inherently spatial format of the NDVI time-series used to index productivity, spatial relationships could not be considered due to the coarse resolution of the satellite imagery. Consequently, only temporal associations were assessed and results of semi-partial correlation analyses are presented in Table 5.3. In addition, multiple correlation coefficients are given for quadratic relations between the NDVI and residuals of linear regressions between the three range use parameters and group size. These latter coefficients specify the strength of quadratic associations between primary productivity and range use whilst controlling for the effect of group size on range use.

Table 5.3 Linear and quadratic relationships between primary productivity and range use, controlling for the effect of group size on range use.

		Core	**DJL**	**Terre**
NDVI $_{\text{linear}}$	r	-.100	***-.619***	***-756***
	Sig.(2-tailed)	.767	.039	< .001
	n	12	12	12
NDVI $_{\text{quadratic}}$	r_{multiple}	.101	***-.860***	***-.868***
	Sig.(2-tailed)	.955	<.005	<.005
	n	12	12	12

Core: monthly core area (ha); DJL: monthly mean day journey length (m); Terre: monthly mean % time the animals spent on the ground; NDVI: monthly Normalised Difference Vegetation Index

Results show that the size of monthly core areas was not related to monthly primary productivity of the annual home range. This may seem unexpected at first since the animals were shown to select the location of their home range in a way that maximised annual productivity (Section 4.2.3.). It is important though, to distinguish between spatial and temporal range selection here. In fact, the animals' faculty of spatial selection, as demonstrated in the previous chapter, may very well be the reason why no temporal association was found in the current analyses. If the animals can select the location of monthly ranging area on the basis of productivity, this would allow them to mitigate the effects of seasonal variation in productivity within their annual range. This has two important consequences. Firstly, being able to select the location of ranging area reduces the need to adjust range size and, secondly, monthly NDVI values averaged over the entire annual home range might be poor estimates of monthly averaged NDVI values experienced by the monkeys in their monthly ranges. For these reasons, it is all the more unfortunate that spatial associations between range use and NDVI could not be investigated. If possible though, it would be expected that NDVI values of monthly areas are less variable (and higher) than those of the annual range. In addition, a negative association between the size and average NDVI values of monthly core areas would seem likely.

Both a strongly negative linear and quadratic association between day journey length and NDVI were detected. A feasible explanation for the linear relationship lies in the association between high levels of productivity and lush, dense green vegetation (Tucker, 1979). When vegetation density is high, habitat visibility is poor and an adaptive behavioural response would be the observed reduction in day journey length to minimise the likelihood of chance encounters with ambush predators (Altmann and Altmann, 1970; Rasmussen, 1983; Lima and Dill, 1990; Cowlishaw, 1997). The quadratic association, on the other hand, is perhaps best interpreted as reflecting a response of the vervets to increased food availability (Section 4.4.4). The negative sign of this relation suggests that the monkeys were able to reduce daily travel distance while still meeting nutritional demands when food availability was high. This interpretation will be considered in more detail in the next subsection where direct estimates of food availability are investigated for their effect on range use.

Increased primary productivity also resulted in the animals spending less time on the ground. Again, both linear and quadratic relationships existed and two similar interpretations to the ones above are given. Reduced habitat visibility increases the risk of attack by terrestrial ambush predators while at the same time reducing the risk of being detected by raptors (Section 5.3.1). The vervets could adaptively have responded to this by more intensely utilising higher strata in the vegetation during periods of high productivity, thereby giving rise to the detected negative linear association between NDVI and the level of terrestriality. If the quadratic relationship on the other hand is again taken to reflect a behavioural response to increased food availability rather than primary productivity *sensu stricto*, the monkeys spent more time in the higher strata of the vegetation where preferred food items (fruits and seeds of trees) are most abundant. Accordingly, the level of terrestriality dropped.

Finally, since day journey length and terrestriality were strongly interrelated (Section 5.2.3), it needed to be assessed whether the reported linear associations with monthly mean NDVI explain unique parts of the variation in both range use parameters. Second-order semi-partial correlations, controlling for the effects of group size and day journey length, indicated that the NDVI indeed accounted for a significant part of the variation in the level of terrestriality ($r_{\text{NDVI}, \% \text{Terre} \cdot \text{GS}, \text{DJL}} = -.557$, $n=12$, $p < .001$). In contrast, no significant relation between NDVI and day journey length was present, when the effects of group size and terrestriality were accounted for ($r_{\text{NDVI}, \text{DJL} \cdot \text{GS}, \% \text{Terre}} = -.090$, $n=12$, $p= .744$). This suggests that primary productivity was only indirectly related to day journey length through its effect on the amount of time the animals spent on the ground. The biologically most preferable interpretation of the reported linear associations between primary productivity and range use would therefore be that, through a decrease in habitat visibility, primary productivity differentially affected perceived predation risk by different predator classes. The study group changed its vertical range use accordingly by spending less time on the ground, which subsequently resulted in shorter day journey lengths. Quadratic relationships between monthly NDVI and range use, on the other hand, were taken to have come about through the quadratic association of monthly NDVI to estimates of local food availability and are discussed in more detail in the following subsection.

5.3.3 Food availability

A final environmental condition that was investigated for temporal associations to monthly variation in parameters of range use was food availability. Monthly food availability was proxied by the two models developed in the previous chapter. Data were logarithmically transformed to correct for deviations from normality prior to analyses and reported correlation coefficients and levels of significance were controlled for the effect of group size on range use (Table 5.4).

Table 5.4 First-order semi-partial correlations between estimated food availability and range use, controlling for the effect of group size on range use.

		Core	**DJL**	**Terre**
Food availability	r	.235	***-.849***	-231
Log (Model $_{\text{field}}$)	Sig.(2-tailed)	.386	< .001	.395
	n	12	12	12
Food availability	r	-.095	***-.616***	-.151
Log (Model $_{\text{NDVI}}$)	Sig.(2-tailed)	.779	.040	.581
	n	12	12	12

Core: monthly core area (ha); DJL: monthly mean day journey length (m); Terre: monthly mean % time the animals spent on the ground

The size of monthly core areas at Lajuma showed no significant association with food availability. In contrast, a positive relationship between food availability and monthly home range size was reported for vervet populations in Kenya, Cameroon and Senegal (Struhsaker, 1967; Kavanagh, 1978; 1981; Harrison, 1983). At these study sites, the animals dealt with low food availability by expanding their monthly ranges. The monkeys at Lajuma, however, changed the location rather than the size of their monthly range in response to changes in food availability (Figure 5.6). This indicates that the study group differentially exploited the distinct habitat types within its home range over the observation period.

In order to be adaptive, this shifting between habitats requires sufficient local ecological heterogeneity in both the temporal and spatial realm (Hemingway and Bynum, 2005), which certainly seemed to be the case at Lajuma (see *e.g.* Figures 4.6 and 4.10). The animals could therefore respond to temporal changes in food availability in the spatially explicit manner they did. A more quantitative analysis of space use in relation to food availability is presented in Section 5.4.2.

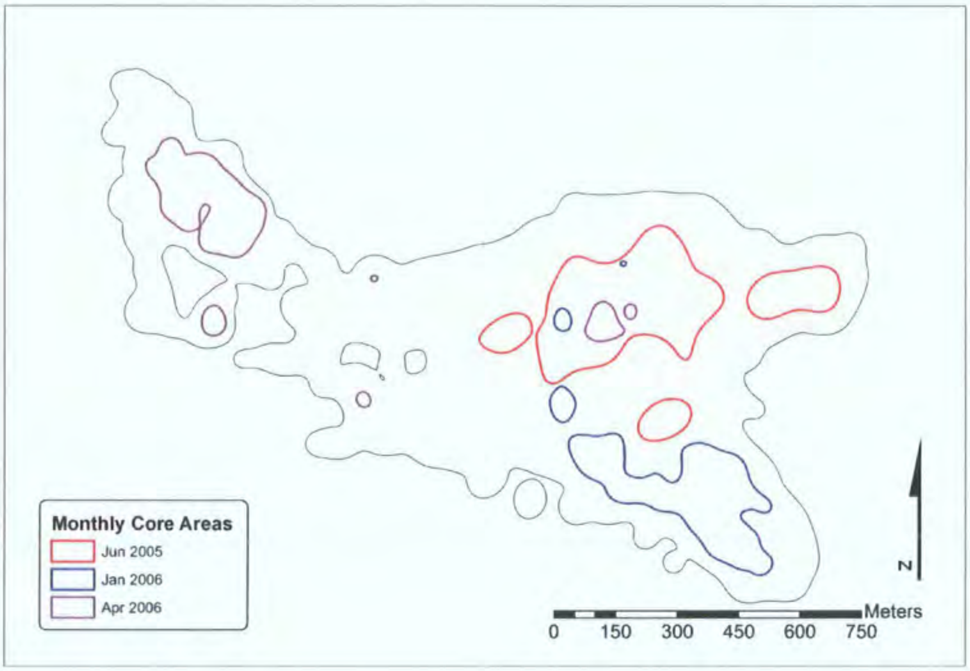

Figure 5.6 Qualitative illustration of how the study group changed location rather than size of monthly core areas in response to changes in food availability.

The significant negative association between day journey length and food availability found here (and in Section 5.3.2), is in contrast to the positive relationships reported for vervet populations in Cameroon and Senegal (Galat and Galat-Luong, 1977; Kavanagh, 1977; Harrison, 1982). This disparity is perhaps best understood by considering other aspects of food resources such as the spatial distribution, quality and overall abundance. Highly relevant in this respect, was the much more pronounced seasonality at the other study sites where overall animal activity (including ranging behaviour) was severely constrained by lack of food during at least part of the year (Kavanagh, 1981; Harrison, 1984; 1985). At one site, this shortage was so extreme that the vervets reduced activity up to the point of complete lethargy (Galat and Galat-Luong, 1977; Fedigan and Fedigan, 1988). In contrast, and possibly because of the absence of a hot dry summer, food was never such a strong limiting factor at Lajuma. Consequently, where the vervets in Cameroon and Senegal had to conserve energy expenditure during periods of food shortage and maximise energy intake during periods of relative abundance, the vervets at Lajuma were far less constrained by food availability and, during periods of maximum food availability, could even reduce day journey length while still meeting nutritional demands. Interestingly, a recent review on range use in primates found only 3 out of 52 studies on African primates (excluding Madagascar) that reported an association between food availability and day journey length (Hemingway and Bynum, 2005). These were all positive but the author is aware of at least one study on an African primate species, in which the same negative association between food availability and day journey length as found here, was reported (Barton *et al.*, 1992). It might be worth noting that this study is one of the very few that measured primate food availability directly in terms of biomass.

The amount of time the animals spent on the ground was not related to estimates of food availability, which is in opposition to what was suggested by the significant quadratic relationship with NDVI in the previous subsection. A possible explanation for this is that, since the modelled estimates of food availability were solely based on phenological observations on trees, they did not take the availability of potential food items in the herb and shrub layers into account. Although this intrinsic simplification of the models was justified by detailed dietary analyses (Section 4.3.2), the ensuing disregard of food items from non-arboreal resources may have prevented the negative association between terrestriality and modelled food availability from reaching statistical significance. Alternatively, given the monkeys' highly flexible feeding behaviour and diverse diet, the absence of this association might be representative of the animals' ability to readily exploit food resources regardless of vegetational stratum and overall availability. An unequivocal conclusion on the relation between food availability and the level of terrestriality can therefore not be reached on the basis of current data.

5.3.4 Regression models for temporal patterns in range use

To determine the extent to which the observed temporal variation in monthly range use can be ascribed to the different environmental conditions discussed in the preceding subsections, regression models were developed. Selection of predictor variables for the full model was based on the preceding correlation analyses and was restricted to environmental conditions that are available in the development of the inter-populational models in Chapter 7. Predictor variables therefore included group size, atmospheric conditions and a linear and quadratic NDVI term. Despite several well-documented problems and inherent biases with stepwise regression methods (Johnson and Omland, 2004; Field, 2005; Whittingham *et al.*, 2006), a combination of forward and backward variable entry procedures was chosen. This was deemed legitimate since current analyses mainly serve exploratory purposes (Wright, 1997). Moreover, the number of potential predictor variables was restricted *a priori* to known predictors (as indicated by first-order semi-partial correlation analyses). Results from these regression analyses are presented in Table 5.5.

Table 5.5 Key parameters and statistics of best-fit regression models developed to quantify the relationship between monthly parameters of range use and local ecological conditions.

		B	**se B**	**β**	**t**	**F_{model}**	**se estimate**	**Adj. R^2**
Core	Intercept	10.15	0.93		10.97^{***}	-	3.21	-
DJL	Intercept	9.82×10^3	2.25×10^3		4.36^{**}	***11.65******	116.37	.659
	NDVI	-24.30×10^3	7.00×10^3	-11.53	-3.47^{**}			
	$NDVI^2$	17.59×10^3	5.35×10^3	10.92	3.29^{**}			
Terre	Intercept	93.89	17.97		5.23^{***}	***50.70******	4.11	.900
	GS	1.26	.68	.199	1.85^{*}			
	NDVI	-117.04	14.74	-.851	-7.94^{***}			

* = $p < .10$; ** = $p < .05$; *** = $p < .01$

It was found that the size of monthly core areas was not influenced by any combination of environmental conditions. As argued before, this is most likely due to the animals' ability to change the location of monthly ranges through habitat switching. Day journey length was mainly driven by food availability and decreased when food was more abundant. The level of terrestriality, finally, increased with group size and decreased with primary productivity. The proximate factor driving this association was thought to be perceived predation risk since the risk of attack by terrestrial ambush predators decreases with group size (Shultz *et al.*, 2004), whereas reduced habitat visibility during months with high productivity increases this risk (Altmann and Altmann, 1970; Rasmussen, 1983; Cowlishaw, 1997). In conclusion, from the current analyses on ranging behaviour of the study group, clear and biologically intuitive expectations may be formulated for the inter-populational model. Potential complications are anticipated though, since vervets at different sites may pursue different locally optimal strategies and global behavioural trends may therefore not exist. This remarkable behavioural flexibility of the vervet super-species complex may very well be the reason for its pan sub-Saharan distribution.

5.4 Spatial associations between annual range use and the environment

Spatial variation within range use is much harder to evaluate quantitatively than temporal variation. Its biological relevance (already alluded to in Section 5.3), is highly significant though and annual associations to spatially varying factors are therefore investigated. In analysing spatial data, assumptions of standard statistical procedures must be met and, in addition, investigations of spatial autocorrelation are necessitated. If uncontrolled for, spatial autocorrelation may result in severe pseudo-replication, inflated significance values and inaccurate parameter estimates (Clifford *et al.*, 1989; Legendre, 1993; Lennon, 2000). Because of this, it is often removed from data by a sub-sampling routine. Chapter 3, however, already demonstrated that even in the absence of significant autocorrelation, spatially explicit analyses may still be preferable over standard statistical procedures (*e.g.* Section 3.4). What is more, in the case of animal ranging it has been contended that spatially independent data can not sufficiently capture the biological essence of the animals' behaviour since range use is an intrinsically non-independent serial event (Lair, 1987). Not explicitly accounting for the spatial structure of range use data would, therefore, considerably compromise biological significance of analyses (De Solla *et al.*, 1999) and, because of this, spatially explicit procedures were used where required throughout this section. Given the complexity and extreme computational demands of these techniques however, a random sub-set of 1,000 locations was generated (Figure 5.7) and reported results from all spatial analyses are obtained from these sample points.

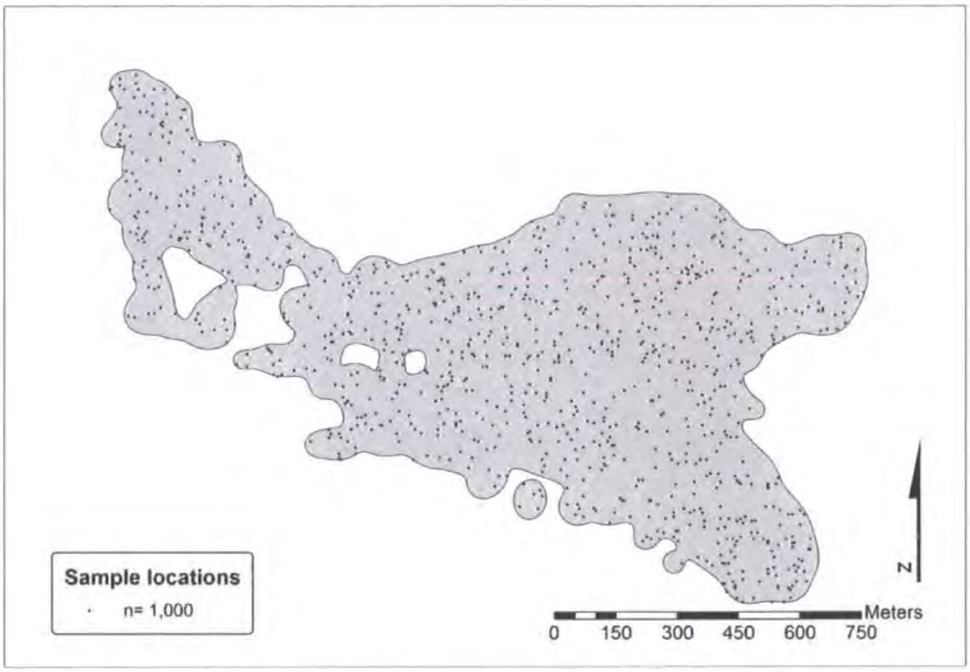

Figure 5.7 Map showing the location of the 1,000 randomly selected sample points upon which all spatially explicit analyses presented in this section are based.

The section starts off with a traditional goodness of fit analysis to investigate potential habitat preferences of the study group. Subsequently, spatial associations between the intensity of range use, indexed by the annual utilisation distribution, and the availability of key resources and perceived predation risk are assessed.

5.4.1 Habitat selection

Utilisation and availability data of habitat types typically show a distinctly multinomial distribution. A goodness of fit analysis was therefore conducted to test whether the amount of time spent in each habitat type (utilisation) was proportionate to the respective true surface area of each habitat (availability). It should be recognised that an implicit assumption of utilisation-availability analyses is that all habitat types are equally accessible at all times and that the animals have knowledge of this. In other words, an ideal free distribution (Fretwell and Lucas, 1970) is assumed and modulating effects of *e.g.* landscape connectivity (Tischendorf and Fahring, 2000; Moilanen and Hanski, 2001), predation risk (Lima, 2002; Brown and Kotler, 2004) and competition (Koops and Abrahams, 2003; Ruxton and Humphries, 2003) are alleged to be negligible. Traditionally, this type of analysis has relied on discrete point observations from telemetric measurements (Alldredge and Ratti, 1986, 1992) but here information on range use was extracted from the annual utilisation distribution. Advantages of this include: 1) an increased sensitivity of analysis; 2) a reduced impact of location error; 3) no concerns about interdependence between data points (Swihart and Slade, 1997) and; 4) correctly treating the study group as the unit of analysis rather than individual sample points (Marzluff *et al.*, 2004).

The initial analysis revealed that habitat types were not used in proportion to their availability in terms of true surface area ($\chi^2_{(9)}$= 40.2, p< .001). To determine preference or avoidance of individual habitat types, post-hoc analyses (Neu *et al.*, 1974) compared the proportion of the home range area comprised by each habitat type to Bonferroni adjusted 95% confidence intervals of observed use. The results of this procedure are presented in Table 5.6.

Table 5.6 Availability and utilisation data of the different habitat types within the animals' home range over the period May 2005 - Apr 2006.

Habitat	**Total area (ha)**	**% total area (availability)**	**% time spent (utilisation)**	**95%-c.i. time spent (utilisation)**	**Habitat selection**
Cliff	3.3	2.9	0.4	0.0 - 0.8	avoided
Marshland	2.8	2.4	4.5	3.2 - 5.8	preferred
Grassland	9.8	8.6	5.5	4.1 - 6.9	avoided
Shrubland	7.5	6.5	2.6	1.6 - 3.6	avoided
Bushland	14.6	12.8	4.3	3.0 - 5.5	avoided
Woodland	2.0	1.7	1.4	0.7 - 2.1	neutral
Thicket	32.5	28.4	48.6	45.5 - 51.7	preferred
Riverine forest	8.6	7.5	15.2	13.0 - 17.5	preferred
Low/short forest	28.3	24.8	16.0	13.7 - 18.2	avoided
Tall forest	4.8	4.2	1.5	0.8 - 2.3	avoided
Total	**114**	**100**	**100**		

The table shows that the animals preferentially used the Marshland, Thicket and Riverine forest habitats within their home range, whilst avoiding Cliff, Grass-, Shrub- and Bushland, Low to short forest and Tall forest. In interpreting these results though, it is important to bear in mind that selection processes form a hierarchical structure (Johnson, 1980). Investigations into habitat selection within a home range (third-order) should therefore always acknowledge that selection of the home range area (second-order) within the geographical range of the species (first-order) has already occurred (Johnson, 1980; Buskirk and Millspaugh, 2006). In this instance this implies that, although data indicate that the animals used marshlands within their home range more than would be expected on the basis of availability, this does not automatically justify a claim of habitat preference for this habitat type. In fact, in selecting the location of the home range an active avoidance of Marshland was apparent as large stretches of the west and south-west boundary of the home range were Marshland. It is therefore concluded that the true preferred habitats of the vervets at Lajuma were Thicket and Riverine forest. Potential causes for why these habitats were preferred are examined in the following two sections.

5.4.2 Access to resources

Spatial associations between annual range use and access to key resources such as food, surface water and sleeping trees are investigated. Information on the spatial distribution of food availability was gathered from the two habitat specific models developed in the previous chapter. In addition, access to water and sleeping sites was expressed as the shortest Euclidean distance of each location within the animals' home range to year-round water streams and the nearest known sleeping tree. Graphical representations of the spatial distribution of food and Euclidean distance landscapes are given in Figure 5.8. Spatial correlation coefficients, geographically effective degrees of freedom (Dutilleul, 1993) and significance values of the associations found between the annual utilisation distribution and these variables are presented in Table 5.7.

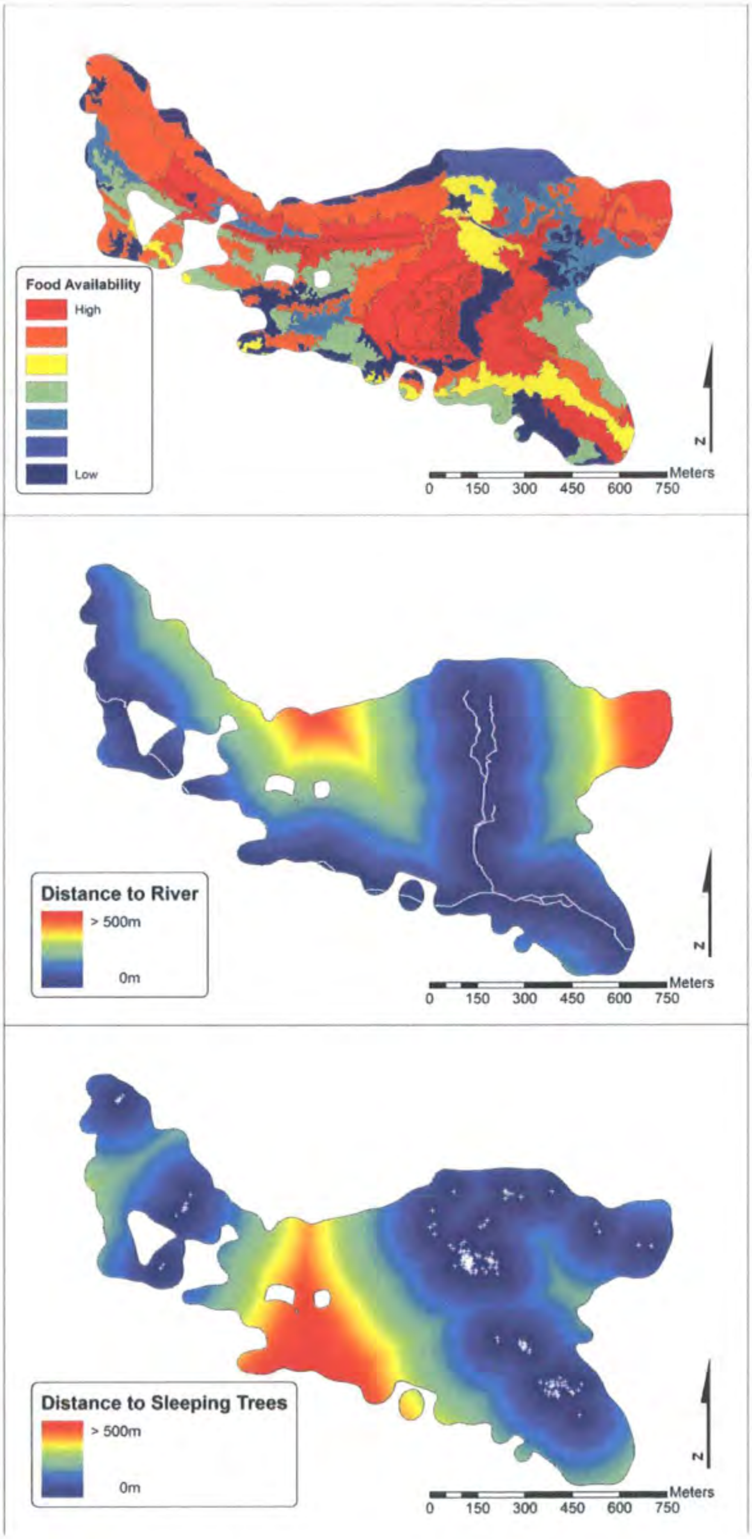

Figure 5.8 Graphical representation of the spatial distribution of food and Euclidean distance landscapes from surface water and sleeping trees. Surface water and sleeping trees in the distance landscapes are represented by white lines and crosses respectively.

Table 5.7 Spatial correlations (Dutilleul, 1993) between range use intensity and two estimates of food availability, distance to permanent surface water and sleeping trees (n= 1,000).

		Food availability (model $_{\text{field}}$)	**Food availability (model $_{\text{NDVI}}$)**	**Distance to river**	**Distance to sleeping trees**
Range use intensity	r	***.363****	***.371****	***-.341***	***-.404***
	df	336.89	492.51	60.61	49.07
	Sig. (2-tailed)	<.001	<.001	<.005	<.005

*=Spearman correlation coefficient (r_s)

The results from these spatial analyses are in line with what was anticipated from previous primatological work (Barton *et al.*, 1992). Arguably though, the value of the coefficients reported here might be more indicative of the true strength of association since the effect of space was explicitly accounted for (Legendre, 1993; Lennon, 2000). In short, the study group spent significantly more time in areas where food was more abundant whereas areas closer to permanent water sources and sleeping trees were more intensively used than would be expected by chance alone. Annual range use of the study group was thus clearly influenced by access to the resources considered here.

5.4.3 Perceived predation risk

Space use by animals is influenced by both lethal and non-lethal costs of predation (McNamara and Houston, 1987; Lima and Dill, 1990; Brown and Kotler, 2004; Thomson *et al.*, 2006) and primates are known to adapt their range use in a predator sensitive way (Cowlishaw, 1997; Enstam and Isbell, 2002; Miller, 2002). It is furthermore generally agreed that the selective significance of predation is best assessed by considering perceived predation risk from the primate's point of view (Hill and Dunbar, 1998), ideally in a predator specific manner (Lima, 1992; Shultz *et al.*, 2004). Hence, in this study perceived predation risk was estimated by *ad libitum* recordings on alarm responses by the study group during complete follow days.

Vervet monkeys use predator specific alarm vocalisations to elicit adaptive responses among conspecifics (Struhsaker, 1965; Seyfarth *et al.*, 1980; Cheney and Seyfarth, 1981) and these can be recognised by human observers. Geographic coordinates of alarm events were calculated from the two GPS fixes immediately preceding and following an event. A total of 385 alarm responses were recorded and categorised into predator specific classes (eagle, n= 215; baboon, n= 57; leopard, n= 15; snake, n= 12 and unknown, n= 86). Kernel density estimation (see Section 5.2.1) was subsequently employed to create predator specific density distributions of perceived risk per time spent at each location in the home range area (here after 'landscapes of fear' (Laundre *et al.*, 2001); Figure 5.9). The outcomes of spatial correlation analyses between the annual utilisation distribution and predator specific landscapes of fear are presented in Table 5.8.

Table 5.8 Spatial correlations (Dutilleul, 1993) between range use intensity and predator specific perceived predation risk (n= 1,000).

		Eagle	**Baboon**	**Leopard**	**Snake**
Range use intensity	r	-.063	***-.245***	***-.389***	.084
	df	292.27	85.02	115.71	153.44
	Sig. (2-tailed)	.282	.022	<.001	.297

The lack of a significant negative relation between the intensity of range use and perceived predation risk by eagle was, at first, surprising. More than two-third of all alarm responses that could be attributed to a predator class was elicited by a perceived potential aerial predator, yet the vervets appeared to have been unable to adjust their ranging behaviour in a way to reduce this risk. Three explanations seem plausible. First, the effectiveness of reducing perceived predation risk by eagle through changes in range use may have been severely restricted by the presence of a breeding pair of crowned eagle within the home range of the study group. Consequently, and given that aerial predators typically monitor areas much larger than the home ranges of their primate prey (Shultz and Noë, 2002), the monkeys may have been approximately equally susceptible to predation throughout their home range. Circumstantial statistical evidence for this

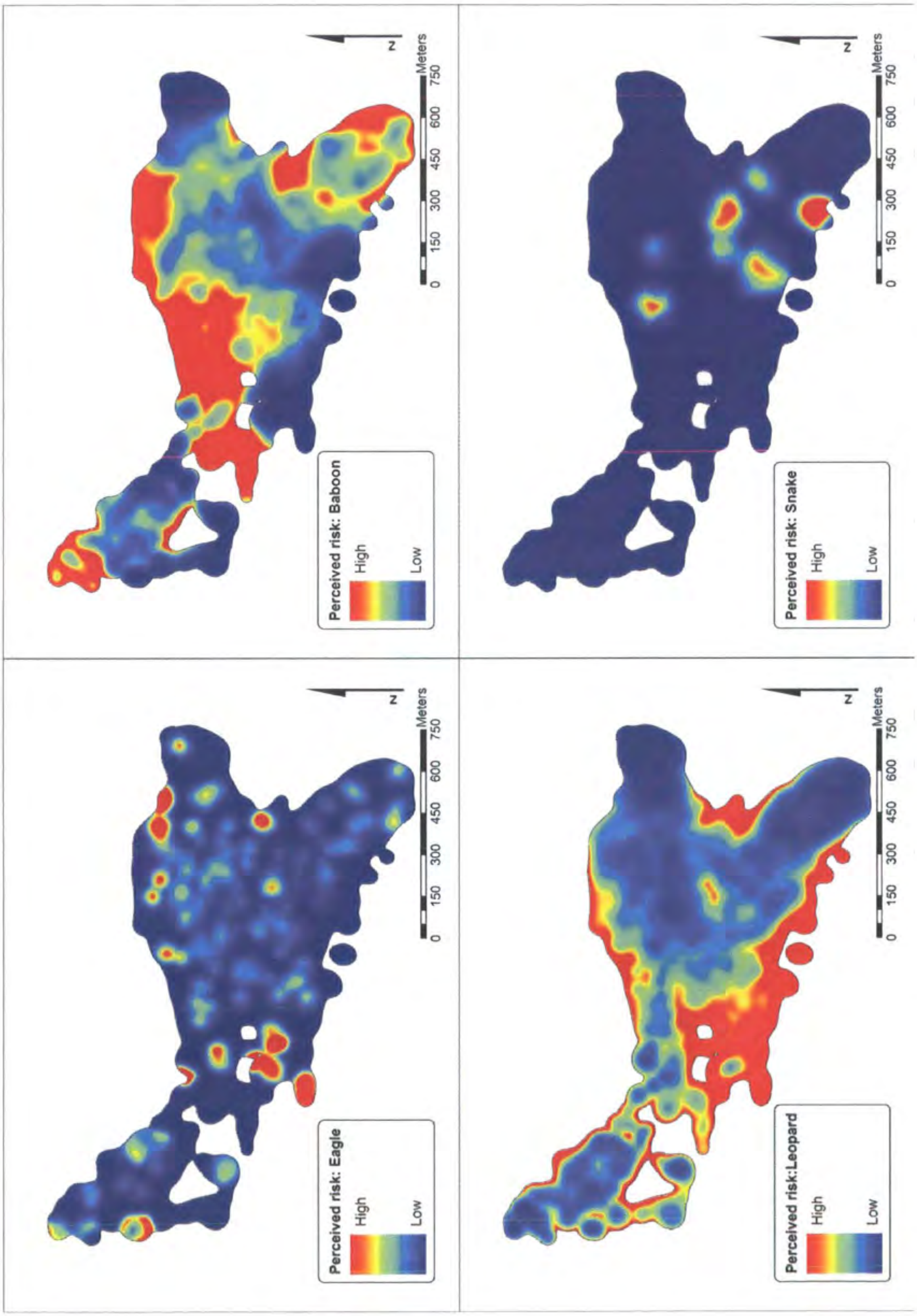

Figure 5.9 Illustrative representations of predator specific landscapes of fear, based on alarm responses by the study group within their home range over the observation period (note that the scale in colour coding differs between the four images).

comes from the comparatively high number of geographically effective degrees of freedom (Table 5.8). This suggests that spatial autocorrelation within alarm responses to eagle was relatively low and hence, that perceived risk of predation by eagle was fairly homogeneously distributed over the entire home range area. A second explanation for the lack of a negative association between the annual utilisation distribution and perceived predation risk by eagle is that the vervets may have responded by adjusting vertical substrate use (Section 5.3.2) rather than horizontal range use. The third explanation might be that eagles can be spotted from far away when soaring high over the canopy. In this respect, the location of alarm calls may not have been as indicative for the location of eagles as it was for other predators. If these explanations are taken into consideration, the current result is perhaps less surprising.

Perceived predation risk by baboon and leopard were both negatively associated to the intensity of range use thereby illustrating that, with regards to these two confirmed terrestrial and arboreal predators (Section 2.3.1), the study group was actively avoiding areas of high perceived risk.

Finally, no significant association was found between the intensity of range use and alarm responses caused by encounters with snakes. In combination with qualitative observations on the nature of these encounters, this was taken to suggest that the vervets did not perceive snakes as a serious threat once detected. This substantiates the notion that most on-site species of snake were not actively predating vervet monkeys, although they do pose a potential cause of mortality (Section 2.2.4). The only species of snake at Lajuma that is known to prey on vervet monkeys, the African rock python, was never encountered by the animals during a follow day.

5.4.4 Regression model for spatial patterns in annual range use

A spatial regression model was employed to determine the extent to which the observed variation in annual range use could be ascribed to the different environmental conditions discussed in the preceding analyses. Given the presence of significant spatial autocorrelation in both the response and predictor variables (Table 5.9), the most appropriate theoretical framework for analysis was a mixed regressive-spatial regressive (Anselin, 1988; Florax and Folmer, 1992) or lagged predictor model (Rangel *et al.*, 2006).

Table 5.9 Global Moran's *I* and associated Monte Carlo p-values (n permutations= 200) indicating the high level of positive spatial autocorrelation within all variables. Moran's *I* has an expected value close to zero in the absence of autocorrelation whereas values close to 1 are indicative of very strong positive spatial autocorrelation. The lag distance upon which statistics are based, was set to the mean nearest neighbour distance between sample points (17.08 m).

	Moran's *I*	$\mathbf{p_{Monte\ Carlo}}$
Utilisation distribution	1.05	<.005
Food availability (model $_{\text{field}}$)	.87	<.005
Food availability (model $_{\text{NDVI}}$)	.84	<.005
Distance to surface water	.97	<.005
Distance to sleeping trees	.90	<.005
Perceived predation risk by eagle	.77	<.005
Perceived predation risk by baboon	1.05	<.005
Perceived predation risk by leopard	.63	<.005
Perceived predation risk by snake	.87	<.005

In matrix notation the general specification of a mixed regressive-spatial regressive model is expressed by:

$$y = \rho Wy + X\beta + WX\gamma + \varepsilon$$

where, y is the n x 1 vector of observations on the response variable, ρ is the spatial autoregressive parameter, W is an n x n weights matrix that formalises the spatial relationships between sample points, X is the n x k matrix of observations on the predictor variables, β is the k x 1 vector of regression parameters associated to X, γ is the k x 1 vector of spatial cross-regressive parameters associated to X and ε, finally, is the n x 1 vector of independent and normally distributed error terms.

Conceptually, this model can be understood as a normal regression model (the regressive term; $X\beta$) complemented by two spatial sets of predictor variables. The first of these (the autoregressive term; ρWy) is derived from the average values of the response variable at neighbouring sample points, whereas the second (the cross-regressive term; $WX\gamma$) incorporates the average values of all predictor variables at neighbouring sample points. The degree to which neighbouring sample points influence the predicted values of the model is defined by the row-standardised weights matrix W (Anselin, 2002; 2006). In the model developed here, this matrix contained non-zero neighbour weight elements (w_{ij}) that specified the relationships among all sample points by a simple distance decay function. The effect of neighbour j on location i was set to be equal to the inverse geographical distance between location i and neighbour j ($w_{ij}= 1/d_{ij}$). Results from ordinary least square estimation are presented in Table 5.10.

Table 5.10 Key parameters and statistics of the lagged predictor model that was developed to quantify the relationship between the annual utilisation distribution of the study group and five ecological conditions.

	B	se B	β	γ	se γ	t	p
Food availability (model $_{\text{field}}$)	.170	.020	.218	.685	.278	8.33	<.001
Distance to surface water	-.167	.045	-.099	.940	.013	-3.68	<.001
Distance to sleeping trees	-.447	.045	-.281	.932	.016	-9.83	<.001
Perceived predation risk by baboon	-.142	.026	-.144	.814	.111	-5.43	<.001
Perceived predation risk by leopard	-.198	.024	-.239	.723	.224	-8.36	<.001

$\rho \pm$ se= .820 ± .105
n= 1,000, Adj. R^2= .795, p< .001

The outcome of the model is in line with what was anticipated on the basis of the preceding correlation analyses and the extensive literature on primate range use. The intensity of space use within the annual home range of the study group was positively associated with food availability, while at the same time the animals stayed close to water and sleeping trees and avoided areas of high perceived predation risk by baboon and leopard. It deserves mention that the inclusion of food availability as assessed by the model based on field observations rather than NDVI values, yielded the best fit (although the difference between the two was marginal). In addition it might be interesting to note that when perceived predation risk by eagle and snake were included as predictor variables, their associated probability values were not significant (p_{eagle}= .09, p_{snake}= .98). Moreover, the resulting increase in the model selection criterion (ΔAICc= 5.28) did not seem to justify the inclusion of these two variables either.

In a comparison of the lagged predictor model to a standard regression model based on the same predictor variables, model selection criteria (ΔAICc= 942.84) indicated that the spatial approach was to be preferred. Moreover, a substantially larger proportion of the variation in the annual utilisation distribution of the study group, as reflected by the respective coefficients of determination (79.5% and 45.9% respectively), was accounted for. Most importantly however, visual inspections of the spatial structure of model residuals (Figure 5.10) suggested that the vector of error terms of the lagged predictor model met the crucial assumption of an independent and identically normal distribution (Anselin, 2006), whereas residuals of the standard regression model did not. Unfortunately, formal statistical tests to assess the significance of autocorrelation in regression residuals to substantiate this claim are unknown to the author (Lichstein *et al.*, 2002).

5.5 Discussion

This chapter set out to identify some of the ecological and social factors influencing the way in which the study group utilised its environment over time and space. Where appropriate a GIS was used to calculate commonly reported parameters of range use and, in addition, a within primatology relatively unexplored measure of space use (the utilisation distribution) was computed. Proceeding from the extensive examinations in the previous two chapters, the usefulness of the NDVI in understanding primate socio-ecology was also examined.

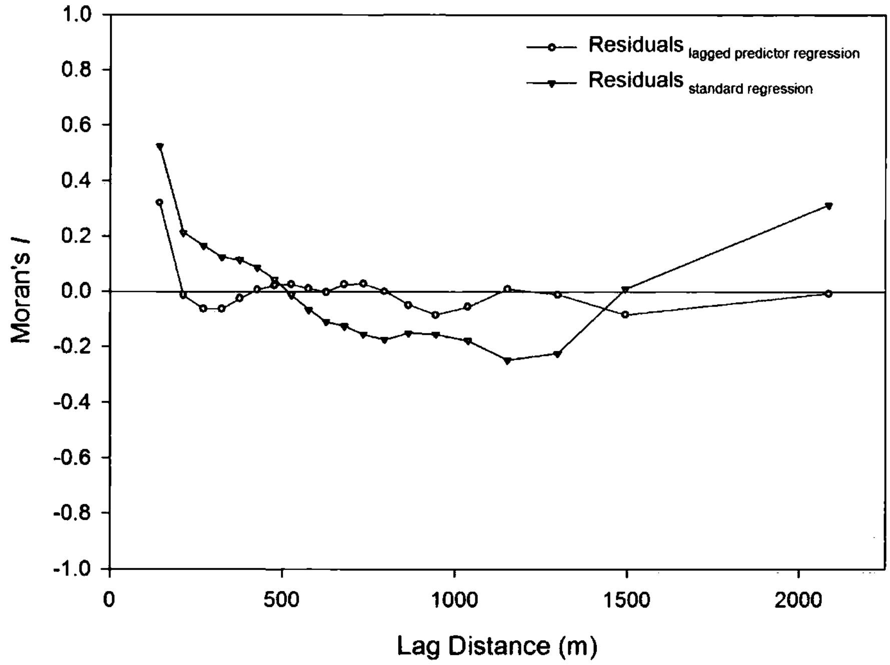

Figure 5.10 Moran's *I* correlograms of residual values of the lagged predictor model and a standard regression model. Moran's *I* has an expected value close to zero in the absence of spatial autocorrelation whereas strongly negative and positive values are indicative of negative and positive spatial autocorrelation respectively. The figure shows that all spatial patterning was effectively removed from the lagged predictor residuals from the second lag onwards. This strongly suggests that the model was statistically appropriate. Residuals of the standard regression in contrast show a distinct spatial pattern.

Temporal associations between the size of monthly core areas and group size, atmospheric conditions, primary productivity or food availability were not detected. Especially the lack of a correlation with the latter two environmental factors was unexpected given previous reports from vervet populations in which monthly ranging areas increased in response to reduced food availability (Struhsaker, 1967; Kavanagh, 1978; 1981; Harrison, 1983). In contrast to this the study group pursued a different behavioural strategy: rather than adjusting the size of monthly core areas, the group adjusted the location of monthly ranging areas within their annual home range. This phenomenon has been observed in other primate taxa as well (Hemingway and Bynum, 2005) and is known as adaptive habitat switching. The disparity in behaviour between different populations strongly suggests that local associations need not have global validity. In other words, the accuracy or indeed plausibility of a global (pan sub-Saharan

Africa) model of vervet socio-ecology may be compromised by the behavioural flexibility of the species. The effect of spatial heterogeneity (Fotheringham *et al.*, 2002) in the socio-ecology of vervet monkeys, therefore, deserves serious consideration in Chapter 7.

In contrast to the size of monthly core areas, monthly averaged day journey length and level of terrestriality did show significant temporal associations to the social and ecological environment. Step-wise regression analyses revealed that day journey length was best explained by a quadratic function of monthly NDVI, whereas the level of terrestriality was best expressed by a linear function of group size and NDVI. Interestingly then, the remotely sensed NDVI was the single-most important explanatory environmental variable to which the study group appears to have been responding. Expectations about the NDVI's potential value in the development of inter-populational models for primate socio-ecology, therefore, were strengthened.

Lastly, the internal spatial structure of the home range was quantified by a probabilistic measure of range use. This annual utilisation distribution was successfully linked to several spatially varying environmental conditions within the animals' home range. A mixed regressive-spatial regressive model demonstrated that annual space use by the study group was strongly influenced by annual food availability, distance to surface water and sleeping trees and perceived risk of predation by baboon and leopard. Although methodologically quite distinct from previous studies on range use in primates, findings from current analyses are in line with what has commonly been reported in the primatological literature (Harrison, 1983; Isbell, 1991; Barton *et al.*, 1992; Cowlishaw, 1997; Enstam and Isbell, 2002; Isbell and Enstam, 2002). However, both statistically and biologically current analyses may be more valid in that they explicitly account for the effect of location in socio-ecological processes. The added value of these spatial techniques may very well prove crucial in the development of effective conservation strategies, based on statistical models of species specific range use.

6 Time allocation

6.1 Introduction

Time is an important resource affecting primate activity and, as is true for most resources, is usually limited (Dunbar, 1992b). To maximise inclusive fitness, animals must allocate the time available during their daily activity period adaptively over different behavioural activities. For social animals, such as the majority of primate taxa, this entails that apart from investing time to meet nutritional and thermoregulatory demands whilst avoiding predation (Schoener, 1971; Pulliam, 1973; Caraco, 1979b; 1979a; Iwamoto and Dunbar, 1983; Mangel and Clark, 1986; Mitchell and Lima, 2002), a significant amount of the active period has to be dedicated to maintaining social relationships (Janson and Boinski, 1992; Dunbar, 1993; 1996). Based on these basic demands on time allocation in the primate time budget, four broad behavioural categories are generally distinguished. These categories incorporate time spent on feeding, moving, social and resting activities and together typically account for more than 95% of total animal activity (Dunbar, 1988). It is important to emphasize that, since an animal can only allocate 100% of its available time over these four mutually exclusive categories, the different time budget components are inherently non-independent.

Numerous studies on time allocation in primates have suggested relationships between time budget components and ecological and demographic factors (Crook and Gartlan, 1966; Crook, 1970; Clutton-Brock and Harvey, 1977). Activity patterns have been found to vary seasonally in response to changes in food availability (Kavanagh, 1978; Harrison, 1985; Isbell and Young, 1993; Doran, 1997; Williamson and Dunbar, 1999; Nakagawa, 2000) and atmospheric conditions (Fa, 1986; Baldellou and Adan, 1997; Hill *et al.*, 2003). Diurnal variation (Hall and Gartlan, 1965; Harrison, 1985; Baldellou and Adan, 1998; Hill, 2005) and inter-populational differences (Dunbar, 1992b; 1992a; Williamson, 1997) have also been linked to local atmospheric conditions. In addition, demographic factors such as reproductive status, age-sex class, social rank and group size also influence the primate time budget (Whitten, 1982; 1983; Chapias and Schulman, 1983; de Ruiter, 1986; Isbell and Young, 1993; Dunbar, 1996; Nakagawa, 2000). Ultimately then, the amount of time available does not only shape differences in behavioural patterns within and between groups or populations, but also defines the habitat specific maximum tolerable group size and potential geographic distribution of a species (Janson and Goldsmith, 1995; Dunbar, 1998; Hill *et al.*, 2003; Korstjens *et al.*, 2006). Identifying the factors that determine how time is allocated over the different time budget components, therefore, is fundamental to primate socio-ecology.

This chapter is the first of two that investigate patterns in vervet monkey time allocation in relation to local ecological and demographic conditions. Here, activity patterns of the study group are investigated. The next chapter will use reported time budget components from other field sites in an inter-populational modelling approach to predict the maximum ecologically tolerable group size and geographic distribution of the *Cercopithecus aethiops* species complex over the whole of sub-Saharan Africa. The current chapter starts off by characterising basic time allocation by the study group at the Lajuma Research Centre and establishing monthly and daily patterns of activity. Subsequently, ecological correlates are identified and, as a precursor to the development of the predictive model in the next chapter, regression models for the four time budget components are constructed. Finally, functional aspects of the time budget components are investigated to gain a fuller understanding of the mechanisms underlying time allocation decisions by the study group.

6.2 Activity patterns

Daily averaged values of the four time budget components were calculated from instantaneous group scan samples on all age-sex classes (Chapter 2). To get a general impression of the overall activity budget, average annual values are presented for the group as a whole as well as for the three constituting age-sex classes (Figure 6.1).

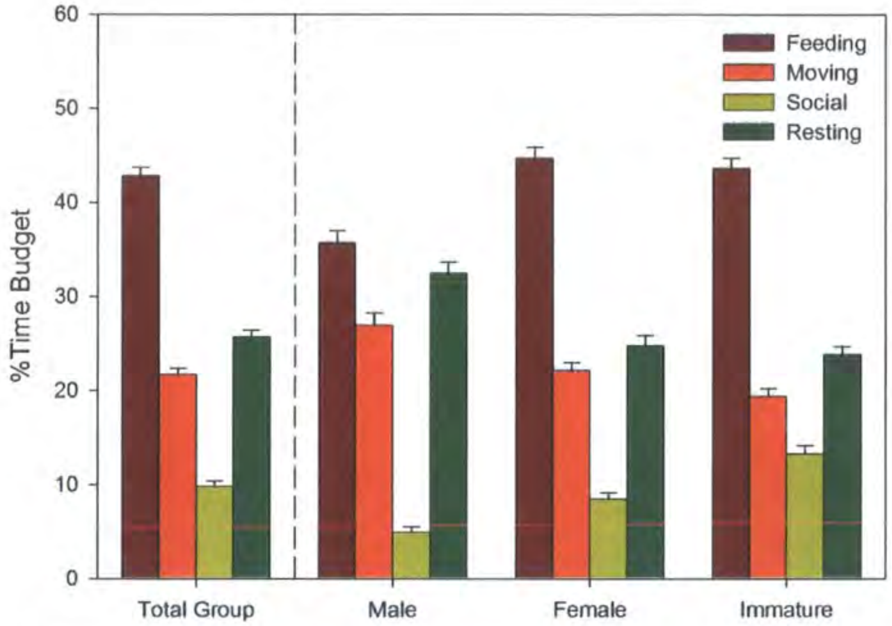

Figure 6.1 Bar charts of the annual average proportion of time allocated to the four time budget components by the group as a whole and the three constituting age-sex classes (error bars represent +1 se).

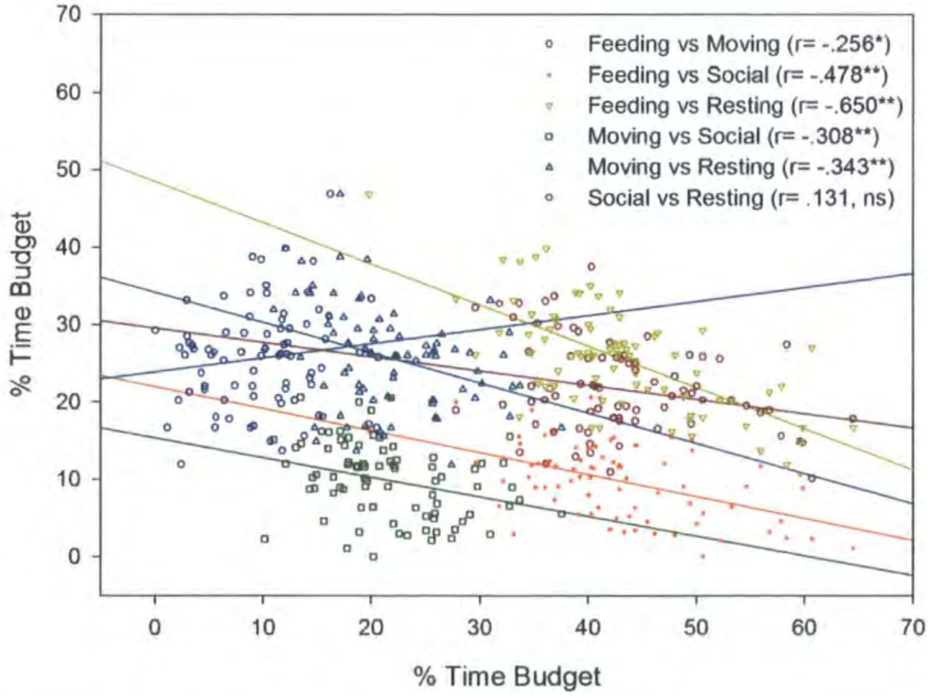

Figure 6.2 Illustration of the inter-dependency between daily time budget components of the whole group over the observation period. Note that the only positive association -between time spent in social activities and time spent resting- was not significant (* significant at p= .05; ** significant at $p_{\text{Bonferroni-corrected}}= .0083$)

Differences in time allocation between males, females and immatures will be briefly discussed (Section 6.2.1), but the main focus here lies on establishing patterns of diurnal and seasonal variation in time allocation by the study group. In doing so, and given the inherent inter-dependency between the four time budget components (illustrated in Figure 6.2), a multivariate approach is taken throughout this section.

6.2.1 Age-sex class variation in time allocation

Annually averaged time allocation by males, females and immatures (Figure 6.1) was compared and found to be significantly different (one-way MANOVA; $V= .377$, $F_{(6,466)}= 18.03$, $p< .001$). Subsequent Bonferroni-corrected univariate analyses revealed that the three age-sex classes differed in the amount of time allocated to each of the four time budget components (Feeding: $F_{(2,234)}= 16.19$, $p< .001$; Moving: $F_{(2,234)}= 14.02$, $p< .001$; Social: $F_{(2,234)}= 30.03$, $p< .001$; Resting: $F_{(2,234)}= 19.79$, $p< .001$) and post-hoc investigations showed that males spent less time feeding than females and immatures (Tukey HSD; $p< .001$, in both comparisons), more time moving than females (Tukey's HSD; $p< .005$) and immatures (Tukey's HSD; $p< .001$) and more time resting (Tukey's HSD; $p< .001$, in both comparisons). Immatures spent more time in social activities than either males or females (Tukey's HSD; $p< .001$, in both comparisons) and females were more social than males (Tukey's HSD; $p< .005$).

These differences between the age-sex classes reflect some interesting disparities between the respective time budget requirements. In order to assess these findings on their adaptive value however, a more detailed functional insight into the time budget components is required. This will be the topic of Section 6.4 and a more in depth discussion of current findings is postponed till then.

6.2.2 Diurnal variation in time allocation

Diurnal rhythms in the behaviour of the study group were investigated by aggregating annual scan data on an hourly basis. Given the considerable variation in on-site day length, analyses were restricted to observations made between 06:00 and 18:00 in order to keep sample size over the hours roughly equal. A potential danger of this is that by lumping data from long and short days together, the clarity of reported diurnal patterns may have been obscured. On an annual basis however, it is fair to assume that the effect of day length variation levels itself out. The potentially confounding effect of variation in group size over the study period, on the other hand, had to be controlled for and was included into the analyses as a covariate. Resulting estimates on the annually averaged diurnal pattern in the behaviour of the study group are reported in Figure 6.3.

A multivariate analysis indicated significant variation in time allocation over the day (one-way MANCOVA; Hour (factor): $V= .435$, $F_{(36,411)}= 1.94$, $p< .005$; Group size (covariate): $V= .072$, $F_{(3,135)}= 3.47$, $p< .05$). Bonferroni corrected univariate analyses revealed that this variation could be ascribed to differences in two of the four time budget components (Moving: $F_{(12,137)}= 2.71$, $p< .005$; Social: $F_{(12,137)}= 2.56$, $p< .005$). Interestingly and in contrast to the commonly reported feeding peaks in the early morning and late afternoon and resting peak at the middle of the day (Hall and Gartlan, 1965; Clutton-Brock and Harvey, 1977), the proportion of time devoted by the study group to these behavioural categories did not show statistically significant variation over the day (Feeding: $F_{(12,137)}= 2.07$, $p= .023$; Resting: $F_{(12,137)}= 1.30$, $p= .223$). Note, however, that feeding time did show substantial variation over the day which only failed to reach significance due to the strict application of Bonferroni corrections.

Statistical significance of daily patterns in the hourly proportion of time spent moving or in social activities was assessed by polynomial contrast analyses (Figure 6.4). This revealed a quadratic trend in the estimated marginal mean proportion of moving time ($p< .001$) and a 4^{th} order trend in time spent in social activities ($p< .05$). The first trend came about through a minimum proportion of time allotted to moving at midday (12:00) followed by a marked increase over the second half of the day. The second reflected the

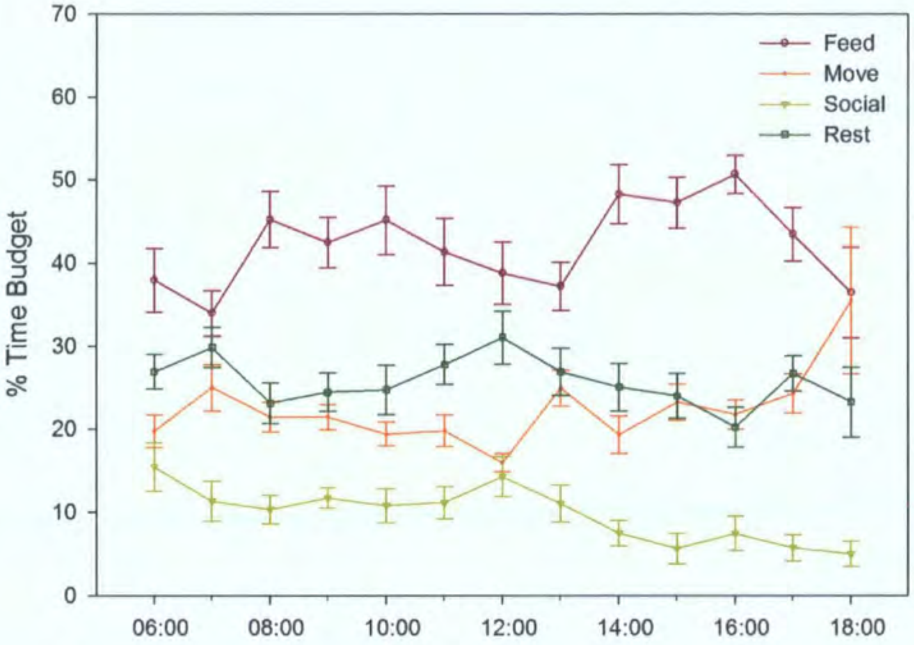

Figure 6.3 Hourly averaged proportion of time allocated to the four time budget components by the study group over the observation period (error bars represent ± 1 se).

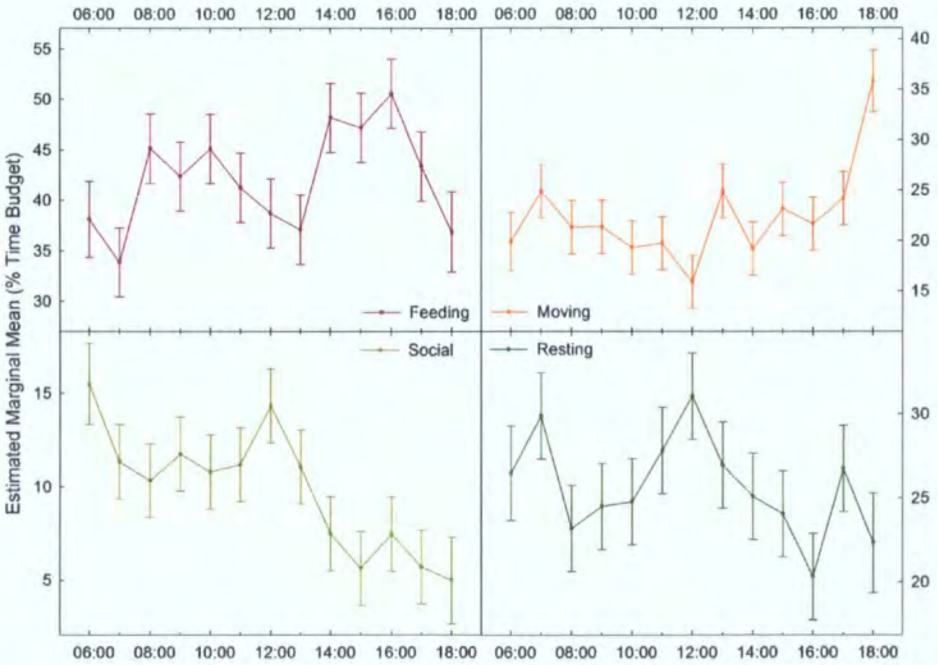

Figure 6.4 Estimated hourly marginal mean (mean after removing the effect of group size) proportion of time allocated to the four different time budget components (error bars represent ± 1 se).

the presence of two distinct peaks in social activity, one in the early morning (at 06:00, shortly after the average onset of activity) and another at midday (roughly at 12:00). Potential environmental correlates of these temporal patterns are assessed in Section 6.3.1.

6.2.3 Monthly variation in time allocation

Apart from diurnal variation within the proportion of time devoted to the different time budget components, animals may also display distinct seasonal patterns in activity. Two complications in investigating seasonal patterns, however, should be dealt with prior to analysis. Firstly, the substantial variation in monthly averaged day length will render comparisons of monthly proportions of time spent in each activity misleading (Hill, 1999). This is perhaps best illustrated by the following example. Exploratory analyses revealed that in June 2005 the study group spent roughly 50 % of its activity period on feeding, whereas in December 2005 this proportion had dropped to around 40 %. Given the difference in average day length between these two months (10.74 and 13.52h, respectively) the actual amount of time the animals spent feeding remained remarkably constant (5.37 and 5.40h). Because of this, investigations of monthly time allocation should consider monthly averaged number of hours per day, rather than the daily proportion of time, spent in each behavioural category (Hill *et al.*, 2003; 2005). A second complication in seasonal analyses of time allocation lies in variation in the demographic composition of the study group over the observation period. Section 6.2.1 illustrated how the age sex classes differed in the way in which they allocated time over the four main behavioural activities and, given changes in group size over the observation period, the relative contribution of the different age sex classes to monthly estimates of time allocation by the study group may have had an undue influence. To eliminate this concern, seasonal analyses were constrained to time budgets of adult females only. An additional advantage of this restriction lies in focusing on, what in conceptual models of primate socio-ecology has sometimes been referred to as the ecological sex (Chapter 1). This may have increased the power of the current analyses of ecological determinants of time allocation.

The daily number of hours that adult females allocated to the respective time budget components was averaged on a monthly basis to assess seasonal variation (Figure 6.5). While controlling for the effect of variation in group size, the amount of time spent in the four behavioural categories was found to vary significantly over the months, (one-way MANCOVA; Month (factor): $V= 1.546$, $F_{(44,264)}= 3.78$, $p< .001$; Group size (covariate): $V= .292$, $F_{(4,63)}= 6.50$, $p< .001$). Bonferroni-corrected univariate analyses subsequently showed that this monthly variation was only significant for the amount of time spent resting (Feeding: $F_{(11,66)}= 1.46$, $p= .168$; Moving: $F_{(11,66)}= .58$, $p= .598$; Social: $F_{(11,66)}= 2.17$, $p= .027$; Resting: $F_{(11,66)}= 5.08$, $p< .001$), whereas the overall significant effect of group size as covariate could entirely be ascribed to its positive effect on the amount of time spent in social activities (Feeding: $F_{(1,66)}= 0.68$, $p= .414$; Moving: $F_{(1,66)}= .57$, $p= .452$; Social: $F_{(1,66)}= 15.24$, $p< .001$; Resting: $F_{(1,66)}= 1.26$, $p= .265$). The significant cubic trend in monthly estimated marginal mean values of resting time revealed by polynomial contrast analysis ($p< .05$) suggested a distinct seasonal pattern.

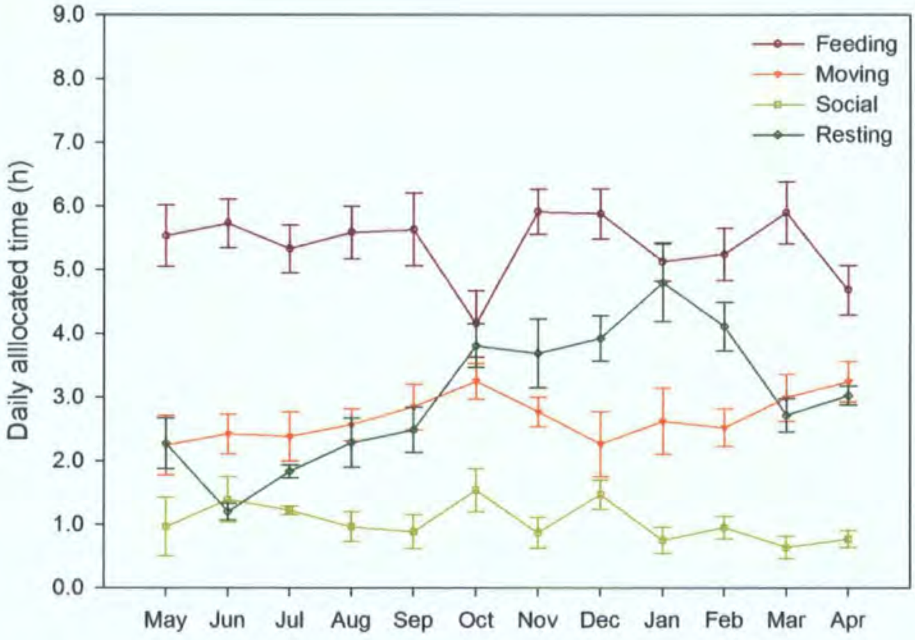

Figure 6.5 Monthly averaged daily time allocated to the different time budget components by adult females in the study group (error bars represent ± 1 se).

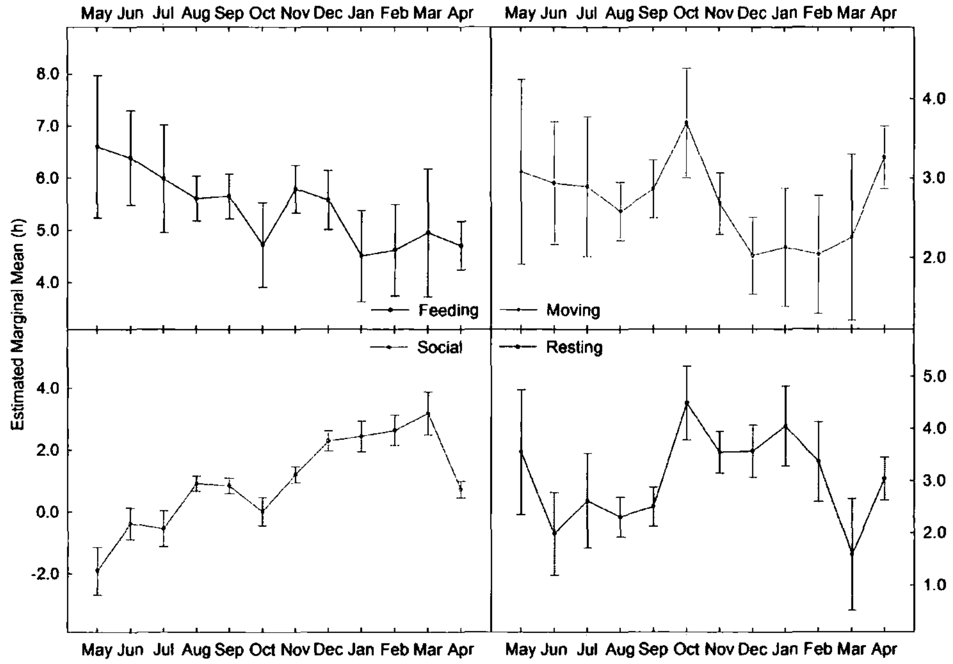

Figure 6.6 Estimated monthly marginal mean (mean after removing the effect of group size) proportion of time allocated to the four different time budget components (error bars represent ± 1 se).

6.3 Ecological conditions affecting time allocation patterns

As both diurnal and seasonal rhythms were observed within the behaviour of the study group, it is attempted here to identify environmental conditions to which the animals may have been responding. This will first be done for daily patterns in relation to hourly averaged weather conditions. Monthly time allocation is subsequently linked to monthly weather conditions, primary productivity and food availability. Towards the end of this section, regression models are developed to express monthly time budget components as functions of group size and environmental conditions. This latter exercise mainly serves as a prelude to the development of the inter-populational model of vervet monkey socio-ecology in the next chapter.

6.3.1 Correlates of diurnal variation in time allocation

Weather conditions were the only environmental factor in this study measured over the day and, given the considerable diurnal variation within these variables, it was assessed whether the study group adjusted proportional hourly time allocation accordingly. To be able to control for the effect of changes in group size over the observation period, Pearson correlation coefficients were calculated between estimated hourly marginal mean values of time budget components (Figure 6.4) and concurrent weather conditions. Results are presented in Table 6.1.

Table 6.1 Investigation of potential associations between the estimated hourly marginal mean (*i.e.* mean after controlling for the effect of group size) proportion of time dedicated to each of the four main time budget components and concurrent weather conditions.

		Thermal environment							**Precipitation**	
		T_{min}	**T_{mean}**	**T_{max}**	**WC**	**HI**	**THW**	**THSW**	**P**	**Mist**
Feeding (%)	r	*.477*	*.483*	.471	*.479*	.476	*.477*	*.534*	-.159	*-.514*
	Sig. (2-tailed)	.099	.095	.105	.097	.100	.100	.060	.603	.073
	n	13	13	13	13	13	13	13	13	13
Moving (%)	r	-.019	-.076	.010	-.066	-.071	-.053	-.289	.034	.101
	Sig. (2-tailed)	.952	.806	.974	.832	.817	.864	.338	.913	.744
	n	13	13	13	13	13	13	13	13	13
Social (%)	r	*-.527*	*-.479*	*-.553*	*-.486*	-.475	*-.493*	-.310	.273	*.502*
	Sig. (2-tailed)	.064	.098	.050	.092	.101	.087	.302	.366	.080
	n	13	13	13	13	13	13	13	13	13
Resting (%)	r	-.188	-.159	-.194	-.162	-.160	-.170	-.091	-.089	.145
	Sig. (2-tailed)	.538	.604	.525	.597	.601	.578	.767	.772	.635
	n	13	13	13	13	13	13	13	13	13

$T_{min/mean/max}$: mean minimum/mean/maximum temperature (°C); WC: Wind Chill (°C); HI: Heat Index (°C); THW: Temperature-Humidity-Wind Chill index (°C); THSW: Temperature-Humidity-Solar radiation-Wind Chill index (°C); P: rainfall (mm); Mist: mean mist-likelihood index

No significant linear associations were found nor did inspections of scatter plots reveal the need to consider non-linear relationships. The only known previous study to directly correlate diurnal activity of vervet monkeys to environmental conditions (Harrison, 1985) found monthly differences within the strength and sign of association between the proportion of time spent feeding and ambient air temperature. Although this claim was based on just 3 out of 12 significant correlation coefficients, monthly variation in the strength and sign of association between diurnal time allocation and weather conditions may have prevented current findings from reaching statistical significance. In addition, diurnal variation in other environmental conditions (*e.g.* quality of food items (Robinson, 1974) or in the metabolic demands of the animals and other endogenous cycles (Baldellou and Adan, 1998; Erkert, 2003) are likely to have obscured possible significant associations. Tentatively then, the apparent increase in feeding time with temperature mirrored by a roughly equal decrease in social time, and the opposite association between these two time budget components and mist precipitation (Table 6.1), may have just failed to reach statistical significance because of these confounding factors. The findings furthermore suggest a trade-off between the hourly proportion of time the animals spent feeding and the hourly proportion spent in social activities.

6.3.2 Correlates of monthly variation in time allocation

Associations between the monthly averaged daily number of hours that adult females allocated to the four time budget components and environmental conditions were assessed by semi-partial correlation analyses controlling for the effect of group size on time allocation. Results of these analyses are presented in Table 6.2.

Out of the four time budget components, only monthly resting time showed significant associations to atmospheric conditions as it increased with day length and temperature. However, Section 5.3.1 pointed out that day length and temperature are strongly inter-related and unless both parameters are considered simultaneously (as will be done in Section 6.3.3) caution is needed in speculations about the causative mechanisms underlying the observed association with resting time. For now it may be said that the extra time available on longer days allowed the animals to spend more time resting and, in addition or alternatively, that thermoregulatory demands due to high ambient temperatures may have restricted animal activity. Given the sub-optimal thermal environment for vervet monkeys at the Lajuma Research Centre though (Section 5.3.1), an association with day length seems the biologically more plausible.

Table 6.2 First-order semi-partial correlations between monthly environmental conditions and time allocation by adult females in the study group, controlling for the effect of group size on time allocation.

		Feeding (h)	**Moving (h)**	**Social (h)**	**Resting (h)**
Photoperiod	r	-.268	.059	.402	***.716***
	Sig. (2-tailed)	.413	.860	.143	< .001
	n	12	12	12	12
T_{min}	r	-.287	.210	.190	***.599***
	Sig. (2-tailed)	.380	.524	.509	.009
	n	12	12	12	12
T_{mean}	r	-.280	.207	.185	***.596***
	Sig. (2-tailed)	.391	.531	.522	.010
	n	12	12	12	12
T_{max}	r	-.275	.205	.181	***.592***
	Sig. (2-tailed)	.402	.535	.530	.010
	n	12	12	12	12
WC	r	-.274	.179	.172	***.608***
	Sig. (2-tailed)	.402	.589	.551	.008
	n	12	12	12	12
HI	r	-.337	.184	.205	***.657***
	Sig. (2-tailed)	.298	.577	.475	.002
	n	12	12	12	12
THW	r	-.327	.134	.187	***.674***
	Sig. (2-tailed)	.313	.686	.517	.001
	n	12	12	12	12
THSW	r	-.344	.144	.187	***.682***
	Sig. (2-tailed)	.287	.665	.517	.001
	n	12	12	12	12
P_{sqrt}	r	-.022	-.378	-.012	.364
	Sig. (2-tailed)	.947	.237	.967	.164
	n	12	12	12	12
Mist	r	-.176	-.147	.049	.058
	Sig. (2-tailed)	.594	.658	.866	.835
	n	12	12	12	12
$NDVI_{linear}$	r	.045	-.330	-.166	-.177
	Sig. (2-tailed)	.892	.308	.566	.519
	n	12	12	12	12
$NDVI_{quadratic}$	r*	.627	***-.852***	-.564	-.636
	Sig. (2-tailed)	.238	.012	.356	.223
	n	12	12	12	12
Food availability Log ($Model_{field}$)	r	***.713***	***-.769***	-.194	*-.425*
	Sig. (2-tailed)	.010	.004	.500	.097
	n	12	12	12	12
Food availability Log ($Model_{NDVI}$)	r	.319	*-.570*	-.058	-.007
	Sig. (2-tailed)	.326	.058	.841	.979
	n	12	12	12	12

* multiple correlation coefficient

$T_{min/mean/max}$: mean monthly minimum/mean/maximum temperature (°C); WC: Wind Chill (°C); HI: Heat Index (°C); THW: Temperature-Humidity-Wind Chill index (°C); THSW: Temperature-Humidity-Solar radiation-Wind Chill index (°C); P_{sqrt}: square root transformed total monthly rainfall (mm); Mist: mean monthly mist-likelihood index.

No linear associations were detected between primary productivity (as indexed by the NDVI) and monthly time budget components but a negative quadratic association to the monthly amount of time allotted to moving, did exist. This relationship was taken to have come about through the quadratic association between NDVI and food availability (Section 4.4.4) and suggests that animals spent less time moving during months with high food availability. This finding corroborates results from Section 5.3.2 in which day journey length was also found to be negatively associated to a quadratic function of NDVI. It is worth noting, moreover, that multiple correlation coefficients with other time budget components were quite high as well (albeit not significant), thereby potentially further substantiating claims about the biological significance of the quadratic NDVI function.

The last environmental factor that was investigated for associations to monthly time allocation was food availability. Log-transformed monthly estimates of food availability as assessed from field observations ($\text{Model}_{\text{field}}$) showed a positive association with the amount of time spent feeding and a negative association with time spent moving. This suggests that adult females in the study group devoted significantly more time to feeding activities when food was more abundant and, therefore, that they may have been pursuing an energy-intake maximising strategy. Alternatively, it could suggest that the animals became more discerning in their selection of food items when food was more abundant. Unfortunately, no data to test for this were collected. The reduction in the amount of time spent moving during months with high food availability may indicate that food was so abundant that the animals could meet nutritional demands without having to travel far (see also Section 5.3.3). However, the decrease in time spent moving may also have been brought about by the negative association to feeding time (Figure 6.2), which increased. The absence of significant associations between monthly time allocation and the second log-transformed estimate of food availability ($\text{Model}_{\text{NDVI}}$) was unexpected and is all the more surprising given the strong relationship between the two log-transformed models ($r= .849$, $n=12$, $p< .001$). If anything, this finding may imply that the log-transformed model based on field observations is the biologically more informative of the two in this particular instance.

6.3.3 Regression models for monthly time allocation

To determine the extent to which variation in monthly time allocation by female vervet monkeys in the study group could be ascribed to group size and the environmental factors discussed in the preceding analyses, regression models were developed. Initial selection of predictor variables considered only those parameters that will be available in the construction of the inter-populational model in the next chapter. Since this yielded no significant equation for the number of hours spent feeding and in social activities, direct estimates of local food availability were subsequently allowed to enter best fit equations as well. Analogous to Section 5.3.4, stepwise variable entry procedures were chosen and resulting parameter estimates and associated statistics are presented in Table 6.3.

Table 6.3 Key parameters and statistics of stepwise regression analyses performed to assess the relationship between monthly time allocation by adult females and demographic and ecological conditions.

		B	**se B**	β	**t**	**F_{model}**	**se estimate**	**Adj. R^2**
Feeding (h)	Intercept	9.70	1.58		6.13^{***}	***4.47*****	0.42	.387
	Food^{+}	$2.53\text{x}10^{-3}$	$8.90\text{x}10^{-4}$	1.11	2.84^{**}			
	Group size	-0.31	0.11	-1.11	-2.84^{**}			
Moving (h)	Intercept	24.50	3.71		6.60^{***}	***11.78******	0.18	.746
	$NDVI^2$	52.28	9.11	18.61	5.74^{***}			
	NDVI	-68.05	11.69	-18.52	-5.82^{***}			
	Rainfall	$-2.78\text{x}10^{-3}$	$1.32\text{x}10^{-3}$	-0.46	-2.10^{*}			
Social (h)	Intercept	-0.29	0.68		$-.42^{*}$	*3.79**	0.27	.202
	Group size	$8.22\text{x}10^{-2}$	0.04	0.52	1.95^{*}			
Resting (h)	Intercept	-8.78	1.52		-5.77^{***}	***60.38******	0.42	.844
	Photoperiod	0.97	0.13	0.93	7.77^{***}			

$^{+}$= Food availability (Model $_{NDVI}$)
* = $p< .10$; ** = $p< .05$; *** = $p< .005$

The monthly averaged daily number of hours spent feeding increased with food availability, suggesting that females either pursued an energy-intake maximising strategy, or that the net energy yield decreased with food available. This latter interpretation, however, seems unlikely and was not tested for. More notably however, the sign of association between feeding time and group size was in the opposite direction of what is typically observed in primates (Janson and van Schaik, 1988; Janson and Goldsmith, 1995). Two speculative explanations for this are offered, but it is immediately conceded that no quantitative data on the study group are currently available to substantiate either. The studies referred to in the remainder of this paragraph though, all reported data from other vervet monkey populations. A first explanation lies in an increased leverage in between group competition for high quality food resources associated with larger group size (Wrangham, 1980; Whitten, 1982; Isbell, 1990). In this scenario, the study group would have been more successful in obtaining access to high quality food resources, at the expense of neighbouring groups, during months in which the number of group members was high. Being able to exploit such preferred resources would result in a decrease in the amount of feeding time required by each individual to meet nutritional demands. A second possibility lies in the seemingly trivial observation that total group size increases during the birth season. This means that an annually recurring increase in group size coincides with a period of increased nutritional demands on adult females due to lactation. Indeed, lactating female vervets have been observed to spend more time feeding than non-lactating female group members (Whitten, unpublished data). Both explanations could account for the observed negative association between total group size and feeding time observed in the study group.

Moving time decreased with food availability (as indexed by a quadratic function of NDVI) and monthly rainfall. As described earlier, this first association suggests that the animals could reduce the proportion of time dedicated to moving during periods of high food availability while still meeting nutritional demands. In terms of this time budget component, it can be said that the animals are minimising time expenditure. The negative association with rainfall is perhaps best interpreted as an energy expenditure minimising response to increased cold stress.

The monthly averaged number of hours that females spent in social activities was a positive function of group size and although this association just failed to reach statistical significance, it is in line with the general pattern observed in Old World monkey and ape societies (Lehmann *et al.*, 2007b). It underlines that larger groups pose higher demands on the amount of time that females have to allocate to maintain social relationships within the group (Dunbar, 1991,Janson, 1992 #698; Janson and Boinski, 1992).

Monthly variation in resting time was largely accounted for by photoperiod, strongly suggesting that resting time during months with long days chiefly consisted of uncommitted time (Dunbar, 1988; 1992b; 1996).

To summarise the main findings from these regression analyses it may be said that time allocation by adult females in the study group could be related to biologically intuitive local environmental conditions and group size. Whether or not the construction of regression models for time allocation by vervet monkeys on a global (*i.e.* inter-populational) scale will be feasible, however, remains to be ascertained. Two out of four regression models developed here (for feeding and social time) did not reach statistical significance if predictor variables were restricted to environmental conditions that are available for the whole of sub-Saharan Africa and perhaps additional information (such as dietary composition and range use) should be incorporated in inter-populational models (Korstjens and Dunbar, 2007; Korstjens *et al.*, submitted; Lehmann *et al.*, 2007a).

6.4 Functional aspects of time budget components

So far, both demographic (*i.e.* age sex-class) and temporal variation in time allocation have been demonstrated and environmental conditions affecting activity patterns of the study group were identified. A final logical step then, is to look at possible functional aspects of the different time budget components. This is of particular relevance for the proportion of time dedicated to resting as this behavioural category is relatively poorly understood. Whereas feeding, moving and social time are commonly recognised to be of eminent importance in day to day survival (Pulliam, 1973; Caraco, 1979a; 1979b), time dedicated to resting has often been taken to constitute a reservoir of uncommitted time from which the animals can draw during periods of time stress (Dunbar, 1988; 1992b; 1996). This may be true to a certain extent, but resting time clearly serves important functions in its own right (Herbers, 1981; Korstjens *et al.*, submitted). To explore different functional aspects of the main time budget components, subcategories were distinguished within behavioural data collected by focal animal sampling. Recall from Section 2.6.1 that only adult males and females were monitored in this way and, therefore, the in depth investigation of functional aspects of time allocation presented here is limited to these two age-sex classes.

6.4.1 Functional subcategories within time budget components

The behavioural subcategories recognised within each of the four time budget components are briefly described in a functional context and an overview of the respective proportions of time spent in each subcategory is presented in Table 6.4.

Table 6.4 Proportional allocation of time over the different subcategories within the four main time budget components. Percentages are given for adults as well as for males and females separately and stem from focal animal observations.

Feeding			
Subcategory (%)	**Adults**	**Male**	**Female**
Bite	24.9	24.0	25.3
Chew	32.0	36.7	30.1
Drink	0.2	0.3	0.2
Lick	0.7	0.6	0.7
Reach	29.4	30.4	29.1
Retch	0.0	-	0.0
Search	12.7	8.0	14.6

Moving			
Subcategory (%)	**Adults**	**Male**	**Female**
Forage	36.8	28.5	39.9
Locomotion	63.2	71.5	60.1

Social			
Subcategory (%)	**Adults**	**Male**	**Female**
Allogrooming	95.9	91.5	97.2
Play	0.7	2.4	0.2
Sexual	0.8	1.8	0.5
Aggressive	2.6	4.2	2.1

Resting			
Subcategory (%)	**Adults**	**Male**	**Female**
Vigilance	24.9	35.1	19.8
Forage	11.6	7.8	13.4
Pause	20.6	16.0	22.9
Inactivity	42.9	41.1	43.8

Feeding

The primary function of feeding is nutrient acquisition although three of the behavioural subcategories distinguished within this time budget component here, were not directly related to the ingestion of food items (Table 6.4). The *retch*, *reach* and *search* subcategories did not necessarily immediately translate into the actual intake of nutrients.

Moving

Two functional subcategories were recognised (Table 6.4): 1) *forage* included all movements related to the search for food items and; 2) *locomotion* encompassed movements related to day journey progression as well as predator avoidance (fleeing, evasive manoeuvres) and intra-group spacing.

Social

Within the social time budget component a distinction was made between three affiliative and one agonistic subcategory (Table 6.4). Of the three affiliative categories, *allogrooming* is most important in maintaining social relationships and group cohesion although it also serves hygienic purposes (Boccia, 1983; Dunbar, 1991). *Play* behaviour in adults may also help maintain social unity within the group, although it was a rare phenomenon. *Sexual* behaviour in vervet monkeys seems strictly related to reproduction and only accounted for a marginal proportion of total social time. *Aggressive* interactions, lastly, serve to establish and maintain dominance relationships. Apart from sexual interactions then, the overwhelming majority of social activities primarily acted to maintain relationships and, thereby, group cohesion.

Resting

Resting behaviour constitutes the functionally most complicated time budget component. In the light of this chapter, the most desirable distinction would be between enforced and uncommitted resting time (Korstjens *et al.*, submitted), where the former encapsulates all functional aspects in terms of recuperation, vigilance, digestion and thermoregulation (Herbers, 1981) and the latter the surplus of time, available for reallocation to other activities when the need arises (Dunbar, 1992b; 1993; 1996). Unfortunately, this distinction can not be made unambiguously on the basis of purely behavioural observations. Instead, four approximately functional subcategories were distinguished (Table 6.4). Two of these mainly represent enforced resting time: *vigilance* comprised the social and anti-predatory monitoring of the environment whereas *forage* included scanning for food and slight pauses in foraging behaviour. In contrast, the *pause* subcategory was taken to chiefly reflect uncommitted resting time since it comprised brief time gaps between successive bouts of activity. The *inactivity* subcategory, lastly, inevitably consisted of both enforced and uncommitted resting time; partly it may have arisen through endogenous (recuperation or digestion) or exogenous (thermal stress) factors, and partly through a surplus of time. Very little can be said about the exact proportions of enforced and uncommitted resting time within the inactivity subcategory however, the following can be deduced. Over the observation period a minimum proportion of total resting time, equal to the sum of the vigilance and forage subcategories (assuming the inactivity subcategory consists solely of uncommitted time), was used in a functional manner. Also, a maximum proportion of total resting time, equal to the sum of the vigilance, forage and inactivity subcategories (assuming the latter consists solely of enforced resting time), can be said to have been used functionally. From Table 6.4 it then follows that the actual proportion of enforced resting time lies somewhere between 36.5-79.4 % of total resting time. In terms of the annual overall activity budget, this translates to a figure for enforced resting time roughly between 10-20 % of the total activity period. This figure, although specific for the study group over the observation period, may serve as a directive in the parameterisation of the inter-populational model that will be developed in the next chapter.

6.4.2 Sex-related and monthly variation in functional time allocation

Equipped with a functional perspective on the four time budget components, differences in time allocation between the sexes and over the months were investigated. This was done for each time budget component separately and since analyses considered monthly patterns, average monthly duration, rather than proportion of time (see Section 6.2.3), was considered (Figure 6.7).

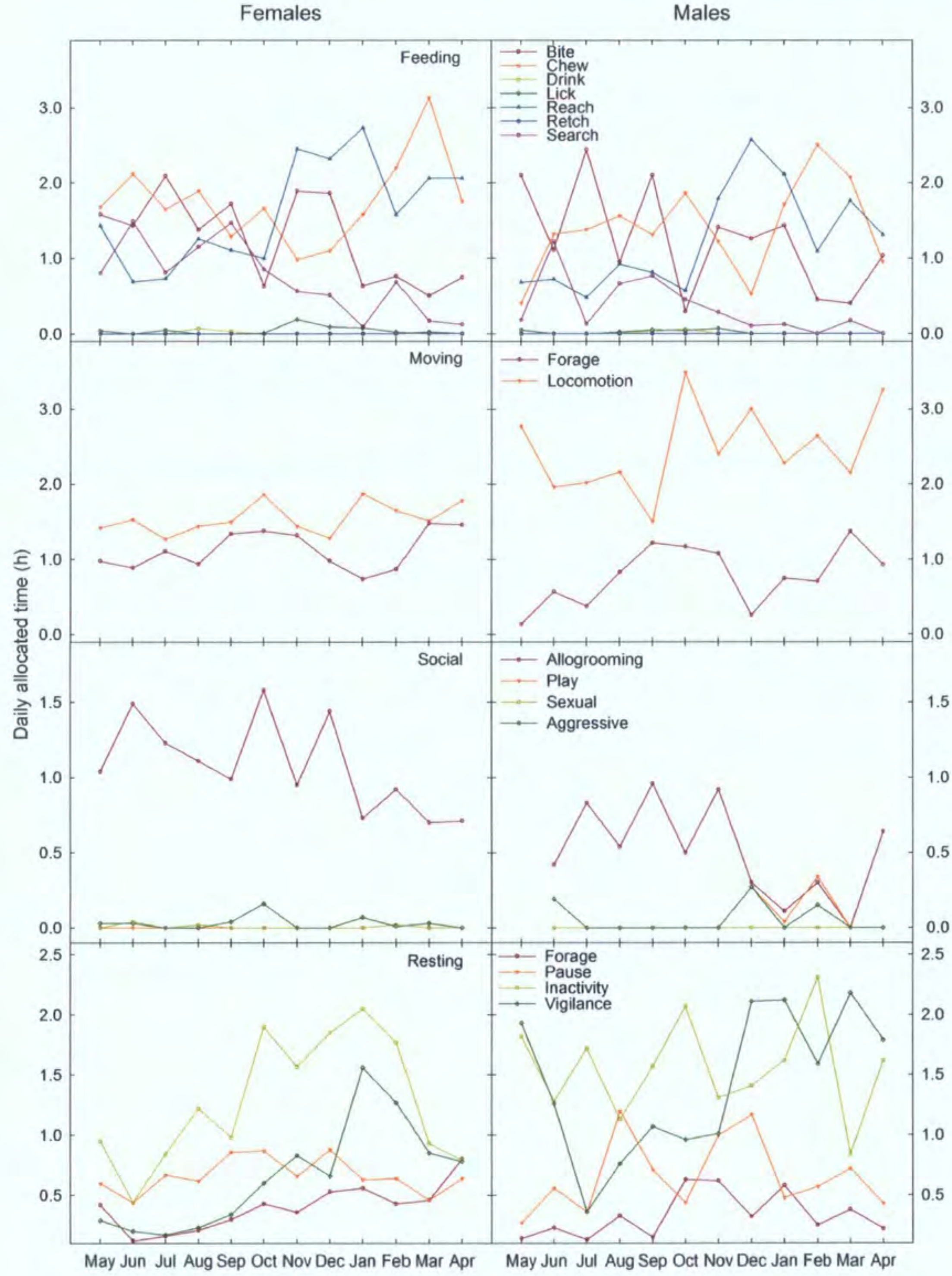

Figure 6.7 Sex specific time allocation over the functional subcategories distinguished within each of the four main time budget components over the observation period (error bars omitted for clarity).

The amount of time dedicated to the different behavioural subcategories within feeding differed significantly between the sexes (two-way MANCOVA; Sex (factor): *V*= .258, $F_{(7, 119)}$= 3.52, p< .001) and over the months (Month (factor): *V*= 1.179, $F_{(77, 875)}$= 2.30, p< .001) whilst controlling for the effect of group size (Group Size (covariate): *V*= 0.210, $F_{(7, 119)}$= 4.53, p< .001). No significant interaction effect between sex and month was detected (*V*= .491, $F_{(77, 875)}$= 0.86, p= .801), indicating that males and females adjusted time allocation to the different behavioural subcategories in a similar manner over the months. Bonferroni-corrected univariate analyses subsequently revealed that the difference in time allocation between males and females was due to the amount of time spent reaching and searching for food items (*reach*: $F_{(1,125)}$= 9.14, p< .005; *search*: $F_{(1,125)}$= 9.64, p< .005). Females spent more time reaching (mean ± se= 1.65h ± 0.11) and searching (mean ± se= 0.73h ± 0.10) than males (mean ± se= 1.26h ± 0.11 and 0.35h ± 0.09, respectively). This may be taken to suggest that males were more efficient (or less selective) at acquiring food items whilst feeding than females. It, however can not support the notion that males may have had priority of access to high quality food items since, although individually dominant over females, males were frequently displaced from food patches by female coalitions. Monthly variation, on the other hand, could be attributed to differences in the amount of time dedicated to *bite* ($F_{(11,125)}$= 3.39, p< .001), *chew* ($F_{(11,125)}$= 2.68, p< .005), *lick* ($F_{(11,125)}$= 3.27, p< .001), *reach* ($F_{(11,125)}$= 5.12, p< .001) and *search* ($F_{(11,125)}$= 3.17, p< .001) which was taken to reflect changes in the manipulation techniques required for seasonally varying food items. In addition it is reported that contrast analyses revealed a significant quadratic trend (p<.001) within monthly variation in the amount of time dedicated to *search*, possibly suggesting a response to seasonal changes in food availability.

Within the moving time budget component, males dedicated less time to foraging (mean ± se= 0.83h ± 0.11) and more time to locomotion (mean ± se= 2.48h ± 0.17) than females (mean ± se= 1.12h ± 0.07 and 1.56h ± 0.08, respectively; two-way MANCOVA; Sex (factor): *V*= .171, $F_{(2,122)}$= 12.61, p< .001). Variation in time allocation over the months just failed to reach statistical significance (Month (factor): *V*= .237, $F_{(22,246)}$= 1.50, p= .074) and no interaction effect between sex and month was detected (*V*= .084, $F_{(22,246)}$=

0.49, p= .975). Group size did not have a significant effect on time allocation within the moving time budget component either (Group Size (covariate): V= .008, $F_{(2,122)}$= 0.50, p= .610). These findings indicate that males are not only more mobile than females in terms of overall time allocation (Figure 6.1) but also in a manner less related to nutrient acquisition (Figure 6.7). Moreover, since there was no difference between the sexes in estimated net day journey length (group cohesion was usually maintained), this result indicates that males are more mobile within the group and may explain why they are often more peripheral than females. Males therefore seem to be more actively 'patrolling' the environment, possibly to gauge external (predation, extra-group competition) and internal (group members) factors.

The only difference between the sexes in time allocation over the social subcategories was that females spent more time allogrooming (mean ± se= 1.06h ± 0.09) than males (mean ± se= 0.49h ± 0.10; two-way MANCOVA; Sex (factor): V= .218, $F_{(4,68)}$= 4.73, p< .005; significant follow-up ANCOVA; Allogrooming: $F_{(1,71)}$= 14.38, p< .001). Hence, females do not only invest a larger proportion of their overall time budget to social activities (Figure 6.1), but also dedicate relatively more of their social time to positively reinforcing relationships (Figure 6.7). This finding is well-established and believed to arise from the asymmetry between what the sexes stand to gain from social alliances within a group (Wrangham, 1980). Monthly variation in the amount of time dedicated to the different functional subcategories of social behaviour was not detected (Month (factor): V= .597, $F_{(44,284)}$= 1.13, p= .271), nor was there evidence for an interaction effect between sex and month (V= .528, $F_{(40,284)}$= 1.08, p= .351). The covariate, group size, did have a significant effect (V= .182, $F_{(4,68)}$= 3.79, p< .01) which could entirely be attributed to more time being dedicated to allogrooming when group size was larger ($F_{(1,71)}$= 15.42, p< .001).

Lastly, while controlling for the potential effect of group size (two-way MANCOVA; Group Size (covariate): V= 0.011, $F_{(4,\ 123)}$= 0.34, p= .860), the amount of time dedicated to the behavioural subcategories within total resting time was found to differ significantly between the sexes (Sex (factor): V= .290, $F_{(4,\ 123)}$= 12.57, p< .001) as well as over the months (Month (factor): *V*= 0.625, $F_{(44,\ 504)}$= 2.12, p< .001). No evidence for an interaction between sex and month was found (*V*= .358, $F_{(44,\ 504)}$= 1.13, p= .273). Follow up Bonferroni-corrected univariate analyses subsequently revealed that the difference between males and females arose entirely from the amount of time both sexes dedicated to vigilance ($F_{(1,94)}$= 34.60, p< .001) as males were more vigilant (mean ± se= 1.46h ± 0.12) than females (mean ± se= 0.67h ± 0.08). Monthly variation was also entirely accounted for by the amount of time dedicated to vigilance ($F_{(11,126)}$= 2.64, p< .005), although the amount of time spent inactive was close to significance as well ($F_{(11,126)}$= 2.24, p= .016). Monthly variation in vigilance, in addition, displayed a significant cubic trend (p< .005) suggestive of a seasonal pattern.

A clear -and familiar- general picture emerges from these analyses. Time allocation by females in the study group was largely driven by nutrient acquisition and the maintenance of social relationships. Males on the other hand, were both overall and proportionally the more mobile and vigilant sex. In addition, males were more efficient (or less selective) whilst feeding which may suggest that they experienced more time stress than females. The high male turnover rate over the observation period (Table 2.2) may be indicative of this.

6.4.3 Ecological correlates to functional aspects of monthly time allocation

After having established that monthly variation occurs within time allocation over the different functional aspects of the main time budget components, ecological correlates were sought to ascertain to which environmental conditions the animals may have been responding. For consistency with Section 6.3.2 investigations were restricted to females only, even though analyses in the previous subsection found no statistically significant difference between the sexes in terms of time allocation adjustments over the months. As before, the potentially confounding effect of variation in group size on time allocation was controlled for by calculating semi-partial correlation coefficients. The set of environmental conditions considered was the same as in Section 6.3.2, although the presented tables only report significant results.

Table 6.5 Significant semi-partial correlations between monthly environmental conditions and functional components of time allocated to feeding by adult females in the study group, controlling for the effect of group size on time allocation.

		Feeding				
		chew	*drink*	*lick*	*retch*	*search*
Photoperiod	r	***-.651***	-	***.611***	-	-
	Sig.(2-tailed)	< .05	-	< .05	-	-
	n	12	-	12	-	-
P_{sqrt}	r	-	***-.758***	-	-	***-.577***
	Sig.(2-tailed)	-	< .01	-	-	< .05
	n	-	12	-	-	12
Mist	r	-	***-.636***	-	-	***-.600***
	Sig.(2-tailed)	-	< .05	-	-	< .05
	n	-	12	-	-	12
Food availability	r	-	-	-	***-.635***	-
Log(Model$_{NDVI}$)	Sig.(2-tailed)	-	-	-	< .01	-
	n	-	-	-	12	-

P_{sqrt}: square root transformed total monthly rainfall (mm)
Mist: mean monthly mist-likelihood index

Recall from Section 6.3.2 that the total amount of time dedicated to feeding was positively associated to monthly food availability. Interestingly, none of the individual functional subcategories displayed the same relationship and in fact, retching showed an opposite association to food availability (Table 6.5). This could suggest that in times of low food availability females had to resort to less preferable food resources, high in secondary compounds and toxins, thereby increasing the occurrence of regurgitation. Alternatively and given the rarity with which retching was observed (Table 6.4), this association may also have come about through chance. During months with longer days the animals were observed to spend less time chewing and more time licking, which was probably effectuated by the seasonal shift in diet composition, rather than a direct causative relationship between day length and these behavioural subcategories. Lastly, during months with high levels of rain and mist precipitation, females spent less time drinking and searching. The former association is intuitively understood in that the animals will have had an increased water intake through their diet during months with lots of precipitation which reduces the need to drink, while a causative mechanism underlying the latter association may be absent.

Table 6.6 Significant semi-partial correlations between monthly environmental conditions and functional components of time allocated to moving and social interactions by adult females in the study group, controlling for the effect of group size on time allocation.

		Moving	**Social**
		forage	*aggression*
Food availability	r	***-.636***	***-.685***
Log(Model$_{\mathrm{field}}$)	Sig.(2-tailed)	< .05	< .05
	n	12	12
Food availability	r	***-.661***	***-.597***
Log(Model$_{\mathrm{NDVI}}$)	Sig.(2-tailed)	< .05	< .05
	n	12	12

Table 6.2 already showed that the overall amount of time dedicated to moving decreased with increasing food availability. Here it was found that this could solely be attributed to the subcategory of moving time that was functionally related to nutrient acquisition (*i.e. forage*; Table 6.6). This finding lends additional support to the interpretation that females in the study group were able to cut down on the amount of time spent moving during periods of high food availability as nutritional demands were more easily met.

Interestingly, and despite the absence of an association between food availability and social activity in general (Table 6.2), the amount of time females spent in agonistic interactions decreased during months with high food availability. This indicates that competition for access to food resources between adult females within the study group was most pronounced during periods when food was scarce.

Within resting time, three functional subcategories were related to environmental conditions (Table 6.7). The total duration of time gaps between sequential bouts of activity (*pause*) was larger during months with longer days. This is a logical corollary of

Table 6.7 Significant semi-partial correlations between monthly environmental conditions and functional components of time allocated to resting by adult females in the study group, controlling for the effect of group size on time allocation.

			Resting	
		pause	*inactivity*	*vigilance*
Photoperiod	r	*.652*	*.792*	-
	Sig.(2-tailed)	< .05	< .001	-
	n	12	12	-
T_{min}	r	-	*.673*	-
	Sig.(2-tailed)	-	< .01	-
	n	-	12	-
T_{mean}	r	-	*.670*	-
	Sig.(2-tailed)	-	< .01	-
	n	-	12	-
T_{max}	r	-	*.666*	-
	Sig.(2-tailed)	-	< .01	-
	n	-	12	-
WC	r	-	*.676*	-
	Sig.(2-tailed)	-	< .01	-
	n	-	12	-
HI	r	-	*.713*	-
	Sig.(2-tailed)	-	< .005	-
	n	-	12	-
THW	r	-	*.723*	*.419*
	Sig.(2-tailed)	-	< .005	< .05
	n	-	12	12
THSW	r	-	*.732*	*.420*
	Sig.(2-tailed)	-	< .005	< .05
	n	-	12	12
P_{sqrt}	r	-	-	*.432*
	Sig.(2-tailed)	-	-	<.05
	n	-	-	12

$T_{min/mean/max}$: mean monthly minimum/mean/maximum temperature (°C); WC: Wind Chill (°C); HI: Heat Index (°C); THW: Temperature-Humidity-Wind Chill index (°C); THSW: Temperature-Humidity-Solar radiation-Wind Chill index (°C); P_{sqrt}: square root transformed total monthly rainfall (mm)

the increased duration of the total animal activity period on longer days (Section 2.4.2). The longer activity period entails that more time is spent between successive bouts of activity, merely because more bouts of activity occur on a single day. Similar to overall resting time, *inactivity* was strongly related to both day length and the thermal environment. As argued before though (Sections 6.3.2 and 6.3.3), the strong inter-relatedness between these two environmental conditions and the sub-optimal thermal environment for vervet monkeys at the Lajuma Research Station meant that the biologically most plausible interpretation is that the monkeys spent more time inactive on longer days. This suggests that the majority of resting time spent in *inactivity* could be classified as uncommitted time and implies that the proportion of enforced resting time is probably closer to 10% than 20% of the total annual time budget (Section 6.4.1). *Vigilance*, lastly, was positively associated to two indices of apparent temperature (THW and THSW) and rainfall. Again, a direct causative mechanism may be lacking, but proximately it may be suggested that females increased vigilance at the onset of the warm wet summer (as suggested by the reported associations) which coincides with the birth season.

6.5 Discussion

This chapter investigated several aspects of time allocation by the study group over the observation period. Diurnal and seasonal rhythms were established and the demographic and ecological conditions underlying these detected patterns were identified. In addition, an in depth investigation of functional aspects of the four main time budget components was undertaken to allow a better understanding of what the monkeys are pursuing when scored to be engaged in one of the four main behavioural categories. The main results are briefly reiterated below.

Diurnal variation in the proportion of time spent in different activities has frequently been reported for vervet monkeys (Harrison, 1982; Baldellou and Adan, 1997; 1998). The patterns observed in this study though (Figure 6.3) deviated slightly from the general diurnal primate activity pattern (Clutton-Brock and Harvey, 1977) in that peaks in feeding and resting time were not detected. In the case of feeding this could be ascribed to the conservative analytical approach taken here (strict application of Bonferroni corrections), whereas hourly variation in the proportion of time allocated to resting appeared genuinely absent. A likely explanation for this latter finding is the low ambient temperature at the study site. Where peaks in primate resting time are often ascribed to high thermal loads at the hottest time of day (Hill, 2005), maximum temperatures at Lajuma may not have been high enough to force the animals into thermoregulatory inactivity. Moreover, diurnal time allocation of the study group was not related to any of the investigated hourly weather conditions, suggesting that other environmental (Robinson, 1974) or endogenous factors (Baldellou and Adan, 1998) were of more importance at Lajuma.

Monthly variation in the proportion of time spent in each of the four time budget components has been reported for a number of vervet populations (Kavanagh, 1977; Isbell and Young, 1993; Nakagawa, 2000) yet only one previous study attempted to relate this to environmental conditions (Harrison, 1985). Unfortunately, this study considered diurnal rather than monthly averaged values (see Section 6.3.1) and direct comparisons to the results of the current chapter are therefore not possible. Monthly time allocation by adult females in the study group could be expressed in terms of local demographic and ecological conditions (Section 6.3.3). In anticipation of the next chapter though, it is important to emphasise that this was only true for the amount of time spent moving and resting when predictor variables were limited to environmental conditions for which data are available at the extent of sub-Saharan Africa. Interestingly, these two time budget components of the study group could be related to two of the monthly range use parameters investigated in the previous chapter. The amount of time allocated to moving was positively associated with day journey length (Pearson's correlation test; $r = .649$, $n=12$, $p < .05$) whereas resting time showed a negative relation with the size of monthly core areas (Pearson's correlation test; $r = -.702$, $n=12$, $p < .05$). This illustrates that time allocation and range use, although treated in separate chapters here, are intrinsically inter-related aspects of the socio-ecology of a species and information on range use may therefore be useful in the development of an inter-populational time budget model for vervet monkeys.

Investigations into functional aspects of the main time budget components, lastly, helped interpret differences in time allocation between the sexes. Time allocation by females was found to be mainly aimed at nutrient acquisition and the maintenance of social relationships, whereas males are the more mobile and vigilant sex. This consolidates implicit assumptions of the socio-ecological model of primate societies on the surmised evolutionary differences between the sexes (Trivers, 1972; Clutton-Brock and Harvey, 1977; Emlen and Oring, 1977; Wrangham, 1980; van Schaik, 1983; 1989; Janson and Goldsmith, 1995; Sterck *et al.*, 1997). Perhaps the most interesting result from the monthly analyses on variation in the functional aspects of time allocation and their ecological correlates, was the derivation of a figure of the proportion of enforced resting time (Herbers, 1981). It was estimated that 10-20% of the total activity period of the study group consisted of enforced resting time which acts as a considerable constraint on the locally maximum ecologically tolerable group size, or indeed primate biogeography in general (Korstjens *et al.*, submitted). All in all then, the scene now seems set to apply findings from all previous chapters to the construction of the inter-populational systems model of vervet monkey socio-ecology.

7 Maximum ecologically tolerable group size

7.1 Introduction

Group size in animals is commonly considered to pose an optimisation problem in which individuals have to balance the benefits of group living (*i.e.* reduced predation risk or increased leverage in between group competition) with its associated costs (Pulliam, 1973; Caraco, 1979; Wrangham, 1980; van Schaik, 1983; 1989; Pulliam and Caraco, 1984; Terborgh and Janson, 1986; Dunbar, 1988). As argued in the previous chapter, an important resource over which group members inadvertently are competing is time and as demands on individual time budgets typically increase with group size, a maximum ecologically tolerable group size may eventually be set by time constraints (Dunbar, 1992b; 1993; 1998; Janson and Goldsmith, 1995). Since both the amount of time available and required to maximise individual fitness are determined by local ecological conditions, primate group size may thus be regarded as a habitat-specific behavioural adaptation of a species (Eisenberg *et al.*, 1972; Clutton-Brock, 1974).

This relationship between time budget requirements, environmental conditions and group size has frequently been used in primatology to develop taxon-specific models to quantify the maximum ecologically tolerable group size and the associated potential geographic range of a species (Chapter 1). Given the extensive use of the time budget approach, it is perhaps surprising to find that the basic model has changed relatively little since its first inception 15 years ago (Dunbar, 1992b). As a consequence, the physical environment in most quantitative models of primate socio-ecology has almost exclusively been expressed in terms of local climatic conditions. This, as pointed out in Chapter 3, is a potentially undesirable omission of a key factor in the causal cascade underpinning primate behaviour and may compromise model accuracy.

The preceding chapters have repeatedly demonstrated the usefulness of a remotely sensed index of primary productivity in interpreting key aspects of the behavioural ecology of a group of vervet monkeys inhabiting a South-African mountain environment. Here, it is investigated whether local findings from this population also hold on a more global, inter-populational scale. More specifically, a time budget model for the maximum ecologically tolerable group size and potential distribution of vervet monkeys will be developed for the whole of sub-Saharan Africa. In doing so, measures of both climate and primary productivity are related to time allocation as observed in a sample of free-ranging vervet populations. Resulting regression models are incorporated into a time budget model to generate predictions on the maximum ecologically tolerable group size of the species. The attempted incorporation of primary productivity as an environmental factor into the model may not only enhance model performance, but also aid understanding the mechanisms that determine time allocation and group size in vervet monkeys. Since the main merit of the time budget model over other, more conventional, species distribution models lies exactly in its ability to provide an insight into these proximate mechanisms, results from this chapter may constitute a noteworthy contribution to the model.

In the first section, the behavioural and environmental input data for the model are briefly described. Multiple regression analyses are subsequently performed to generate the best-fit equations that lie at the heart of the time budget model. After biological interpretation and validation of these equations, predictions from the time budget model of maximum ecologically tolerable group size and potential geographic range of vervet monkeys are presented and subsequently tested for accuracy and validity in three different ways.

7.2 Data collection

Perhaps the most important step in any modelling exercise is the collection of empirical data from which to estimate model parameters. Ideally, large quantities of high quality data are collated but in reality this is rarely achieved. Inevitably then, compromises have to be made and details are given below on how the behavioural and environmental input data for the time budget model were obtained.

7.2.1 Behavioural data

Information on presence, group size, time allocation, diet and range use was collected from as many African populations as possible (Figure 7.1). Data were collated in an extensive literature review and complemented by kind donations of unpublished data by Drs. L.A. Isbell, P.C. Lee, N. Nakagawa, D.J. van der Post, P.L. Whitten and T.R. Turner. Additional information on the documented presence of vervet monkeys was acquired from an extensive primate database compiled by Drs. A.H.M Korstjens and J. Lehmann and the African Mammals Databank (IEA, 1998a; 1998b). Perhaps the most striking outcome of this was that, although vervet monkeys have been studied extensively in the wild over the last 4.5 decades, detailed behavioural data were relatively scarce. The highly adaptive and opportunistic ecology of vervet monkeys, moreover, meant that a number of studies reported data on groups living under disturbed or semi-natural conditions (Henzi and Lucas, 1980). Groups in certain populations were reported to have incorporated crop raiding into their behavioural repertoire (Dunbar, 1974; Saj, 1998) or to have been actively provisioned by nearby human communities (Kavanagh, 1977; Cambefort, 1981; Brennan *et al.*, 1985). Another issue was the substantial disparity in definitions and methodologies used in the different studies, compromising commensurability of the reported behavioural information. Although Dunbar (1988) justly points out that this is unlikely to introduce a systematic bias to inter-populational models such as the one developed here, it undeniably contributes to the amount of noise in the data. Bearing in mind though that the behavioural data sets used in the construction of previous time budget models suffered from similar complications, for the moment these issues are taken to pose no serious cause for concern. Given its very nature though, one study was excluded *a priori* from the analyses (Brennan *et al.*, 1985) as it focussed on the ecology and behaviour of a group of vervet monkeys living in a tourist lodge environment.

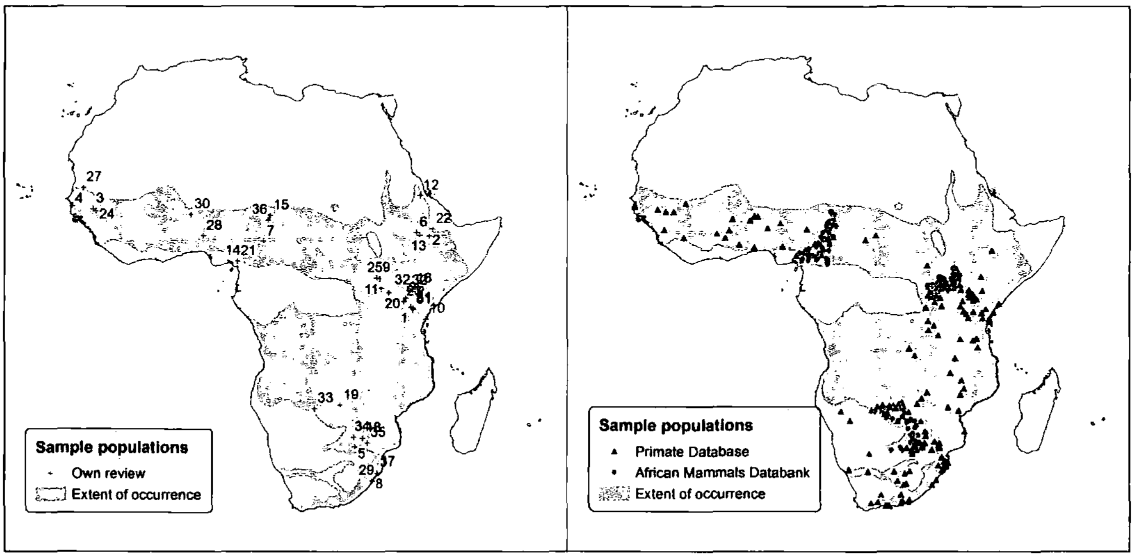

Figure 7.1 Locations throughout Africa where the presence of vervet monkeys has been documented. Numbered sites (left figure; n= 37) indicate those populations for which information on group size and time allocation was available and that were used in the development of the time budget model (Table 7.1). Locations for which only presence of vervet moneys had been reported are presented separately for reasons of clarity (right figure; n= 339).

In total, information on at least group size was available from an estimated 182 groups, representing 37 populations (Figure 7.1). Sufficiently detailed data to calculate the best-fit regression equations of the time budget model, however, were available for 14 populations only (Table 7.1). Careful inspection of regression diagnostics was thus deemed pivotal before generalising the obtained equations over the whole of sub-Saharan Africa (Section 7.3.1).

7.2.2 Environmental data

Environmental information was factored into the model using the spatially explicit datasets on climatic conditions and primary productivity developed in Chapter 3. In addition, information on the local annual range in day length was incorporated here. The inclusion of this last variable was motivated by previous studies on primate socio-ecology

(Hill, 1999; Hill *et al.*, 2003; 2005) and findings in Chapters 5 and 6. Local values of the environmental conditions thus considered in model development, are presented in Table 7.2. It is perhaps interesting to note that the latest generation of time budget models has recently (and independently) started implementing spatial datasets as well (Korstjens *et al.*, 2006; Korstjens and Dunbar, 2007; Korstjens *et al.*, submitted; Lehmann *et al.*, 2007a, b), although environmental variables entered into those models were limited to climatic conditions only.

7.3 Model development

The principal aim of the time budget model is to quantify the maximum group size at which individual vervet monkeys can still meet habitat-specific time budget requirements. It approaches this problem by firstly establishing the relationships between local environmental conditions, time allocation and group size in a number of sample populations using multiple regression analyses. Subsequently, the obtained best-fit equations are used to predict time allocation by vervet monkeys over the whole of sub-Saharan Africa and interpreted for their biological validity. Then, the inter-populational time budget model is developed and predictions on maximum ecologically tolerable group size presented.

Table 7.1 Overview of the behavioural information that was available for the construction of the time budget model. Presented data are weighted averages for each population in case information was available from multiple groups and/or different time periods. This weighting scheme assured that the influence of each population on the model was equal -continued on next page-.

Map nr.	**Site**	**Country**	**Lat**	**Lon**	**Alt**	**GS**	**Time Allocation**				**Range Use**				**Diet**		
							Feed	*Move*	*Social*	*Rest*	*DJL*	*HR*	*Fruit*	*Seed*	*Flower*	*Leaves*	*Animal*
1	Amboseli	Kenya	-2.40	37.17	1189	15.6	35.4	14.3	13.6	36.8		27.3	11.5	24.9	14.9	22.5	7.7
2	Awash	Ethiopia	8.85	40.00	956	18.0											
3	Badi	Senegal	13.17	-13.25	41	11.4	13.0	17.0	13.0	57.0	550.0	20.0					
4	Bandiala	Senegal	13.65	-16.55	4	33.0	8.1	20.6	7.6	63.7		138.0					
5	Blydeberg	South Africa	-24.43	28.19	1229	33.0	42.0	15.0	26.0	17.0		77.0	48.9	18.4	1.4	1.4	3.9
6	Bole Valley	Ethiopia	9.42	38.00	2232	18.8	28.0	28.9	11.4	31.8	700.0	30.0			17.6	18.7	7.4
7	Buffle Noir	Cameroon	8.10	13.87	380	18.0					2374.4	102.5	26.8	1.0	34.3	5.1	29.0
8	Burman Bush	South Africa	-29.85	31.02	13	25.0						15.0					
9	Chobi	Uganda	2.20	32.17	983	18.0						243.5					
10	Diani Beach Forest	Kenya	-4.24	39.55	79	14.0							55.3	21.3	6.4	10.6	
11	Entebbe	Uganda	0.60	32.45	1210	21.0	19.7	12.5	17.2	50.6	596.0	12.0					
12	Eritrea (survey)	Eritrea	15.30	38.55	1440	9.1											
13	Holota	Ethiopia	9.03	38.47	2341	36.7											
14	Kak, Bakossi	Cameroon	4.87	9.70	832	8.0											
15	Kalamaloue	Cameroon	12.15	14.88	294	47.3	23.4	19.8	5.0	49.9	1429.4	94.6	59.5	9.5	10.1	12.9	6.6
16	Kimana	Kenya	0.50	37.50	1025	13.3											
17	Krantzkloof	South Africa	-28.58	31.77	171	36.0											
18	Lajuma	South Africa	-23.04	29.43	1381	17.8	42.8	21.7	9.8	25.7	1580.7	114.1	51.0	25.0	0.9	14.5	0.3
19	Livingstone	Zambia	-17.85	25.87	926	20.0						30.0		50.6	17.6	18.7	7.4
20	Lolui Island	Uganda	-0.12	33.67	1139	12.7					824.6	155.4	30.9			58.9	
21	Meket Mbeng, Bakossi	Cameroon	4.88	9.68	633	14.5						13.4					
22	Metahara	Ethiopia	10.00	40.53	572	22.0											
23	Mosiro	Kenya	-1.50	36.00	1571	12.5											
24	Mt. Assirik	Senegal	12.88	-12.77	174	25.5			8.5	46.7	1515.0	178.4	50.0	13.0	13.0	7.0	13.0
25	Murchison Falls	Uganda	2.28	31.68	693	11.0											
26	N'Dioum	Senegal	16.55	-14.74	8	39.5	27.0	41.0	7.0	25.0			26.6		2.7	37.1	13.1
27	Naivasha	Kenya	-1.00	36.33	1638	14.7											
28	Old Oyo	Nigeria	8.97	4.30	364	20.0	52.7	30.2	7.5	9.7							
29	Palmiet Valley	South Africa	-29.83	30.93	223	26.0											
30	Park W	Niger	12.35	2.35	256	14.0											
31	Samburu, Isiolo	Kenya	-2.56	37.50	1180	32.7	37.5	12.2			1500.0	81.0	7.8	24.9	49.9	16.6	0.8
32	Segera, Laikipia	Kenya	0.25	36.83	1791	17.5	23.8	11.7	15.9	48.6	1328.5	25.0	4.4	8.4	4.9	3.0	2.9
33	Shakawa	Botswana	-18.42	21.88	995	35.8											
34	Stevensford	Botswana	-22.90	28.04	775	27.5											
35	Tzaneen	South Africa	-23.83	30.17	696	36.0											
36	Waza	Cameroon	11.42	14.58	303	23.0											
37	Windy Ridge	South Africa	-28.58	31.77	171	23.0	32.8	21.2	22.6	23.4							

Table 7.1 -continued- Reference list.

Map nr.	Site	References
1	Amboseli	Struhsaker, 1965, 1967c, b, a, 1969, 1973, 1976; Klein, 1978; Lee, 1982; Isbell, 1990b; Isbell and Young, 1993; Isbell, unpubl.
2	Awash	Turner, 1977
3	Badi	Dunbar, 1974
4	Bandiala	Galat and Galat-Luong, 1976
5	Blydeberg	Barrett, 2005
6	Bole Valley	Dunbar and Dunbar, 1974
7	Buffle Noir	Kavanagh, 1977, 1978, 1980, 1981
8	Burman Bush	Henzi and Lucas, 1980
9	Chobi	Gartlan, 1966
10	Diani Beach Forest	Moreno-Black and Maples, 1977
11	Entebbe	Saj, 1998
12	Eritrea (survey)	Zinner *et al.*, 2002
13	Holota	Shimada and Shotake, 1997
14	Kak, Bakossi	Kavanagh, 1977, 1978, 1980, 1981
15	Kalamaloue	Kavanagh, 1977, 1978, 1980, 1981; Nakagawa, 2000; Nakagawa, unpubl.
16	Kimana	Turner *et al.*, 1994, 1997; Turner, unpubl.
17	Krantzkloof	Tollman and Simpson, 1975
18	Lajuma	Current study
19	Livingstone	Lancaster, 1971
20	Lolui Island	Gartlan, 1966
21	Meket Mbeng, Bakossi	Gartlan 1973; cited in Kavanagh, 1977
22	Metahara	Shimada and Shotake, 1997
23	Mosiro	Turner *et al.*, 1994, 1997; Turner, unpubl.
24	Mt. Assirik	Harrison, 1982; Harrison, 1983b, a, c, 1984, 1985
25	Murchison Falls	Hall, cited in Kavanagh, 1977
26	N'Dioum	Galat and Galat-Luong, 1977
27	Naivasha	Turner *et al.*, 1994, 1997; Turner, unpubl.
28	Old Oyo	Adeyemo, 1997
29	Palmiet Valley	Harrison, 1997
30	Park W	Poché, 1976
31	Samburu, Isiolo	Turner *et al.*, 1997, 1994; Whitten, 1981; Whitten, 1982b; Whitten, 1983; Whitten, 1984; Whitten, 1988; Whitten unpubl.
32	Segera, Laikipia	Isbell and Pruetz, 1998; Isbell *et al.*, 1998; Isbell *et al.*, 1999b; Isbell *et al.*, 1999a; Pruetz, 1999; Pruetz and Isbell, 2000; Enstam and Isbell, 2002a; Enstam, 2002; Enstam and Isbell, 2002b; Isbell and Young, 2002; Isbell unpubl.
33	Shakawa	van der Post, *pers. com.*
34	Stevensford	van der Post, *pers. com.*
35	Tzaneen	Cambefort, 1981
36	Waza	Gartlan 1973; cited in Kavanagh, 1977
37	Windy Ridge	Baldellou and Henzi, 1992; Baldellou and Adan, 1997, 1998

Table 7.2 Overview of the environmental information that was considered in the time budget model for maximum ecologically tolerable group size.

Site	$\text{Photoperiod}_{\text{range}}$	T_{min}	T_{mean}	T_{max}	T_{sd}	$T_{\text{daily range}}$	P_{total}	$P_{\text{driest month}}$	$P_{\text{wettest month}}$	P>2T	P_{Shannon}	P_{CoV}	NDVI_{min}	NDVI	$\text{NDVI}_{\text{range}}$	INDVI
Amboseli	0.28	13.6	21.4	30.3	13.7	12.1	607	2	124	7	0.85	80	0.28	0.36	0.08	3.33
Awash	1.03	12.8	24.8	35.6	20.6	15.0	535	4	132	3	0.88	82	0.34	0.40	0.06	4.08
Badi	1.55	15.7	28.2	39.4	24.3	13.6	873	0	244	5	0.67	124	0.41	0.71	0.30	5.28
Bandiala	1.61	16.5	26.8	34.7	12.2	12.4	795	0	295	4	0.59	146	0.18	0.22	0.04	3.67
Blydeberg	3.03	1.8	18.4	29.4	41.7	15.9	619	4	123	7	0.84	83	0.42	0.55	0.13	5.02
Bole Valley	1.10	7.6	17.1	27.0	12.3	14.5	1049	6	267	8	0.80	98	0.44	0.65	0.21	5.50
Buffle Noir	0.94	15.6	26.2	36.1	16.3	12.8	1328	0	278	7	0.77	96	0.47	0.71	0.24	6.67
Burman Bush	3.84	11.3	20.9	28.1	26.3	8.6	972	30	125	4	0.96	42	0.04	0.13	0.09	1.78
Chobi	0.25	16.6	23.7	32.6	9.2	12.5	1258	25	165	9	0.95	44	0.66	0.77	0.11	8.09
Diani Beach Forest	0.49	19.9	26.0	32.7	14.6	8.2	1226	19	293	6	0.91	74	0.50	0.58	0.08	4.09
Entebbe	0.07	14.9	21.5	28.7	5.3	11.6	1260	47	157	12	0.98	32	0.71	0.72	0.01	8.06
Eritrea (survey)	1.82	11.3	22.4	33.4	16.6	15.4	608	15	164	3	0.89	95	0.25	0.36	0.11	2.84
Holota	1.05	6.3	16.3	25.8	11.1	14.3	1118	8	263	8	0.83	92	0.45	0.55	0.10	5.09
Kak, Bakossi	0.56	17.0	22.2	28.6	9.3	8.8	2721	16	474	10	0.89	71	0.47	0.64	0.17	6.21
Kalamaloue	1.43	13.8	27.9	40.8	29.2	15.3	486	0	169	1	0.64	137	0.28	0.46	0.18	3.19
Kimana	0.06	14.1	23.2	33.3	7.0	16.9	619	7	151	6	0.84	90	0.44	0.51	0.07	4.21
Krantzkloof	3.64	10.8	21.1	29.4	26.5	10.7	982	34	123	12	0.96	42	0.67	0.73	0.06	7.20
Lajuma	2.83	3.8	17.0	26.1	33.4	12.9	807	7	168	6	0.85	82	0.42	0.54	0.12	5.93
Livingstone	2.14	6.7	22.6	35.5	35.9	15.6	693	0	176	5	0.71	116	0.33	0.57	0.24	4.99
Lolui Island	0.01	15.6	22.3	29.4	5.6	11.8	1180	40	194	0	0.95	50	0.28	0.34	0.06	3.27
Meket Mbeng, Bakossi	0.57	18.5	23.5	30.0	9.0	8.8	2877	23	486	10	0.89	68	0.47	0.64	0.17	6.15
Metahara	1.17	13.5	25.4	36.9	23.3	14.3	464	6	135	3	0.86	90	0.33	0.39	0.06	3.85
Mosiro	0.17	11.8	20.1	29.0	10.5	13.8	712	13	156	7	0.91	70	0.33	0.56	0.23	4.72
Mt. Assirik	1.52	16.3	27.7	39.0	23.0	13.1	1068	0	295	5	0.68	121	0.41	0.71	0.30	5.53
Murchison Falls	0.26	17.2	25.1	33.7	9.9	12.2	1152	22	148	9	0.96	43	0.59	0.73	0.14	7.37
N'Dioum	1.97	12.6	27.5	39.9	34.8	15.6	246	0	93	2	0.60	143	0.18	0.22	0.04	1.92
Naivasha	0.12	10.2	18.7	28.5	11.4	14.5	756	21	165	9	0.93	68	0.27	0.42	0.15	3.80
Old Oyo	1.05	17.4	26.3	35.7	14.6	11.8	1180	6	237	7	0.85	78	0.34	0.56	0.22	5.15
Palmiet Valley	3.84	11.4	20.2	27.1	22.8	8.9	964	26	138	10	0.95	46	0.62	0.66	0.04	5.26
Park W	1.45	16.6	28.5	39.8	24.5	13.6	684	0	202	4	0.69	121	0.32	0.62	0.30	4.40
Samburu, Isiolo	0.30	13.6	21.2	30.1	14.2	11.9	720	3	158	7	0.85	85	0.28	0.40	0.12	3.34
Segera, Laikipia	0.03	7.6	17.5	27.5	5.6	16.2	683	19	126	8	0.95	53	0.44	0.60	0.16	4.65
Shakawa	2.21	6.0	22.1	33.8	37.1	15.6	520	0	125	5	0.74	107	0.40	0.64	0.24	5.29
Stevensford	2.81	5.0	21.5	33.0	44.1	15.3	378	1	72	4	0.82	88	0.32	0.43	0.11	3.92
Tzaneen	2.94	6.8	20.3	29.8	32.9	13.6	978	10	215	7	0.85	87	0.63	0.72	0.09	7.48
Waza	1.34	15.8	27.9	40.1	23.2	14.6	651	0	213	4	0.65	130	0.27	0.52	0.25	4.00
Windy Ridge	3.64	10.8	21.1	29.4	26.5	10.7	982	34	123	12	0.96	42	0.67	0.73	0.06	7.20

For details on how these variables were obtained and for definitions (if not self-explanatory), the reader is referred back to Chapters 3 and 4.

7.3.1 Calculation of best-fit equations

Previous time budget modelling studies have commonly incorporated aspects of range use (Dunbar, 1996) and information on local diet (Korstjens and Dunbar, 2007) in addition to the suite of environmental variables as predictor variables into the models. Therefore, and whenever available, information on range use and dietary composition were included in the current analyses as well. The time budget components themselves, moreover, are inherently interdependent (Chapter 6) and may also be used to predict the proportion of time spent in each of the other behavioural activities (for details on this, see (Dunbar, 1992b). A hybrid regression technique, relying on hierarchical and stepwise variable entry procedures, was chosen and key parameters and associated statistics of the resulting best-fit equations are summarised in Table 7.3.

Table 7.3 Parameter estimates and statistics of the regression analyses performed to quantify the relationship between local ecological conditions, group size and time allocation as observed within the sampled populations. The proportion of leaves in the diet was found to be a significant predictor of moving time and is therefore expressed as a function of environmental conditions as well.

		B	**se B**	$\boldsymbol{\beta}$	**t**	**F** $_{model}$	**se estimate**	**Adj. R^2**
Feeding (%)	Intercept	-78.76	13.59		***-5.80******	***17.14******	6.85	.843
	$P_{Shannon}$	130.60	17.52	1.39	***7.46******			
	$NDVI_{min}$	-104.32	17.13	-1.35	***-6.09******			
	T_{sd}	0.96	0.16	0.89	***5.95******			
	P_{annual}	0.03	0.01	0.69	***3.69*****			
Moving (%)	Intercept	10.22	3.52		***2.90*****	***16.12*****	5.63	.716
	Leaves	0.76	0.19	0.87	***4.02*****			
Social (%)	Intercept	-24.86	10.85		***-2.29*****	***9.40******	3.62	.677
	P>2T	1.87	0.38	0.96	***4.99******			
	$T_{daily\ range}$	1.65	0.67	0.47	***2.45*****			
	Photoperiod $_{range}$	2.09	0.94	0.37	*2.22**			
Resting (%)	Intercept	84.60	6.87		***12.31******	***36.28******	6.34	.865
	Feeding	-1.24	0.15	-0.92	***-8.31******			
	Group size	-0.52	0.21	-0.28	***-2.47*****			
Leaves (%)	Intercept	51.74	9.48		***5.46******	***15.25******	8.63	.704
	$NDVI_{min}$	-111.96	25.49	-0.69	***-4.39******			
	$P_{driest\ month}$	0.81	0.21	0.60	***3.82******			

* = p< .10; ** = p< .05; **p< .01; *** = p< .005

Inspections of model diagnostics confirmed the relatively high level of accuracy of all equations as indicated by their respective adjusted R^2 values (Table 7.3). Thus, no statistical complications were foreseen in predicting local time allocation demands beyond the sampled populations. These were subsequently calculated over the whole of sub-Saharan Africa within a GIS (Figure 7.2). Note that local demands on resting time could not be determined, due to the inclusion of group size as an unknown predictor variable. Instead, the proportion of time available to resting after meeting time allocation demands of all other time budget components is presented. It is important to emphasise that this predicted value for total resting time consists of both enforced resting time (local resting time demands) and uncommitted resting time (Section 6.4.1).

A few remarks about Figure 7.2 should be made before biological interpretations of the calculated best-fit equations are offered. The first thing to note is that the calculated local time allocation demands are highly simplified mathematical abstractions of a very complex socio-ecological phenomenon. This means they should be interpreted with care and sound biological reasoning. For example, where the model predicts that the external environment poses no demands on feeding time (*i.e.* values < 0%), real vervet monkeys would obviously still have to spend time feeding to meet internal demands (metabolic and physiological). In other words, minimum time demands on the respective time budget components are not always set by the external environment. On the other hand, where predicted time budget demands exceed 100% (blacked out regions in the maps of feeding and moving time demands), local demands of the individual time budget component can not be met and these areas are unsuitable for occupation by vervet monkeys. Again, however, real animals will be subjected to other constraints as well (such as physiological limitations and indeed the time allocation demands of other time budget components) and therefore the maximum amount of time that may realistically be allocated to each behavioural component will be much lower than 100%. It is important to keep these considerations in mind when using the best-fit equations to calculate maximum ecologically (rather than mathematically) tolerable group size. The most valid way of doing so may be by limiting the range of calculated time allocation demands to the observed minima and maxima in the behavioural database (Section 7.2.1).

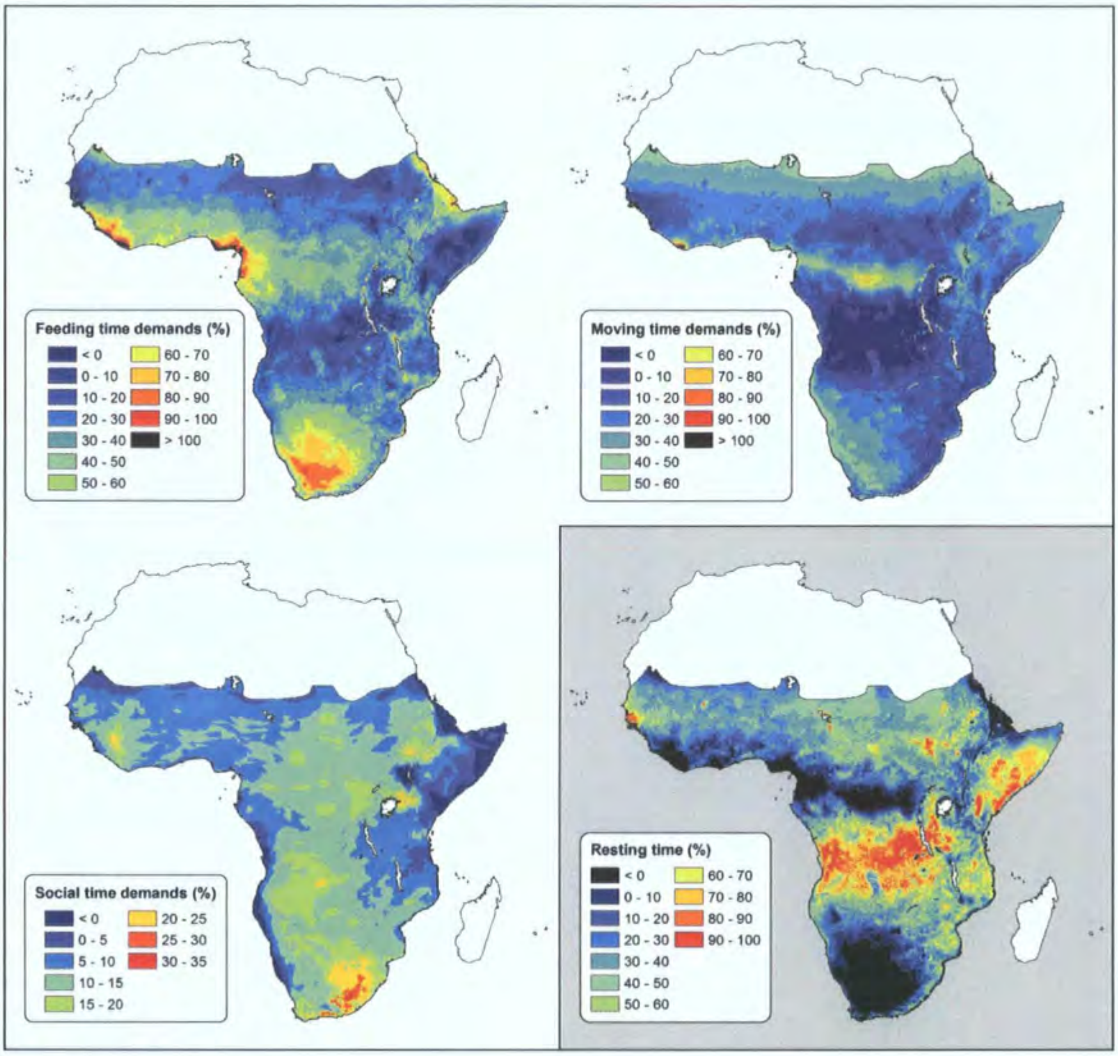

Figure 7.2 Pan sub-Saharan Africa time allocation demands on vervet monkeys of three out of the four main time budget components. The bottom-right graph gives the proportion of local time spent resting, which consists of both enforced resting time and uncommitted time.

7.3.2 Biological interpretation

After establishing the statistically significant relationships between local ecological conditions, group size and vervet time allocation in the previous sub-section, biological significance of the proposed mechanisms underlying these associations is investigated.

Inter-populational feeding time was best expressed by linear relationships to Shannon's index of rainfall evenness, annual minimum NDVI, the annual standard deviation of temperature and total annual rainfall (Table 7.3). The positive association to evenness of rainfall in combination with the negative relationship to minimum annual productivity suggests that the monkeys were forced to spend more time feeding in consistently dry and relatively poor areas in order to meet nutritional demands. On the other end of the habitat quality spectrum, high levels of precipitation and even rainfall throughout the year also increased demands on feeding time. These two trends are nicely illustrated over sub-Saharan Africa by the high demands on feeding time in the deserts of southern Africa and north-western Ethiopia, and the equally high demands over the tropical rainforests of the Congo basin and West Africa (Figure 7.2). Seasonality in annual temperature, lastly, may have contributed to elevated demands on feeding time through its effect on thermoregulatory demands on the animals.

The proportion of time attributed to moving by the sample populations was predominantly ordained by a dietary component. In populations where leaves constituted a large part of the diet, monkeys were found to spend a lot of time moving (Table 7.3). This was a likely response to a relatively poor diet and vervet monkeys in these populations may have been making the best out of a bad situation by exploiting a low quality, but widely available, food resource. The negative association between minimum annual NDVI and the proportion of leaves in the diet supports this interpretation as it suggests that leaves were mostly exploited in relatively poor habitats. Leaves thus constitute a fallback food source under harsh ecological conditions. The amount of rainfall during the driest month of the year also increased the proportion of leaves in the diet. This may denote how leaves were more abundant, and hence more exploited, at low productivity sites with less severe seasonal droughts. On a pan sub-Saharan African scale, the equation for moving time accounts for the observed elevated demands in desert areas and the entire east-west strip of Sahelian savannah fringing the southern edge of the Sahara (Figure 7.2). In highly productive areas though, the interpretation offered above may break down as vervets would switch to other, higher quality, food resources. Predictions on the remarkably high demands on moving time over the central and western

African rainforests may thus require a different interpretation, but nevertheless coincide with areas not exploited by vervet monkeys in the wild.

Animals in the sampled populations spent more time in social interactions at sites with a longer potential growing season (P>2T; le Houérou, 1984), a more pronounced range in daily temperature and greater variation in day length over the year (Table 7.3). In effect, this equation suggests that more time was committed to social activities when demands on other time budget components were more relaxed (if a longer growing season is taken to indicate a longer 'period of plenty') and when more time was available during certain parts of the year (reflected by a more pronounced annual variation in day length). Fluctuations in daily temperature may have imposed thermal constraints on the monkeys, preventing them from engaging in energetically more demanding activities. Mapped over sub-Saharan Africa, the equation for social time generates several distinct patches of elevated social time, the highest values occurring in the Drakensberg mountain range in South Africa. Whether these predicted values of social time represent strict habitat-specific minimum demands on social activity or the intricate trade-offs within the primate time budget, remains tentative. Ultimately, social time in primates serves to maintain group cohesion and is therefore most likely to be driven by social, rather than ecological, demands (Dunbar, 1991; 1992a; Lehmann *et al.*, 2007b).

The observed inter-populational variation in resting time, lastly, was best expressed by negative associations to feeding time and group size. Resting time in vervet monkeys thus illustrates how the time demands of one time budget component (feeding) can take precedence over the proportion of time allocated to another (resting) when the total amount of time available to the animals is limited due to group size (Dunbar, 1992b; 1993; 1998; Janson and Goldsmith, 1995). The equation thereby underlines the notion that resting time partly consists of uncommitted time (Herbers, 1981; Korstjens *et al.*, submitted), which serves as a reservoir from which animals can draw when time allocation demands increase (*e.g.* in larger groups; Dunbar, 1996). In this respect, resting time may be particularly informative as it could be inversely related to the amount of time stress experienced by the animals. The resting time map presented in Figure 7.2 can hence tentatively be interpreted as a habitat quality map in terms of inverse local time stress.

To conclude this section on the biological interpretation of the generated best-fit equations for the individual time budget components, a flow chart of the inferred causal cascade relating environmental factors and time allocation to local group size is presented (Figure 7.3). This chart basically represents the time budget model for the local maximum ecologically tolerable group size that now can be developed.

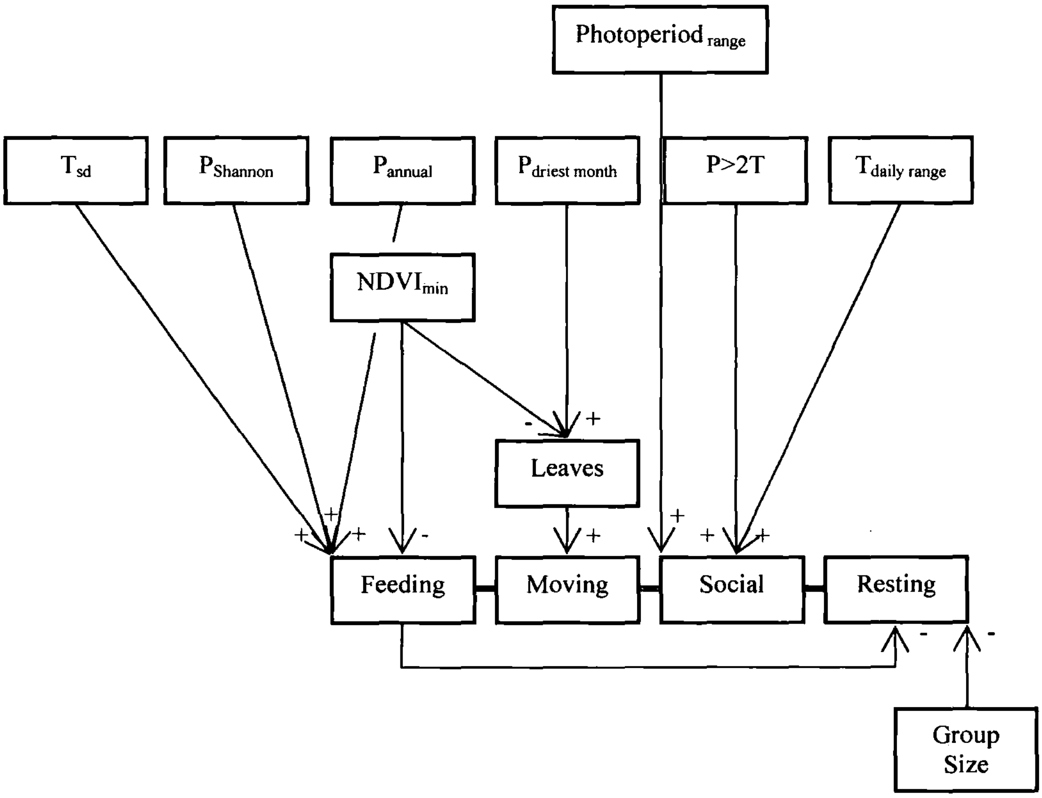

Figure 7.3 Flowchart of the vervet time budget model depicting the inferred causal relationships between climatic conditions, vegetation characteristics, dietary components, time budget components and group size (abbreviations used for climatic conditions are given in Table 7.2).

7.3.3 Maximum ecologically tolerable group size

Best-fit equations for time allocation as presented and interpreted above, are routinely used to estimate the maximum ecologically tolerable group size in primates (Chapter 1). Before presenting the time budget model for vervet monkeys, however, a minor reservation is articulated against this approach. Given the cumulative built-up of errors inherent to the use of calculated best-fit equations to estimate key predictors in the model, and given the small sample sizes on which these equations are typically based, it would seem prudent to be modest about claims on the accuracy and validity of any ensuing predictions.

Typically, time budget models have had to resort to estimation through iteration to quantify the maximum group size primates can maintain under a given set of local environmental conditions (Chapter 1). Small computer programs have been written (in BASIC and Dbase) to perform this task which basically involves the repeated calculation of the sum of local time budget demands at incrementing group sizes until this total exceeds 100%. The largest group size at which the sum of all time allocation demands is less than 100%, thus represents the maximum ecologically tolerable group size. As pointed out in Section 7.3.1, values of the time budget demands in this exercise have to be constrained following both mathematical and biological considerations to warrant meaningful results.

In contrast to previous time budget models, the format of the model for vervet monkeys allowed direct analytical calculation of the maximum ecologically tolerable group size. This fortunate coincidence was due to group size only occurring once in the best-fit equations, effectively reducing the problem to finding the solution to two equations with one unknown variable. The rationale, however, is the same. Taking the best-fit equation for resting time (Table 7.3) as a starting point, the deduction of maximum ecologically tolerable group size in vervet monkeys is as follows:

$$R = 84.60 - 1.24 \times F - 0.52 \times Group\ Size$$

$$\Rightarrow Group\ Size = \frac{84.60 - R - 1.24 \times F}{0.52} \qquad (1)$$

Substituting resting time by its alternative equation,

$$R = 100 - F - M - S$$

results in:

$$Group\ Size = \frac{84.60 - (100 - F - M - S) - 1.24 \times F}{0.52}$$

$$\Rightarrow Group\ Size = \frac{-15.40 + M + S - 0.24 \times F}{0.52} \qquad (2)$$

where *M*, *S* and *F* are the known local demands on moving, social and feeding time.

Finally, the biologically constrained domain of time budget values was set, based on the respective observed minima and maxima in the behavioural database (Table 7.1):

$$\begin{matrix} F \in [\ 8.1;52.7] \\ M \in [11.7;41.0] \\ S \in [\ 5.0;26.0] \\ R \in [\ 9.7;63.7] \end{matrix} \Rightarrow \left.\begin{matrix} F \in [10,55] \\ M \in [10,35] \\ S \in [\ 5,25] \\ R \in [10,65] \end{matrix}\right\} \sum \leq 100\% \qquad (3)$$

In line with previous modelling exercises, convenient but biologically inspired values were chosen. Note that in setting the upper-limit on moving time demands, it was decided to lower this value from a figure of around 40%, as suggested by the data, to 35%. The motivation for this stems from comments by the authors that reported the 41% value on the poor physical condition of the study animals and on starvation and malnutrition being likely causes of observed mortality (Galat and Galat-Luong, 1976, 1977). These remarks strongly suggested that the vervet monkeys in this study were suffering severe ecological stress and since animals were starving, this clearly did not represent a sustainable situation. A more conservative estimate for the maximum sustainable demands on moving time was thus set at 35%.

To estimate the maximum ecologically tolerable group size the minimum resting time demand, representing the point at which all uncommitted time was taken to have been reallocated to functional time budget components, was set to the observed minimum value in the behavioural database. This yielded an estimated figure for enforced resting time of 10%, a value very similar to the one derived for the study group (Section 6.4.1). Implementation of Equation 1 into a GIS, whilst constraining the range of all time budget components to their respective observed ranges (Equation 3), yielded the following result (Figure 7.4).

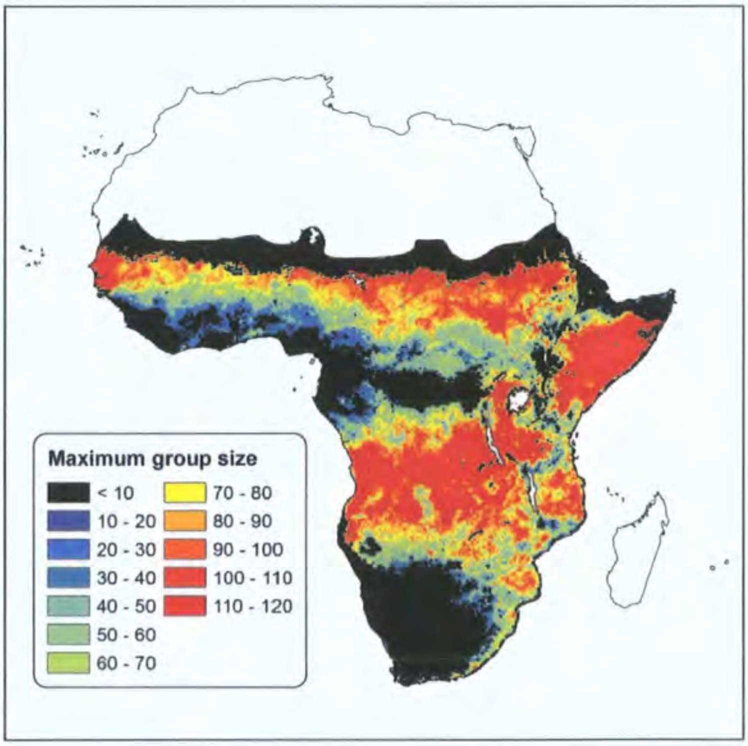

Figure 7.4 Predicted maximum ecologically tolerable group size and associated range of distribution of vervet monkeys over sub-Saharan Africa as predicted by the time budget model.

One thing to note from this figure is that the predicted maximum ecologically tolerable group size was never smaller than 10 individuals when calculated time budget components were within their defined biologically valid ranges. This eliminated the need to impose further restrictions on the model since group sizes greater than 10 individuals seem to be able to sustain considerable predation pressure. In this respect it may be worth noting that the smallest observed group size within the behavioural database consisted of 8 animals only.

7.4 Model validation

To assess the time budget model for its accuracy and validity, three tests are performed. Firstly, it is investigated how well the model predicts the presence of vervet monkeys at sites of known occurrence. Secondly, predicted maximum ecologically tolerable group size is plotted against observed group sizes in a number of sample populations. This serves to ascertain whether vervet monkeys indeed live in groups smaller than the maximum ecologically tolerable values predicted by the model. Thirdly and lastly, the predicted potential geographical range over sub-Saharan Africa is overlaid with a map of known occurrence for a visual comparison.

7.4.1 Predicted presence at sites of known occurrence

In a first, qualitative, examination of the accuracy and validity of the time budget model, predictions were generated on vervet monkey presence at sites of known occurrence. All sites from which information on the presence of vervet monkeys was available (Figure 7.1) were entered into the model. Potentially confounding spatial auto-correlation within these data need not be considered here since the current examination was of a descriptive nature. Findings are summarised in Table 7.4.

Table 7.4 Summary of correctly predicted presence and falsely predicted absence of vervet monkeys at 376 sites throughout sub-Saharan Africa.

	Time budget model
No prediction (environmental information missing)	1.6%
Falsely predicted absence (time budget demand violation)	30.1%
Correctly predicted presence	68.4%
Total	**100%**

At 6 of the 376 sites (representing 1.6% of all sample locations) data on climatic conditions were missing and no predictions could be made. These sites were all very closely situated to coastlines, which strongly suggested that the absence of data was an artefact of the reprojection and resampling algorithms employed in the pre-processing of the climatic dataset (Section 3.3.1). This was indeed found to be the case and a closer examination learned that the highest locational inaccuracy introduced by this was in the order of magnitude of 4km (half a pixel within the GIS). Unfortunately, this kind of spatial error is almost inevitable when working with data on a near-continental scale. It is unlikely, however, to have seriously affected overall model performance.

The model falsely predicted vervet monkey absence at 113 sites (30.1%) due to calculated time allocation requirements falling outside of the defined biologically valid range. This may indicate a serious flaw in the theoretical framework behind the model and calls for furher exploration. At first it may seem that the range of biologically valid time budget demands was set too strictly. Given the high proportion of predicted time budget components falling outside of the valid mathematical range as well though (percentage data can only assume values between 0% and 100%), the validity of the generalised best-fit equations themselves, rather than their output, may be in need of revision. Investigations of model diagnostics in Section 7.3.1 did not reveal any statistical grounds to question the accuracy or generalisability of these equations, so an even more fundamental, biological, explanation may be required. One possibility is that due to the highly adaptive social organisation of vervet monkeys and their opportunistic nature (Struhsaker, 1967; Gartlan and Brain, 1968), the flexibility of their behavioural repertoire was not sufficiently captured by the 14 sample populations upon which the best fit equations were based. Pertaining to this is the notion of potential spatial heterogeneity (Fotheringham *et al.*, 2000, 2002) in vervet monkey socio-ecology, a possibility already alluded to in Section 5.5. This may require serious consideration as its implications for inter-populational analyses can be far-reaching. Spatial heterogeneity is therefore discussed in more detail in Section 7.5.

The time budget model correctly predicted vervet monkey presence in over 68% of all cases. Unfortunately the interpretation of this result is limited by not having data on known absence for which model predictions could be assessed. It appears though that the model performed reasonably well.

7.4.2 Comparison to known group sizes

Perhaps the most straightforward way to assess the accuracy of the time budget model is by comparing predicted group sizes to those observed in vervet monkeys. As mentioned in Section 7.3.1, data on group size were available from 37 sites and here comparisons are presented between model predictions and observed mean and maximum group sizes in these populations (Figure 7.5). The data exhibited no significant spatial autocorrelation (Moran's $I = .07$, $n_{\text{permutations}} = 200$, $p_{\text{Monte Carlo}} = 0.12$).

The first result reported here is that at 4 sites, the model falsely predicted vervet monkeys to be absent. Excluding these sites from the following brief discussion, it is concluded that the model performed well: at only 2 out of 33 sites for which valid predictions were generated, did observed group sizes (mean and maximum) exceed the predicted maximum. Note from Figure 7.5, moreover, that they only did so marginally. Paired sampled t-tests statistically confirmed this. Predicted maximum group size (mean ± se= 68.8 ± 4.3) was significantly larger than both observed mean (mean ± se= 23.1 ± 1.7; $t_{(32)} = 10.45$, $p < .001$) and observed maximum (mean ± se= 27.7 ± 2.4; $t_{(32)} = 8.77$, $p < .001$) group size. Of particular interest here, however, are the populations for which the model generated false predictions and these are presented (Table 7.5) and discussed in more detail below.

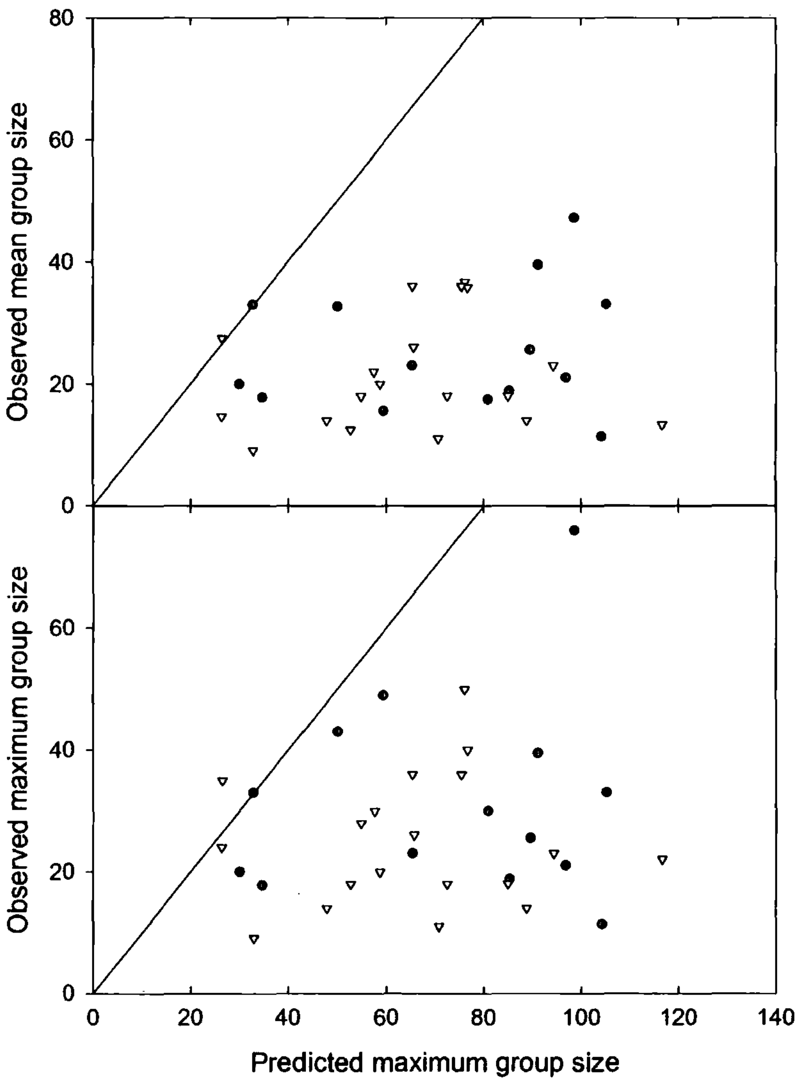

Figure 7.5 Comparison between the predicted maximum ecologically tolerable group size and mean and maximum group sizes observed in 37 vervet monkey populations. Closed circles denote the populations used in the construction of best-fit equations (n=14), whereas the downward pointing triangles signify an independent set of test populations. Solid lines serve as visual aids for interpretation: in areas below the lines, the predicted maximum ecologically tolerable group size exceeds observed group size.

Table 7.5 The 4 populations for which predicted maximum group size violated underlying time budget requirements are presented alongside with the 2 populations in which observed group sizes exceeded the predicted ecologically tolerable group size.

	Observed mean	Observed maximum	Predicted maximum
Burman Bush	25	25	-90.2*
Kak, Bakossi	8	8	-51.7*
Lolui Island	12.7	21	4.4*
Meket Mbeng, Bakossi	14.5	18	-62.7*
Blydeberg	33	33	32.8
Stevensford	27.5	35	26.5

*= falsely predicted absence due to violation of time budget requirements

The population at Burman Bush was studied in a park in one of South Africa's largest cities (Henzi and Lucas, 1980). This clearly represents an unnatural situation and inspections of Table 7.2 reveal very low NDVI values for this site, as would be expected over urban areas. It is therefore not too surprising to find that the model falsely predicted the absence of vervet monkeys under these highly disturbed conditions. The two sites in Bakossi (Cameroon) are interpreted as representing the same population since they are within 3 km distance of each other. Interestingly, both sites just fall outside of the geographical range predicted by the time budget model as well as the known extent of occurrence (IEA, 1998b). This suggests that the Bakossi population was living at the very edge of the species' range of distribution as reflected by excessively high predicted feeding time requirements (over 80%). Again, reports from the original study on the animals inhabiting a mosaic of farmland and secondary forest (Kavanagh, 1977), suggested that local conditions may not have been representative of a natural situation. Falsely predicted absence at Lolui (Uganda) could be ascribed to the fact that this island in the northern part of Lake Victoria has a surface area below pixel resolution of the GIS. Estimated NDVI values therefore suffered from water contamination, which almost certainly resulted in a considerable underestimation of true local primary productivity. Indeed, calculated feeding and moving time requirements exceeded their biologically permitted maximum values (58% and 51% respectively). This population then, revealed a shortcoming in model accuracy due to the coarse pixel size of the NDVI data that were implemented into the model. The two sites at which observed group sizes exceeded the predicted maximum group sizes (Blydeberg in South Africa and Stevensford, Botswana), represented two populations living under fairly undisturbed conditions. The fact that observed group sizes only marginally exceeded the predicted maximum may make the need for an explanation of model breakdown at these sites less urgent, but it is nevertheless reported that data from the Stevensford population stemmed from brief surveys and consequently that group size estimates may have been overestimations of true local group sizes (van der Post, *pers. com.*; *pers. obs.*).

7.4.3 Comparison to known extent of occurrence

In a final test of model performance the level of agreement between the predicted geographical range of vervet monkeys and the known extent of occurrence was visually assessed (Figure 7.6).

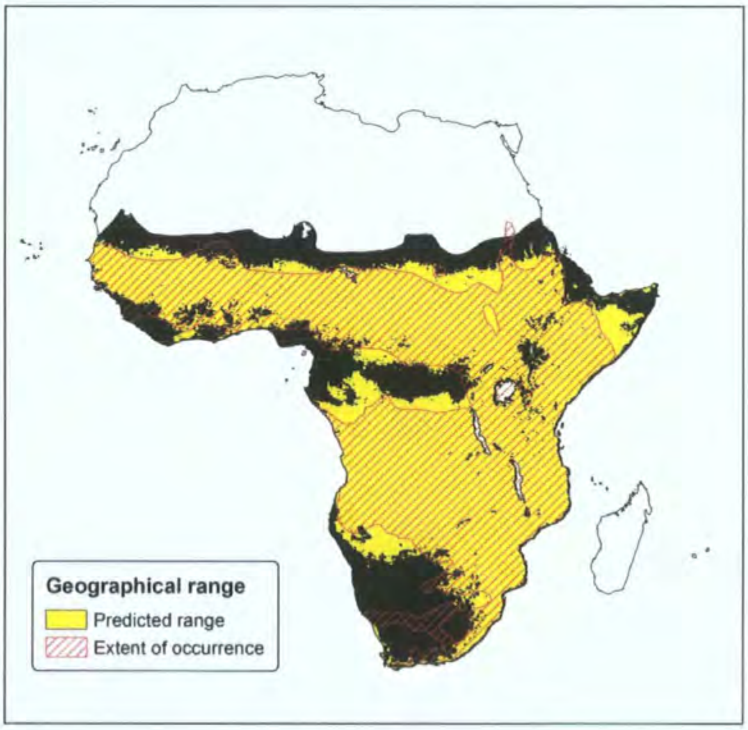

Figure 7.6 Visual comparison between the geographical range of vervet monkeys as predicted by the time budget model and the known extent of occurrence as established by the African Mammals Databank (IEA, 1998a; 1998b).

Overall, the potential range of distribution as predicted by the time budget model is in remarkable agreement with the known extent of occurrence as established by the African Mammals Databank (IEA, 1998a, b). The most conspicuous region of disparity is perhaps the narrow east-west strip in Southern Africa where vervet monkeys are known to occur, but their presence was not predicted by the model. In this area, vervet monkeys are bound to the catchment area of the Orange river, which springs in the Drakensberg mountains of Lesotho and flows westwards into the Atlantic Ocean. As a consequence, environmental conditions experienced locally by these groups will have been poorly represented by the climatic variables upon which model predictions are based. The presence of this river then, offers a biologically feasible explanation for the falsely predicted absence of vervet monkeys in this, otherwise arid, region.

All in all the three tests presented here, have offered at least some qualitative support for the accuracy and biological validity of the time budget model. Substantial material for further discussion, however, was also generated.

7.5 Discussion

A time budget model was developed to predict the maximum ecologically tolerable group size and associated geographical distribution of vervet monkeys over sub-Saharan Africa. Similar models have routinely been constructed for other primate species (Chapter 1) and in this respect the current chapter can be viewed as part of a new series of models that has recently been developed (Korstjens *et al.*, 2006; Korstjens and Dunbar, 2007; Korstjens *et al.*, submitted; Lehmann *et al.*, 2007a, b). The main aim of the current study, however, was to adopt an innovative approach whilst critically assessing model performance and validity.

Encouraged by findings from preceding chapters on the usefulness of the NDVI, a first innovation attempted here was to incorporate direct measures of primary productivity into the best-fit equations that lie at the heart of the time budget model. Typically, time budget models have almost exclusively represented the local environment in terms of climatic conditions. Primary productivity, however, is an important intermediate level in the causal cascade linking climate to primate group size (Figure 1.3) and its successful implementation into the model developed here, offers a more direct and intuitive representation of this key component in models of primate socio-ecology. The biological relevance of this was exemplified by the finding that both local feeding and moving time demands were strongly determined by the annual minimum NDVI value (Table 7.3). Thereby, primary productivity appears to be a pivotal environmental condition in defining the potential range of distribution of vervet monkeys. This was visualised in Figure 7.2 that showed unsustainably high feeding time demands over the deserts in southern Africa and north-western Ethiopia, as well as in the tropical rainforests of the Congo basin and West Africa. High moving time demands limited the biogeographical range of vervet monkeys most notably throughout the Sahel in the north, the Namib and Kalahari deserts in the south-west, and the Congo basin in central Africa. Through its strong association to feeding time, moreover, primary productivity was also a key determinant of the maximum ecologically tolerable group size of vervet monkeys (Equation 1). Vervet monkeys then, are clearly constrained to habitats of intermediate productivity: deserts are unsuitably poor, whereas tropical rainforests are unsuitably rich. The cause for rainforests being unsuitable vervet habitat requires further investigation, but it may very well be that other constraints than time allocation (such as a lack of morphological adaptations required for an arboreal life style or competition from closely related forest specialists) are involved here as well. Rainfall and rainfall seasonality, were other key factors in the socio-ecology of vervet monkey, albeit to an arguably lesser extent and possibly only indirectly, through their effect on local productivity (Chapter 3).

A second important innovation effectuated here, was the integration of the time budget model into a GIS. The GIS offers an ideal modelling environment for inter-populational studies and greatly facilitated visual representation and analysis of key model components and predictions over the entire area of interest. It also holds the promise of an extremely powerful set of spatial statistics, although sample size in the current exercise (as may indeed be true for most inter-populational studies on primate behavioural ecology) was too small to take advantage of this.

Model validation revealed that vervet monkey presence was correctly predicted at over two-thirds of sites of known occurrence and that predicted maximum ecologically tolerable group sizes were significantly larger than observed group sizes. The predicted potential geographical range, lastly, was in strong agreement with the known extent of occurrence. Conversely however, absence was falsely predicted at close to one-third of sites of known occurrence and 6 out of 37 populations for which group size was known proved model predictions wrong. The biological explanations that were subsequently sought for this, all identified the highly adaptable nature of vervet monkeys as the most likely factor limiting model performance. The remarkable behavioural flexibility that allows vervet monkeys to thrive under disturbed ecological conditions may very well be the main reason for their near pan sub-Saharan African distribution. It, however, may also entail a potential problem for inter-populational analyses. Given the vast behavioural flexibility over an extensive geographical range, the mere concept of a single set of global best-fit equations able to express local time allocation demands in terms of local environmental conditions may be misguided. Biologically it is highly unlikely that the behavioural repertoire of a species can be expressed by deterministic rules with global validity. Instead, animals with such an extensive geographical distribution as vervet monkeys, are likely to pursue very different, but always locally adaptive, behavioural strategies to maximise inclusive fitness. The relationships tying local time allocation demands and group size to the local environment, in other words, may thus vary considerably over space and, hence, between populations (see also Section 5.5). This phenomenon of spatially varying relationships is known as spatial heterogeneity (Fotheringham *et al.*, 2000, 2002). One of its many implications is that it renders standard (*i.e.* global) statistical procedures, upon which the time budget model relies, incomplete at best. It is thus expressed that future inter-populational models stand a lot to gain from implementing more suitable statistical procedures (*e.g.* Geographically Weighted Regression; Fotheringham *et al.*, 2002) that, moreover, do more justice to the remarkable flexibility of the socio-ecological systems of primates in general. Unfortunately, data on a species and genus level are typically too few to benefit from these spatially explicit techniques and in that sense, the time may now have arrived to attempt an integration of findings on all separate species (Section 1.1.2) into one coherent framework for general primate socio-ecology.

8 Discussion

This thesis aimed to present an in depth investigation of several key aspects of the socio-ecology of vervet monkeys. It has attempted to do so by presenting findings on a new study population and through the development of an inter-populational model of group size, based on an extensive review of previous research on the species throughout its natural range. Prominent throughout this endeavour has been the exploration of new methodologies to assess their potential to further our understanding of vervet monkey socio-ecology in particular, and that of primates in general. Before synthesising the main findings into some concluding remarks and formulating potentially interesting future directives, a concise synopsis of the main results of each chapter is presented.

8.1 Summary of main results

Starting at the top of the causal cascade underpinning primate socio-ecology (Figure 1.3), Chapter 3 developed extensive spatial datasets for climatic variables and primary productivity over sub-Saharan Africa. It used these data to assess the association between climatic conditions and primary productivity at two, for ecologists highly relevant, spatio-temporal resolutions. On a sub-continental and annual scale, three different levels of aggregation (local, ecoregion and biome) indicated that primary productivity displayed a strong quadratic association to rainfall, a linear association to rainfall seasonality and no association to temperature. On a regional and monthly scale, primary productivity over the ecogeographical region of the study population showed a year-round positive linear association to monthly rainfall and a negative linear association to temperature at the onset of the warm-wet season. The aim of these analyses was not so much to investigate the phyto-physiological mechanisms underlying these relationships, but rather to illustrate the applicability and information content of the compiled datasets. Not only did this validate the biological significance of the NDVI as a remotely sensed index of primary productivity, but it also illuminated the importance of incorporating the implicit spatial character of ecological data into statistical analyses. These proved valuable lessons throughout the remainder of the thesis that may not always have received the attention they deserve in primatological studies.

Following up on this, Chapter 4 assessed the relationship between the NDVI and field observations on phenology and food availability within the home range of the study group. In addition, a geographical information system (GIS) was used in consort with hyper-spatial satellite imagery and extensive ground surveys to construct highly accurate vegetation maps. Possibly the most significant result of the analyses conducted in this chapter was the highly significant quadratic association between field estimates of monthly food availability and remotely sensed primary productivity. The NDVI was moreover successfully implemented into a simple spline-algorithm to model habitat-specific monthly food availability. This model generated biologically valid estimates that offered several analytical advantages over the more standard estimates of food availability as obtained solely from the field. Modelled food availability was consequently used throughout the later chapters to investigate spatio-temporal associations between food availability and the behaviour of the study group.

Chapter 5 investigated temporal and spatial variation in local range use in relation to group size and key environmental factors such as climatic conditions, primary productivity, resource availability and perceived predation risk. Where appropriate, a GIS was used to gain an unprecedented insight into how these variables affected the ranging behaviour of the study group over space and time. The NDVI was found to be a strong predictor of temporal variation in day journey length and level of terrestriality, both directly as a measure of primary productivity, and indirectly as a measure of local food availability. The use of probabilistic techniques to estimate range use intensity and perceived predation risk (in a novel approach to quantify 'landscapes of fear'; Laundre *et al.*, 2001) was found to be particularly useful. Combined with spatial data on food availability and distance to surface water and sleeping trees, these probabilistic measures enabled the assessment of the combined effects of predation risk and access to resources within a single quantitative model of range use. An interesting potential complication with regard to inter-populational studies was briefly highlighted by drawing attention to how associations between range use and environmental conditions differed between vervet populations (*i.e.* spatial heterogeneity; Fotheringham *et al.*, 2000, 2002).

As a prelude to the inter-populational time budget model of vervet monkey group size, Chapter 6 looked at activity patterns of the study group. Marked age-sex class differences were found and diurnal and monthly variation in time allocation could be established. Diurnal and monthly patterns in activity were subsequently related to environmental and demographic conditions. In doing so, the importance of correcting monthly analyses for variation in day length was emphasised. The NDVI featured prominently in best-fit equations that expressed the monthly amount of time spent feeding and moving as functions of local environmental conditions. In addition, an in depth analysis of functional aspects of the different time budget components was undertaken. This revealed some interesting disparities between the ecological factors driving time allocation by adult males and females. Whereas males were found to be more vigilant and mobile, time allocation by females was mainly driven by nutrient acquisition. This confirmed expectations from the general model of primate socio-ecology (Chapter 1). Lastly, an approximate value for enforced resting time, a crucial parameter in the inter-populational time budget model of group size, was derived.

Following three chapters that focussed on aspects of the local socio-ecology of the study group, Chapter 7 zoomed out again to the pan sub-Saharan scale of Chapter 3 to integrate all previous findings into an inter-populational systems model of vervet monkey group size. Information on aspects of the socio-ecology that were investigated in the study population, was now collated for populations throughout the natural range of the species. Best-fit equations were constructed to express inter-populational time allocation over the four main time budget components as functions of local environmental and demographic conditions. NDVI over the least productive month of the year was found to be a key environmental predictor of vervet monkey time allocation and group size. By implementing the obtained best-fit equations into a GIS environment, maps of predicted time allocation over the whole of sub-Saharan Africa were obtained. These maps greatly enhanced model interpretation and illustrated how vervet monkeys were constrained in their potential distribution by differential local demands on individual time budget components. Predictions on the maximum ecologically tolerable group size were lastly validated by three tests. The model was found to correctly predict vervet monkey presence at 257 out of 376 sites of known occurrence (68%) and observed group sizes in 37 populations were significantly smaller than the maximum ecologically tolerable group size as predicted by the model. Moreover, the predicted geographical range showed a remarkable similarity to the known extent of occurrence. It was concluded that, although overall model performance was good, spatial heterogeneity in the causal cascade underpinning the socio-ecology of vervet monkeys may have been a confounding factor that deserves serious consideration in future inter-populational studies.

8.2 Concluding remarks

“Essentially, all models are wrong, but some are useful” (Box and Draper, 1987; p. 424). Clearly, the models developed throughout this thesis to help interpret and predict key aspects of vervet monkey socio-ecology, can not possibly do justice to the complexity of the entire socio-ecological matrix shaping the social organisation of the species. Nevertheless, the innovative approach explored here generated some powerful new insights into the mechanisms underlying range use, time allocation, group size and the biogeography of this primate species. Moreover, the potential scope of the techniques and methodologies employed here, is far from limited to current investigations. In particular, conservation oriented studies may find the use of remotely sensed information within the spatially explicit modelling environment of a geographical information system extremely informative. Other fields of research within primatology that may benefit from adopting these techniques may range from studies on inter-group relationships and predator-prey interactions to investigation into genetic, behavioural and cultural diversity in relation to the local environment. Hopefully, this study may instigate attempts in these directions.

In exploring the usefulness of remote sensing and geographical information systems in the construction of a systems model for vervet monkey socio-ecology, this study has worked its way up from local investigations on a study population, to an inter-populational level to make predictions on an entire species. Perhaps a tentative parallel may be drawn to direct future modelling efforts. Numerous models have been developed over the last 15 years and perhaps it is now possible to integrate these findings on the species level into an 'inter-species' systems model for group size of the entire primate order. Undoubtedly, many complications will arise in this enterprise, but perhaps this study will have contributed to overcome some of these. In the light of the greater research project of which this PhD is part, a general primate model would be an interesting starting point for investigations into the socio-ecology and evolution of our own species.

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Appendix

Tabular summaries of calculated model diagnostics are presented for each of the multiple regression models developed in Section 7.3.1. Reported residual and difference (DF) statistics are standardised values and highlighted numbers indicate cases that required further biological and/or statistical investigation.

Feeding (%) $= -78.76 + 130.60\ P_{Shannon} - 104.32\ NDVI_{min} + 0.96\ T_{sd} + 0.03\ P_{annual}$

Site	Case Number	Residual	Cook's Distance	CLV	DF fit	DF β Intercept	DF β NDVI $_{min}$	DF β P $_{Shan}$	DF β T $_{sd}$	DF β P $_{annual}$
1 Amboseli	2	1.331		0.222						
2 Amboseli	3	-0.471		0.222						
3 Amboseli	4	-0.020		0.222						
4 Amboseli	5	-0.471		0.222						
5 Amboseli	6	-0.621		0.222						
6 Amboseli	7	0.280		0.222						
7 Badi	24	-0.510	0.038	0.254	-0.420	-0.250	-0.199	0.341	0.007	-0.058
8 Bandiala	25	-1.430	0.630	0.379	-2.280	-1.392	0.235	1.227	0.741	-0.542
9 Blydeberg	26	-1.018	0.293	0.365	-1.292	0.686	0.253	-0.541	-1.014	-0.119
10 Bole Valley	27	0.685	0.026	0.105	0.347	0.081	0.026	-0.117	-0.077	0.141
11 Entebbe	32	0.133	0.008	0.447	0.190	0.034	0.110	-0.050	-0.082	-0.017
12 Kalamaloue	36	0.145		0.184						
13 Kalamaloue	37	1.647		0.184						
14 Lajuma	40	-0.415	0.018	0.199	-0.286	0.179	0.103	-0.127	-0.235	-0.115
15 N'Dioum	49	1.017	0.274	0.353	1.245	0.628	0.234	-0.368	0.001	-0.631
16 Old Oyo	50	0.968	0.818	0.546	2.278	-1.228	-1.752	0.946	0.936	1.960
17 Samburu, Isiolo	55	-0.125		0.194						
18 Samburu, Isiolo	56	-0.103		0.194						
19 Segera, Laikipia	57	-0.408	0.073	0.439	-0.579	-0.088	-0.119	-0.155	0.386	0.387
20 Windy Ridge	64	0.190	0.008	0.313	0.183	-0.034	0.095	-0.002	0.038	-0.024
N $_{weighted}$		13	10	13	10	10	10	10	10	10

Moving (%) $= 10.22 + 0.76$ Leaves

Site	Case Number	Residual	Cook's Distance	CLV	DF fit	DF β Intercept	DF β Leaves
1 Blydeberg	26	0.658	0.175	0.203	0.568	0.567	-0.435
2 Bole Valley	27	0.782	0.070	0.018	0.361	0.110	0.121
3 Kalamaloue	36	-0.255		0.005			
4 Kalamaloue	37	0.158		0.038			
5 Lajuma	40	0.069	0.000	0.000	0.027	0.017	-0.001
6 N'Dioum	49	0.445	0.846	0.569	1.252	-0.553	1.119
7 Samburu, Isiolo	55	-2.222		0.005			
8 Samburu, Isiolo	56	-1.574		0.003			
9 Segera, Laikipia	57	-0.008	0.000	0.185	-0.006	-0.006	0.004
N $_{weighted}$		7	5	7	5	5	5

Social (%) = -24.86 + 1.87 P>2T + 1.65 $T_{\text{daily range}}$ + 2.09 Photoperiod $_{\text{range}}$

Site	Case Number	Residual	Cook's Distance	CLV	DF fit	DF β Intercept	DF β P>2T	DF β $T_{\text{daily range}}$	DF β $\text{Photoperiod}_{\text{range}}$
1 Amboseli	2	1.939		0.180					
2 Amboseli	3	2.767		0.180					
3 Amboseli	4	0.696		0.180					
4 Amboseli	5	1.110		0.180					
5 Amboseli	6	1.318		0.180					
6 Amboseli	7	0.282		0.180					
7 Badi	24	0.796	0.019	0.021	0.271	0.097	-0.124	-0.054	-0.009
8 Bandiala	25	0.333	0.011	0.162	0.203	0.163	-0.150	-0.140	-0.011
9 Blydeberg	26	1.456	0.981	0.410	2.540	-1.931	1.155	1.855	1.576
10 Bole Valley	27	-1.356	0.116	0.095	-0.738	0.410	-0.435	-0.452	0.151
11 Entebbe	32	0.112	0.005	0.382	0.132	0.015	0.070	-0.019	-0.072
12 Kalamaloue	37	-0.038	0.000	0.238	-0.030	-0.005	0.021	-0.002	0.002
13 Lajuma	40	-1.017	0.080	0.122	-0.578	-0.116	0.102	0.137	-0.413
14 Mt. Assirik	46	-0.199	0.002	0.041	-0.073	-0.043	0.041	0.033	0.006
15 N'Dioum	49	-0.462	0.027	0.191	-0.313	0.040	0.153	-0.096	-0.066
16 Old Oyo	50	-0.658	0.031	0.110	-0.340	-0.258	0.094	0.238	0.123
17 Segera, Laikipia	57	-0.256	0.041	0.462	-0.387	0.248	-0.202	-0.286	0.175
18 Windy Ridge	64	-0.062	0.006	0.586	-0.141	-0.003	-0.061	0.030	-0.094
N_{weighted}		13	12	13	12	12	12	12	12

Resting (%) = 84.60 - 1.24 Feeding - 0.52 Group size

Site	Case Number	Residual	Cook's Distance	CLV	DF fit	DF β Intercept	DF β Feeding	DF β Group size
1 Amboseli	2	-0.441		0.165				
2 Amboseli	3	-0.895		0.194				
3 Amboseli	4	0.817		0.173				
4 Amboseli	5	0.069		0.278				
5 Amboseli	6	0.137		0.237				
6 Amboseli	7	0.955		0.282				
7 Badi	24	-0.861	0.239	0.293	-0.857	-0.835	0.577	0.531
8 Bandiala	25	1.014	0.494	0.361	1.287	0.303	-0.917	0.640
9 Blydeberg	26	0.305	0.022	0.242	0.245	-0.170	0.140	0.168
10 Bole Valley	27	-1.287	0.065	0.012	-0.465	-0.263	0.061	0.160
11 Entebbe	32	0.234	0.003	0.054	0.095	0.066	-0.059	-0.012
12 Kalamaloue	37	1.373	0.078	0.017	0.520	0.322	-0.102	-0.194
13 Lajuma	40	0.582	0.034	0.113	0.310	-0.030	0.215	-0.079
14 N'Dioum	49	-0.844	0.305	0.342	-0.971	0.459	0.018	-0.867
15 Old Oyo	50	0.180	0.011	0.303	0.172	-0.071	0.152	-0.006
16 Segera, Laikipia	57	0.520	0.013	0.033	0.192	0.141	-0.079	-0.070
17 Windy Ridge	64	-1.324	0.065	0.008	-0.469	0.007	-0.129	-0.065
N_{weighted}		12	11	12	11	11	11	11

Leaves (%) = 51.74 -111.96 $NDVI_{min}$ + 0.81 $P_{driest\ month}$

Site	Case Number	Residual	Cook's Distance	CLV	DF fit	DF β Intercept	DF β $NDVI_{min}$	DF β $P_{driest\ month}$
1 Amboseli	10	-1.222		0.075				
2 Amboseli	11	0.761		0.075				
3 Amboseli	21	0.481		0.075				
4 Blydeberg	26	-0.809	0.032	0.037	-0.305	0.071	-0.155	0.097
5 Bole Valley	27	1.318	0.104	0.058	0.593	-0.241	0.383	-0.107
6 Buffle Noir	28	0.668	0.056	0.148	0.399	-0.184	0.283	-0.188
7 Diani Beach Forest	31	-0.063	0.001	0.220	-0.046	0.029	-0.032	-0.020
8 Kalamaloue	36	-0.468		0.088				
9 Kalamaloue	37	-1.372		0.088				
10 Lajuma	40	0.529	0.013	0.035	0.193	-0.061	0.107	-0.021
11 Livingstone	41	0.428	0.009	0.041	0.159	0.081	-0.036	-0.082
12 Lolui Island	42	0.705	3.757	0.734	3.709	1.031	-1.358	3.389
13 Mt. Assirik	46	0.110	0.001	0.060	0.045	-0.006	0.019	-0.024
14 N'Dioum	49	0.635	0.130	0.299	0.613	0.591	-0.514	-0.127
15 Samburu, Isiolo	55	-0.816		0.093				
16 Samburu, Isiolo	56	-0.848		0.093				
17 Segera, Laikipia	58	-2.122		0.113				
18 Segera, Laikipia	59	-1.427		0.113				
$N_{weighted}$		13	9	13	9	9	9	9

Standardised residuals were used to identify outliers at the 95% confidence interval (values > 1.96), whereas the presence of influential cases was assessed by considering Cook's distances (values > 1.0), Centralised Leverage Values (CLV > 2*(1+n predictors/$N_{weighted}$)) and difference statistics (DF > 1.0). Although several cases showed high DF values, on only one occasion this was accompanied by a worryingly high Cook's distance and CLV (best-fit equation for ***Leaves (%)***, Lolui Island). This particular case is discussed in more detail in Section 7.4.2.

In addition to the diagnostics presented above, levels of multicollinearity were assessed by correlation matrices and Variation Inflation Factors. Independence of error terms was controlled for by considering values of the Durban-Watson statistic (1 < D-W statistic < 3).

The author would explicitly like to express that he would not want to ascribe great statistical or inferential value to multiple regression analyses based on the small sample sizes used throughout this thesis. Interestingly though, previous modelling exercises within primatology relying on the time budget approach do not seem to share this reservation.