The feeding and movement ecology of yellow baboons (Papio cynocephalus) in a primate rich habitat: The Issa Valley of Western Tanzania.

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The feeding and movement ecology of yellow baboons (*Papio cynocephalus*) in a primate rich habitat: the Issa valley of western Tanzania

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THESIS SUMMARY

Baboons are a well studied primate, with extensive data from numerous long-term field sites from various ecological contexts across Africa. Underrepresented in this sample, however, are woodland/forest population. In this thesis I investigated the diet and movement ecology in a woodland/forest population of yellow baboons (*Papio cynocephalus*) at the Issa valley of Ugalla, western Tanzania. I begin by describing the diet of Issa baboons using macroscopic faecal analysis. I show they selectively exploited the environment according to the availability of fruits, and unlike for their savannah conspecifics, there appeared to be sufficient food alternatives during periods of low fruit availability. Using day path lengths (DPL) I examined what factors are important in determining movement of baboons at a continental scale. Using a mixed modelling approach with data from 39 baboon troops form sub-Saharan Africa, I show factors to be important on a continental scale include plant productivity, anthropogenic influence, primate richness and group size. Next, I explored the movement ecology of baboons at a local scale in two ways, using baboons at Issa. First I examined the DPL and Path Trajectories (PTs: speed and tortuosity) where I find they moved slower and over shorter distances on warmer days, and slower and more directly when fruit was more abundant. Second I examined patterns of space use within their home ranges (HR). I find sleep site availability and habitat type significantly influence movement within HRs and that the forest habitat is avoided whilst rocky outcrops are preferred. Additionally, I find PTs were predicted by habitat type, with baboons moving faster and straighter through habitats they tended to avoid. Finally, I explored the potential for competition between baboons at Issa with sympatric chimpanzees (Pan troglodytes) by comparing their diet and patterns of habitat use. I show that despite periods of high overlap in fruits consumed, competition between these primates is unlikely to be important due to key dietary differences and differential utilisation of habitat types.

DECLARATION

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

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STATEMENT 1

This thesis is the result of my own investigations, except where otherwise stated. Where correction services have been used, the extent and nature of the correction is clearly marked in a footnote(s).

Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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Statement of contributions

C. Johnson (CJ) analysed all data and wrote all the thesis with guidance from Andrew King (AK). In Chapter 3 and 6, all faecals were collected by CJ and Field Assistants (FA). In Chapters 4, 5 and 6, GPS data on baboons were collected by CJ and FA's. The content of Chapters 3, 4, 5 and 6 were critically revised by AK, Fiona Stewart and Alex Piel. Chapter 6 was also critically revised by Adriana Hernandez-Aguilar. All chimpanzee, climate, and phenology data were contributed by the Ugalla Primate Project.

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Chapter 1 - Introduction

General Background

Measuring and describing animal movement

All animals have to successfully navigate their environment in search of food, shelter, and mates if they are to survive and reproduce. An understanding of animal space use and the resources therein is therefore crucial to almost every aspect of a species' biology and their conservation (Douglas-Hamilton et al. 2005; Gillies et al. 2007). This requires that biologists are able to track individuals' movements in space as well as through time.

In the early years of animal tracking, the plotting of animal movements was restricted to following the animal, taking a bearing and plotting this on a map (e.g. Blair 1940). In the early 1960's our ability to understand wild animals was revolutionised by the introduction of radio telemetry, which used VHF radio waves to track animals through their natural habitat (Cochran & Lord 1963). Researchers could use these VHF radio waves, transmitted from a collar on the animal, to triangulate its position. This was a cost effective and accurate method but labour intensive. In the 1970's, Buechner (1971) introduced satellite telemetry to animal tracking that allowed researchers to track animals over long distances and in remote areas. Whilst drastically reducing labour intensity, satellite telemetry is expensive (Mech & Barber 2002) and less accurate than Global Positioning Systems (GPS) (Keating et al. 1991) which were developed in 1973 by the United States Department of Defence for military purposes. By the early 1990s GPS devices became available for use in animal tracking, and this tool has revolutionised the study of animal movement and space use: GPS devices can be attached directly onto the animal via a collar or harness (Moen et al. 1996; Li et al. 2000), or carried by the researcher following the animal (Schreier & Grove 2010; Volampeno et al. 2011; Hoffman & O'Riain 2012). This provides high-quality movement data.

Dealing with GPS data has become a field of study of its own. Knowing the location of an animal is just a stepping-stone to understanding the social and ecological factors that determine its movements and the specific tactics it employs to optimise them. A current method that is advancing in describing the animal movements is the use of random walk models (Viswanathan & Afanasyev 1996; Ramos-Fernández & Mateos 2004; Levandowsky et al. 1997), originally borrowed from statistical physics (Patlak 1953). These random walk models assume the movements of animals are comparable to that of particles – i.e. Brownian motion, first described by Robert Brown (1828) – and has been used to describe movement phenomena across disciplines including physics, geology, and ecology.

To understand what can be inferred from these models, a brief description of their mechanisms and historical development is useful. Models of animal movement based on random walks (RW) assume that the direction of an individual is independent of the previous directions in which it moved (uncorrelated) and there is no preferred direction (unbiased) (Codling et al. 2008) (Figure 1.1). These assumptions, however, can prove problematic when applying the models to real animal movement data, since the models do not account for the directional insistence typically observed in their movement (Bartumeus et al. 2005). Correlated random walks (CRWs) compensate for this by incorporating a correlation between sequential step directions. Thus each step inclines towards the same direction as the previous, termed 'persistence' (Patlak 1953).

The application of animal movement models at larger spatial and temporal scales resulted in the development of a random walk model called the Levy walk (LW) (Viswanathan & Afanasyev 1996). LWs are characterised by many small steps joined by rare long steps resulting in step lengths that are not constant but instead are chosen from a probability distribution that is heavy-tailed (Viswanathan & Afanasyev 1996). This signature of movement is predicted to improve efficiency in random search scenarios (Viswanathan et al. 1999). In fact, researchers have gone so far as to suggest a potential convergent evolution of the LW search strategy expected to be found in almost all species (Viswanathan et al. 1999; Viswanathan & Afanasyev 1996; Viswanathan et al. 2008).

The ubiquity of LW search strategies has, however, been questioned by recent research. For example, a recent study on chacma baboons (*Papio ursinus*) has demonstrated that they do not use LW but rather they use a Brownian process which is thought to occur as a consequence of resources being abundant and homogeneously distributed (Sueur 2011). Such studies have broadened our understanding of random walks by forcing us to consider them in an environmental context, with work investigating the movement patterns of marine predators leading the way. For instance, movement patterns of yellowfin tuna (*Thunnus albacares*) and basking sharks (*Cetorhinus maximus*) have been shown to be a reflection of their prey distribution (Humphries et al. 2010). Animal movements are likely, therefore, to be flexible and determined by the habitat and resources they are exploiting (Sueur 2011; Sims et al. 2008; Bartumeus et al. 2002). Accordingly, when studying the movements of an individual fish, bird, or primate, this individual animal can be expected to adopt a LW-like movement in a heterogeneous environment (where resources are sparse and unpredictably distributed), and a Brownian-like movement in a homogenous environment (where resources are evenly distributed) (Sueur 2011). A number of recent studies have correspondingly demonstrated animals switching between LW and Brownian motion to suite resource abundance temporally (Humphries et al. 2010). Thus, such models of animal movements are perhaps less indicative of the "search strategies" or "decision rules" applied by the animal and more indicative of the spatial and temporal distribution of resources within the environment. Consequently, in this thesis, I do not adopt a model-fitting exercise to describe the distribution of step-lengths or turning angles an individual or group makes, but instead assume that animals search their environment in the most efficient way possible (Schoener 1971).

GPS data can be organised temporally in order to provide an indication of patterns of space over different time periods. GPS data over 24 hours can provide an estimate of day path length (DPL), and or over longer periods an indication of home range (HR) use and home range size (HRS). Being able to calculate such measures in wild animals is essential to the understanding of their behaviour, life history, ecology and therefore population dynamics (Rubenstein & Hobson 2004). These two major levels at which we quantify and study animal space use: DPL and HRS are dynamic, emergent patterns of space use (Fieberg & Börger 2012) that are influenced by the availability of environmental resources, climate, habitat quality and potential mate distribution

(Volampeno et al. 2011). Consequently, DPL and HRS offer the potential to indicate resource and behavioural requirements of animals relative to their abundance and distribution in the environment (Perry & Garland 2002). As a result, much emphasis has been placed on understanding the factors capable of predicting DPL and HRS.

What determines how far animals go (day path length)?

Many factors can determine an animal's space requirements, but one of the most important is dietary needs (Garland 1983). Animals search their environment in their daily efforts to fulfil their requirements of essential resources. These resources can be numerous and specific to the species, but one resource required by all animals is energy, which is typically obtained through the consumption of foods. Foods are rarely confined to a single location; instead they are distributed in their availability across the environment. Most animals must, therefore, search their environment in order to locate and consume sufficient foods in order to sate their dietary requirements. Subsequently, an animal's search strategy should therefore be one that is efficient in minimising the energy expended, and maximising energy intake when searching its environment (Schoener 1971), whilst simultaneously avoiding predation (Cowlishaw 1997b).

Energy supply rates, that is the energy an individual gains over the distance it moves (per km^{-2}), decreases significantly between trophic groups (Jetz et al. 2004). Using a comparative analysis across species, Carbone (2004) demonstrated that DPL increases progressively with dietary requirements: Herbivores have the lowest DPL, carnivores have the highest DPL, and frugivores have an intermediate DPL for a given body mass and group size (Figure 1.1). This comparative approach, exploring DPL across taxa, also revealed a suite of other factors that predict DPL, but almost all of which are directly or indirectly linked to diet and energy intake. First, as the mass of an individual increases, so do its energy requirements, thus necessitating a higher food intake (Garland 1983). DPL is therefore seen to increase with body mass (Carbone et al. 2005) (Figure 1.1). Second, seasonal variation in climate and day length can also impact on DPL since these factors will be linked to productivity of the environment, and thus the availability of food (van Schaik et al. 1993). Longer days for diurnal animals also provide a larger time frame in which to forage, often leading to a positive relationship between day length and DPL (Baoping et al. 2009; Gerber et al. 2012). Third, as group size increases, so does the total mass of the group and consequently the total energy requirement. As such, it has been predicted that as group size increases, daily travel distances will increase in the search for the food to satisfy the increased nutritional requirements (Clutton-Brock & Harvey 1979). Additionally, the aforementioned relationships can be less clear-cut when the diet of certain taxonomic groups are considered e.g. carnivores (Carbone et al. 2005), and frugivorous primates (Clutton-Brock & Harvey 1979) (Figure 1.1). Carnivores must travel further in order to encompass sufficient prey with which to support themselves, since energy is lost in the transition between trophic levels (McNab 1963). Similarly, the fruits on which frugivorous primates depend often have a patchy distribution compared to the homogeneous and abundant supply of leaves for primate foliage eaters necessitating increased travel distances (Milton & May 1976). Finally, human disturbance can also significantly impact DPL. For example, chacma baboons, *Papio ursinus* living in human altered habitats have reduced DPLs due to high availability of high quality, human foods in the form of either garbage or crops (Hoffman & O'Riain 2012).

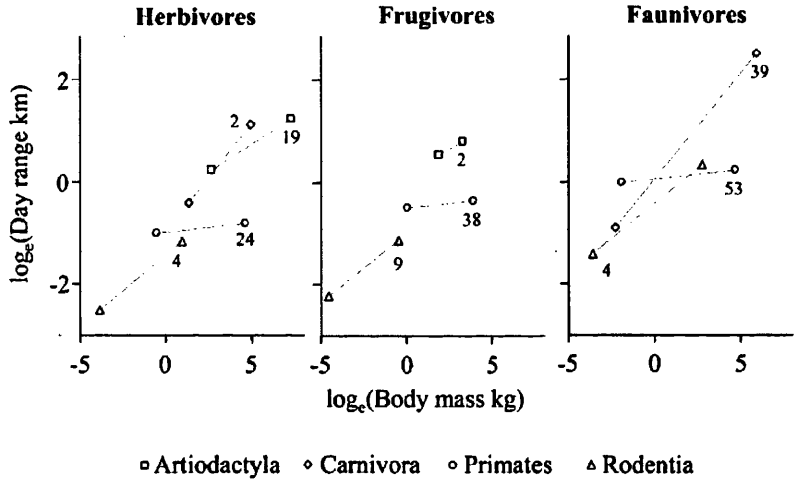

Figure 1.1. Figure taken from Figure 2 of Carbone et al. 2004 showing the slopes of day range length in relation to body mass according to diet and order. Numbers refer to the numbers of species in each group and line coverage illustrates the extreme body mass values in each group.

What determines the space animals use (home range selection and size)?

Measuring an animal's DPL as described above offers a simple, short-term measure of animal space use, which we can use as a building block to understand strategies of resource acquisition as scale-dependent selection behaviours. That is, a selection of habitats or areas within a HR and this HR within the broader landscape (Johnson & Prairie 1980). Charles Darwin (1861) noted that animals rarely wander needlessly; instead they confine their movements to specific HRs. Home ranges have subsequently been defined as "the area occupied by an adult animal in its search of food and mates and caring for offspring but does not include seasonal migrations or occasional sallies outside the usual area" (Burt 1943).

Interspecific variation in HRS can be immense, some are small, $< 0.01\text{km}^2$ for chipmunks (*Tamias striatus,* Mares et al. 1980), some are very large, 1000s of km^2 for polar bears (*Ursinus maritimus,* Amstrup et al. 2011). Intraspecific variation in HRS is also common (Irwin 2008; Alt et al. 1976). Interspecific variance is much more easily explained due to the many morphological/physiological differences/requirements across species, but the reasons behind the observed variance between two individuals/groups of the same species is often much less obvious and the factors responsible are of significant ecological relevance (Morales et al. 2010).

Not to be confused with HR is the concept of a territory. These are two distinct patterns of space use that must be distinguished. As already defined, a HR is the area traversed in an animal's typical behaviours. A territory is the area within a HR that an animal will actively defend and protect by fighting or using threatening gestures (Burt 1943). For an area to be a territory it must have the following characteristics: (1) be a fixed area, (2) be defendable via actual territorial defence and/or warning signals that cause avoidance responses in competitors, and (3) be exclusively used by territory holder (Brown & Orians 1970; Börger et al. 2008). Therefore, HR estimates incorporate all available location data, whereas territory estimation only includes defensive acts and the location of neighbouring competitors to delineate an area of exclusive use (Burt 1943; Brown & Orians 1970; Moorcroft et al. 2006).

As with studies of DPL, studies of HRS have reported relationships between HRS and the individual characteristics of the animal, and characteristics of the environment in which that animal lives. These may include rainfall, temperature, food abundance and availability, mate distribution, intra and inter-specific competition and predation, all of which can be linked to HRS and stability quality (Isbell 1983; Volampeno et al. 2011; Watts 1998). For example, as discussed already with respect to DPL, bigger animals (i.e. body mass) and more social individuals (i.e. larger social group size) have larger HRS. This is likely due to the energy requirements of the animals whereby the larger animals require more food and therefore have larger areas for foraging (Mace et al. 1983; Mysterud et al. 2001). For the same reasons, in social animals, the larger the group the greater the combined metabolic demands and therefore the larger the HRS needs to be to encompass enough food (Clutton-Brock & Harvey 1979), and carnivores will require much larger HRS to sustain themselves than would herbivores (McNab 1963) since energy is lost as it flows up the trophic levels (with up to 90% loss with each successive step: Perry & Garland 2002). However, the single most crucial factor determining HR is the distribution and availability of food. Therefore, anything, which affects the productivity and location of these foods, will inadvertently influence the HR of the animal. A prominent example of which, is seasonal variation in climate. Many animals search their environment seasonally, responding to intra-annual variations in climate. These animals often have to migrate between two or more geographically distinct regions of the world as their habitats become too hot, too cold, or too dry and food availability varies. Classic examples of this are the Caribou (*Rangifer tarandus*) migrations of North America that cover distances of 5,000 km a year in their search for seasonally dependant food sources (Fancy & Pank 1989). More extreme examples include birds like the Arctic tern (*Sterna paradisaea*) that annually migrates between the poles completing a round trip distance of 71,000 km (Egevang & Stenhouse 2010).

The role of competition and risk to animal movement

Above, I introduced how far animals go, and the space they used largely with respect to finding food to eat. But, animals exist in communities, which means they might be prey for other predatory species, and/or have to compete with species with similar ecological requirements. Therefore, in the wake of recent biodiversity crises (McLellan et al. 2014) and climate change (Stocker et al. 2013), a more comprehensive understanding of the role of the structure and function of ecological communities upon species movement ecology is essential.

Communities are a collection of organisms that coexist within a particular habitat together, the structure of which is defined by causal processes such as interspecific competition (Schoener 1983; Alatalo et al. 1986; Roughgarden 1983). Interspecific competition occurs between species that overlap in their resource requirements to the extent the use of a resource by one species reduces its availability for another (Ricklefs & Miller 1999). Accordingly, the presence of a superior competitor can potentially limit the distribution and abundance of a weaker competitor (Webster et al. 2012; Durant 2000). Thus, for two potentially competing species to exist sympatrically, a mode of coexistence is essential. Modes of coexistence are predominantly referred to in terms of niche separation, whereby species with similar requirements coexist via the differential utilisation of three primary niche components: habitat, food type, and activity time (Schoener 1974). Examples of niche separation have been demonstrated in many taxa, for example, African wild dogs (*Lycaon pictus*) exhibit dissimilar spatiotemporal activity patterns to dominant sympatric competitors, including lions (*Panthera leo*) and spotted hyena (*Crocuta crocuta*), without which the African wild dogs would be competitively excluded (Creel & Creel 2002). Spatial data on the movements of sympatric animals are therefore useful in identifying modes of coexistence, and ultimately to build towards a comprehensive understanding of the local community structure, which may allow conservation based predictions to be made (e.g. the likelihood of competitive displacement of certain species (Gause 1932), or feasibility of re-introducing species (Bertram & Moltu 1986)).

An unavoidable outcome of existing within a community for animals is the trophic web of predator-prey interactions into which they must fit. The risk of predation for many animals is a serious selective force that induces behavioural adaptations of prey species that seek to minimise the risk. Consequently, the way in which animals use the space within their habitat has been found to be heavily influenced by the presence of predators (Schoener 1971; Mangel & Clark 1986). The mechanism of this influence is often complex, however. The physical presence and distribution of predators is less important in deciding space-use, Instead, it is the perceived risk of predation that has been found to influence animals to use their space in a way that minimises this risk (Lima & Dill 1990; Brown & Kotler 2004; Cresswell 2008; Willems & Hill 2009). Despite being intrinsically linked, predator presence and perceived risk are slightly different. For example, predator density can be high in open habitats, but due to high visibility, the risk of predation is actually low. To minimise risk, though, often requires a trade-off between the acquisition of food and, in addition to other factors, the cost of predation (Brown 1988). The relatively complex issue of reducing the risk of predation can, therefore, manifest itself in a multitude of species-specific behavioural adaptations in the way animals use their space. For example, animals may avoid vegetation types or areas that are perceived to be high risk, or minimise the time spent there if resource acquisition necessitates they be there. Additionally, the use of refuges to reduce predation risk is a pervasive strategy. For example, many animals exploit the use of refuges such as; trees (Dill & Houtman 1989), cliffs (Berger 1991), burrows (Clarke et al. 1993), rock talus' (Holmes 1991), or thick vegetation (Cassini 1991) in order to either improve their detection of predators, reduce their own detection by predators or even to protect them directly from predators.

Moving forward: management strategies and conservation

The study of HRS is implicit in the development of modern management strategies and conservation (i.e. for creating corridors for elephants) (Douglas-Hamilton et al. 2005). By better understanding the space requirements, learned from HR studies, it is possible to define a range of habitats and/or an area of space, which is important to the resident animals. From this, it is possible to assign protection status to the areas that will result in the more effective conservation of an animal (e.g. Yellowstone National Park, Newmark 1985). Contemporary conservation of endangered species relies on the formulation of legal mandates (e.g. Endangered Species Act of 1973, USA), therefore a more comprehensive understanding of the spatial requirements of the individual or population is becoming increasingly important. The spatial requirements of animal behaviour are essential in the preservation of threatened species (Seminoff et al. 2002), and in the management of threats, such as invasive species (Gillies, P J Graham, et al. 2007).

Specific Background

Primates and patterns of space use

This current thesis focuses on the diet (see Chapter 3) and ranging behaviour (see Chapters 4 and 5) of yellow baboons (*Papio cynocephalus*), and how they coexist with other sympatric primate species (see Chapter 6) in the Issa valley of western Tanzania. In this section, I provide a brief review of our understanding of space-use, diet and coexistence in primates and conclude the chapter by outlining the organisation of my thesis and the objective of my chapters.

Assessing variations in space-use allows key influences on primate movement to be identified and may consequently then allow a better understanding of population dynamics (Morales et al. 2010). Consequently, spatial ecology has been a prominent facet of study in primatology since the 1940's (e.g. Carpenter 1940). An obvious, reoccurring theme that has been documented is the extensive intra- and inter-specific variability in the ranging patterns across the order (Clutton-Brock & Harvey 1977a). The factors accountable for the variation in primate ranging behaviours are best understood as elements of resolution. At a coarse level, factors such as dietary preference (i.e. folivory v.s. fruigivory) and ecological niche habitation (e.g. terrestrial or arboreal, diurnal or nocturnal) offer substantial explanation to inter-specific ranging variability when considered with the imposed constraints of each condition. At a finer level ecological factors including the distribution and availability of food (Hemingway & Bynum 2005), surface water (Altmann 1974), sleep sites (Anderson 1998), predation risk (Boinski et al. 2000; Cowlishaw 1997b), and competitive interactions within (Isbell 1983; Goodall 1986; Clutton-Brock & Harvey 1979) and between species (Holenweg et al. 1996) can explain intra-specific ranging variability.

Group size and diet

Primate group size and diet have long been known to influence DPL and HRS in primates (Clutton-Brock & Harvey 1979). Intragroup feeding competition correlates positively with group size (Isbell 1991) especially for frugivorous primates. Fruit is a highly nutritious and highly important food source of many primates, which occurs ephemerally in finite, clumped patches distributed heterogeneously. This forces frugivorous primates to travel between these patches in relation to the availability of fruit within them. Primates with a larger group compete internally for fruits more intensely, thus exhaust patches much faster and forcing the group to expand their range in order to encompass more fruit patches (Isbell 1991; Hoffman & O'Riain 2012; Chapman et al. 1995). Therefore group size is often found as a positive function of HRS in frugivorous primates (Chapman & Chapman 2000). In contrast however, folivorous primates have HRS that are not as readily influenced by group size (e.g. *Brachyteles arachnoides hypoxanthus*: Dias & Strier 2003; *Colobus badius tephrosceles*: Isbell 1983). This is due to leaf-based and herbaceous foods having a homogeneous distribution compared to the clumped and temporally dependant distribution of foods like fruits. Intra-group competition is therefore much less intense and the group need not range further to meet the increased dietary requirements of a larger group.

Food abundance and distribution

Typically, primate ranging patterns are dictated by a compromise between the cost of travelling and the intake of energy. The energy required to move between resources directly impinges on the energy balance of the primate individual, or group and consequently their fitness. As a result, ranging in primates is primarily constrained by the distribution and abundance of food (Clutton-Brock & Harvey 1977b; Isbell 1983; Li et al. 2000).

The presence and distribution of food in habitats is rarely consistent, and in most habitats it varies significantly as a result of temporal fluctuations in rainfall, temperature and day length. These in turn are subject to annual rhythms of seasonal variation (Hemingway & Bynum 2005), greatly affecting the availability of food in the environment and consequently illicit any combination of possible responses in the primates inhabiting them (Gerber et al. 2012). In times of low food abundance primates may respond by either 1) increasing the size of their HR and/or (2) extend their DPL in search of higher quality food items in attempts to maximise energy consumption (van Schaik et al. 1993) or by (3) decreasing the size of their HR and/or (4) reduce their DPL to reduce energy expenditure and therefore the need for more resources (Fan et al. 2008).

Seasonality

The importance of seasonality on primate behaviour and ecology is widely acknowledged by primatologists (White 1998). Food abundance in relation to nutritional requirements has been assessed as seasonally insufficient in many primates (van Schaik et al. 1993). Depleted supplies of food as a result of seasonality (Clutton-

Brock & Harvey 1977a) can result in reduced rates of growth, fecundity, growth and survival in primates (Altmann 1974). Such a large effect of seasonality upon primate ranging is perhaps unsurprising given that phenological monitoring has shown that plant production of consumable resources to vary spatially and temporally in virtually all forests studied (van Schaik et al. 1993; Hemingway & Bynum 2005). Strongly implicated in the phenology patterns of forests are abiotic factors including rainfall patterns, temperature, day length and daily sunlight (van Schaik et al. 1993).

Various responses have been studied with regards to food scarcity as a result of seasonality in vertebrate consumers. Van Shaik et al. (1993), in a seminal review of phenology patterns, recognised seven responses to food scarcity: occasional famine and mass mortality, dietary switching, seasonal breeding, seasonal movements, nomadic behaviour, altitudinal migration, and hibernation. Primates in particular exhibit a remarkable range of behavioural and physiological responses, which fully encompass those seen in vertebrates (Hemingway & Bynum 2005). Decreased food abundance has repeatedly revealed numerous and complex responses in both Old and New World primates, especially with regards to ranging. Primates may adapt their foraging behaviour depending on food abundance. In response to low food availability some taxa reduce their DPL (*Nomascus concolor jingdongensis*: Fan et al. 2008; *Saimiri oerstedi*: Boinski 2008) whereas other taxa extend their DPL and expand their HRS (*Eulemur flavifrons*: Volampeno et al. 2011; *Papio hamadryas ursinus*: Pebsworth et al. 2012). Primates also shift their HRs to encompass areas that contain higher quality food items (Hemingway & Bynum 2005).

Predation risk and refuge availability

The selection of sleeping sites is of vital relevance to the avoidance of predators, especially for diurnal primates, the majority of which demonstrate a propensity for site-relevant considerations (*Presbytis aygula*: Ruhiyat 1983; *Trachypithecus pileatus*: Stanford 1991; *Macaca fuscata*: Takahashi 1997; *Pan paniscus*: Kanō 1992; *Pan troglodytes*: Goodall 1968, Hernandez-Aguilar 2009) and sleeping site fidelity (*Papio cynocephalus*: Rasmussen 1978; *Hylobates klossii*: Tenaza 1975; *Trachypithecus poliocephalus*: Huang et al. 2003). However, having to return to a central place every night poses a constraint that strongly influences the choice of foraging sites (Stephens & Krebs 1986). Therefore primates will move between sleep-sites that are close to resources they want to exploit in order to minimise travel time, increase potential foraging time (e.g. spider monkey, *Ateles geoffroyi*: Chapman et al., 1989) and avoid resource depletion (Chapman 1988).

For similar reasons, “habitat types” in diverse environments are often used preferentially with respect to one or more of the aforementioned ecological factors. For example, dense forest habitats can be both productive (because they have lots of available food items), and dangerous (as a consequence of the ambush hunting tactics that some primate predators employ: e.g. baboons by lion, *Panthera leo* and leopard, *Panthera pardus*: Cowlishaw, 1994). Consequently, primates demonstrate differential exploitation of habitat types in accordance with such trade-offs and select habitats based on food productivity (Stevenson et al. 2000; Albernaz 1997; Hill 1999), and perceived risk of predation (e.g. chacma baboons, *Papio cynocephalus*: Cowlishaw, 1997 a; vervet monkey, *Cercopithecus aethiops*: Willems & Hill, 2013).

Competition and coexistence in primates

Primates frequently exist sympatrically with at least one other primate species, and occasionally with >10 other species. In conjunction with pervasive similarities in the dietary requirements of the taxon (Ganzhorn 1999), primates can offer a constructive perspective from which to consider modes of coexistence. Dietary overlap, niche separation and interspecific competition are all critical issues in explaining patterns of coexistence (Head et al. 2011; Schreier et al. 2009). Due to the similarities in diets between many primate species, it is the limited supply of food that most drives competition between species, particularly in times of low availability (Ganzhorn 1999). Fruit in particular, which comprises a substantial component of the diet in many primate species (Wrangham et al. 1998), invariably undergoes periods of seasonal scarcity (van Schaik et al. 1993). To reduce competition at these times, primates with similar diets must separate their niches by broadening the diversity food species consumed in order to reduce dietary overlap (Tutin et al. 1991; Tutin & Fernandez 1993; Head et al. 2011; Lambert 2002), or simply by dividing the habitat spatially and/or temporally (Schreier et al. 2009). The necessity of coexistence, in the case of many sympatric primate species, can subsequently lead to niche separation within individual forests (Stevenson et al. 2000; Rodman 1973; Terborgh 1984; Ganzhorn 1989) and therefore hugely influence space-use within them.

Thesis Aims

In this thesis, I investigate the diet and patterns of space-use in yellow baboons (*Papio cynocephalus*), and how they coexist with other sympatric primate species in the Issa valley of western Tanzania. Diet and ranging, in baboons, is a well-studied topic of research with extensive data from long-term field sites across Africa. The ranging and dietary behaviour of baboons is particularly well described in populations in savannah environments (e.g. Amboseli: Altmann & Altmann 1970; Post 1978; Gilgil: Harding 1976; Chololo: Barton et al. 1992; Mikui: Rasmussen 1979; Norton et al. 1987), forests (Ransom 1981a; Okecha & Newton-fisher 2006), deserts (Cowlishaw 1997a) and highlands (Swedell 2002; Sigg & Stolba 1981). Under represented in this sample though, are woodland/forest populations such as those found at Issa, Ugalla. These environments are unique in the resources that they offer and the numerous other sympatric primate species they support (Wahungu 1998; Ransom 1981a).

In the following chapters of this thesis, I therefore aim to contribute to our overall understanding of baboon ecology by providing diet and ranging data for non-savannah baboons. This will hopefully prove useful to understanding baboon ecology and how it varies across a more complete multitude of ecological contexts. These chapters each contain introductions and background specific to the aspects of baboon ecology that they address. A summary outline for each chapter is provided below.

This chapter (Chapter 1) has provided an introduction to space-use patterns in animals very generally, and primates specifically. It has highlighted the importance of understanding animal movement with regards to species ecology, population dynamics and conservation.

Chapter 2 will provide specific details of the study site, study subjects and the general methods of data collection and analysis that I have undertaken.

Chapter 3 is the first of four data chapters, and describes the dietary preferences of baboons at Ugalla. I examine the diversity of the diet and how this changes in accordance with the variation of ecological factors at the site.

Chapter 4 tests the hypothesis that ecological factors determine variation in short-term movement patterns in baboons at a continental, and local scale. I test the prediction that DPL will be reduced under conditions in which resources are expected to be plentiful. I then investigate how the DPLs of troops at Issa compare to those from across Africa whilst controlling for an array of *a priori* selected ecological determinants.

Chapter 5 tests the hypothesis that ecological factors determine longer-term variations in patterns of Ugalla baboon space use. To test this hypothesis I explore home range size and characteristics and how these vary seasonally, as well as examining specific patterns of space-use within and between habitat types.

Chapter 6 then explores the potential for Ugalla baboons to be in conflict with the sympatric chimpanzee in this primate-rich environment. With chimpanzee locational data, I test whether baboon movement patterns show evidence of actively avoiding chimpanzee-utilised space in Ugalla. I then determine the overlap in the diet of the two primates to test whether competition for diet could likely explain any observed differences in habitat utilisation between the species.

Chapter 7 provides a summary of my thesis in which I combine and discuss the main findings.

Chapter 2 - General Methods and Study Location

Study Animals

Baboons

There are 79 different species of primate in Africa spread over 19 genera (Grubb et al. 2003). Of these, baboons comprise the genus *Papio*, which includes five generally accepted species: *Papio papio*, *Papio hamadryas*, *Papio anubis*, *Papio ursinus* and *Papio cynocephalus* (Grubb et al. 2003). The *Papio* genus is arguably the most successful in Africa, being the most widespread and commonly found across sub-Saharan Africa (Kingdon 2003) (Figure 2.1). These baboons are large, mostly terrestrial, social primates that are known to exploit a diverse selection of habitat types including scrubland, savannah, forest and woodland. The colonisation of such a diverse array of habitats is likely made possible by their dietary and behavioural flexibility (Swedell 2011; Bronikowski & Altmann 1996). Consequently, baboons are a well-studied genus with descriptions of diet, ecology, social behaviour and ranging existing for a number of long-term study sites across an array of habitat types (Amboseli: Altmann & Altmann 1970; Post 1981; Cape Point: Davidge 1978; Gilgil: R. Harding 1976; De Hoop: Hill 1999; Cape Peninsula: Hoffman & O'Riain 2010; Chololo: Barton 1992; Mikumi: Rasmussen 1979; Okavango: Hamilton et al. 1976; Mt Assirik: Sharman 1981; Tsaobis: Cowlishaw 1997; Suikerbosrand: Anderson 1981) (Figure 2.1).

The diet of baboons largely consists of fruits, flowers, seeds, pods, leaves, gum, and tubers from a variety of plant taxa in addition to any small animal that can be caught (Rowell 1966; Altmann & Altmann 1970; Davidge 1978; Norton, Rhine, et al. 1987; Whiten et al. 1987; Whiten et al. 1991; Altmann 1998; Johnson et al. 2013; Okecha & Newton-fisher 2006; Bentley-Condit 2009; Johnson et al. 2012). As such, they have been attributed with being dietary generalists, eclectic omnivores, and extractive foragers (Altmann 1998), but that also selectively exploit their habitat according to a variety of factors (Norton, Rhine, et al. 1987; Hamilton et al. 1978; Whiten et al. 1991). As a result of this, and the variation in the distribution and abundance of plant foods spatially and temporally (van Schaik et al. 1993), baboons are documented to demonstrate huge dietary flexibility within and between populations (Norton, Rhine, et al. 1987; Whiten et al. 1991).

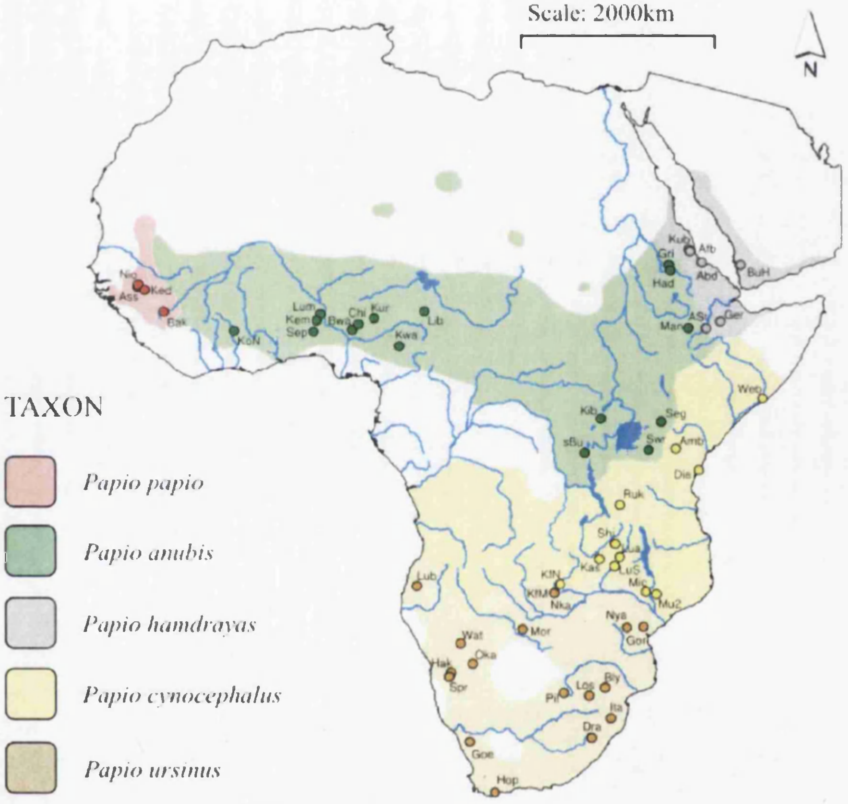

Figure 2.1. Geographical distribution of baboons in Africa. Figure adapted from Figure 2 in Zinner (2009). Baboon study sites are signified by coloured points and an associated three-letter code (please refer to Zinner (2009)).

As with other primates, the ranging behaviour of baboons has been found to respond primarily to intrinsic social factors, and extrinsic variation in biotic and abiotic factors which often arise as a result of the seasonal environments where they exist (Swedell 2011; Dunbar 1992). For example, home range sizes (HRS) and day path lengths (DPLs) of baboons have been shown to correlate positively with group size (Barton 1992; Hoffman & O'Riain 2012; Stacey 1986; Bettridge et al. 2010), and negatively with habitat quality (Dunbar 1992; Barton 1992). More specifically, the availability of food within a habitat and the seasonal fluctuations it undergoes (van Schaik et al. 1993) causes differential patterns of space-use within baboon troops. In response to reduced food availability, baboons tend towards an energy maximising strategy (Gerber et al. 2012) whereby, they expand their HRS and DPL in search of preferred food items (Altmann 1974; Wahungu 2001; Barton 1992; Harding 1976; Pebsworth, MacIntosh, et al. 2012).

In this thesis, I focus on the diet and ranging behaviour of a previously unstudied population of yellow baboons (*Papio cynocephalus*). Yellow baboons are ubiquitous across their geographic range, which extends across central Africa from west to east in Angola, Ethiopia, Kenya, Malawi, Mozambique, Somalia, Tanzania and Zambia (Groves 2001) (Figure 2.1). I continue now by describing the study subjects at the study site and an overview of the primary methodology applied in order to provide context for the ensuing thesis.

The Study Site

The Issa study area (05° 23.34 S 30° 35.04 E) is situated in the Ugalla region of western Tanzania (Hernandez-Aguilar 2006). The region is situated between the village of Uvinza to the North, and the town of Mpanda to the South. Primatological and phenological data have been collected at the Issa study area since it was established in 2001 by Hernandez-Aguilar (Hernandez-Aguilar 2006). From 2003-2005 there was no research presence and since 2008 there has been a permanent presence. The primary research area is an 85km^2 area situated in the western part of the Ugalla region, 81km East of Lake Tanganyika (Figure 2.2). "Ugalla" became known as such following extensive surveys of western Tanzania conducted between 1956 and 1967 by Kano (1972) and while much of the Ugalla region now lies inside the Tongwe East Forest Reserve, Issa itself is situated on 'general land', which gains it no official protection or status.

The Ugalla region has come under increasing pressure from anthropogenic factors in recent years (Stewart 2011). The most pervasive threats, outlined in a conservation action plan for the region, include cattle herding, agriculture, fire, logging, and poaching. Since Ugalla is a forest reserve, not a National Park, it does not have the financial investment associated with that status, and whilst there is no fixed human habitation within the Ugalla region, temporary camps do exist. These act as a base for honey gatherers, loggers, hunters, and people fishing in the rivers. Permits for these activities can be obtained from forestry officials in nearby Mpanda and Uvinza, but during the study period (dates) there were no active patrols by guards to inhibit illegal poaching. As a consequence, permits were rarely obtained, and I regularly observed honey gathering, logging and hunting during the study period.

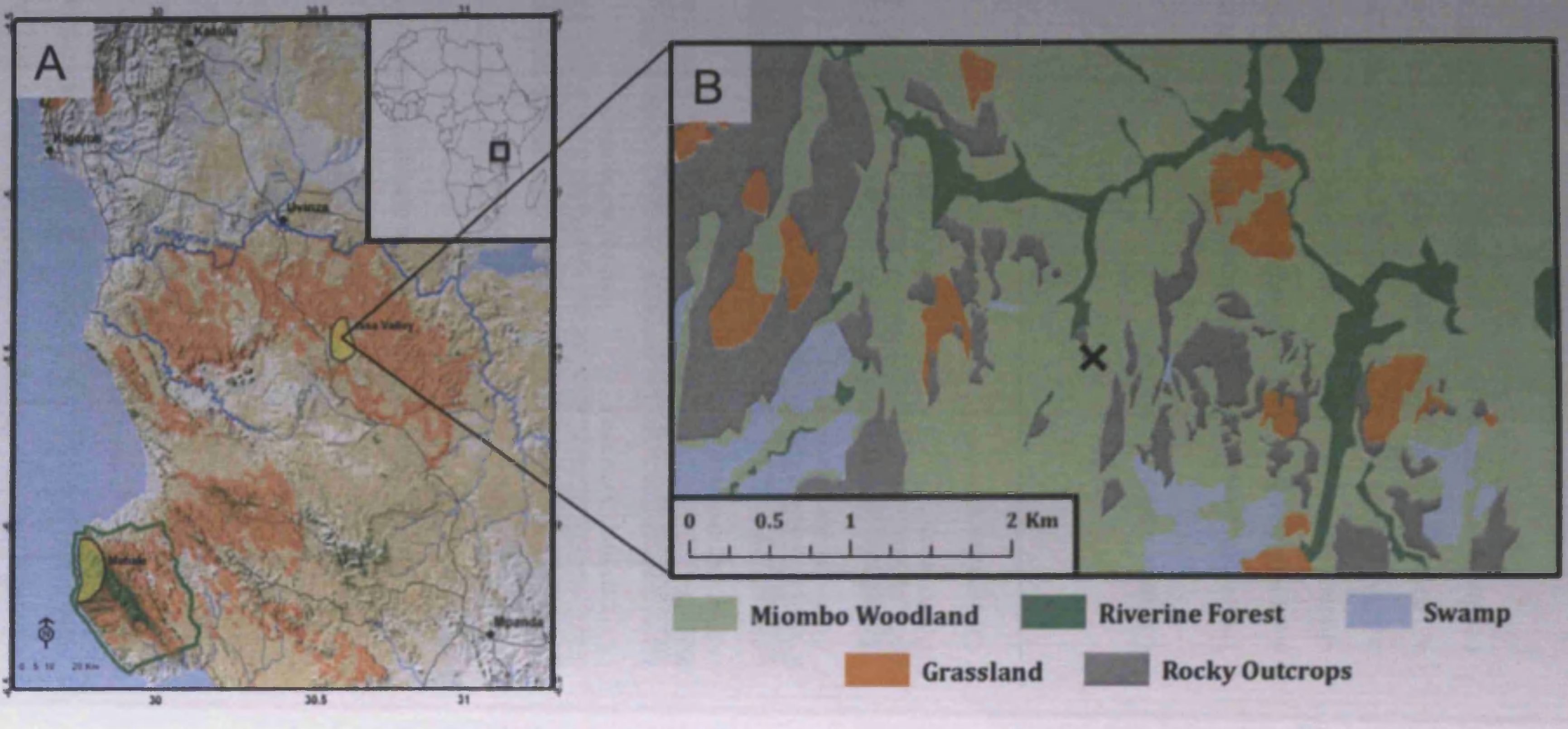

Figure 2.2. Study site location. (A) Western Tanzania. The Issa Valley study area is highlighted in yellow. Gombe and Mahale Mountain National Parks are shown in green on the lake shore (Image contributed by Lilian Pintea, Jane Goodall Institute) (B) The home ranges of the two study troops are shown on the right in relation to camp.

Despite increasing pressure from human disturbance, Issa remains a healthy ecosystem supporting a broad biodiversity. These include a full array of potential baboon predators including lion (*Panther leo*), leopard (*Panthera pardus*), hyena (*Crocuta crocuta*), and wild dog (*Lycaon pictus*). Evidence of leopards was frequent, with scat, footprints and vocalisations being documented several times per month, whilst lion and hyena traces were rare. The collection of mammal density data is continuous at Issa in order to monitor anthropogenic threats (Piel et al., 2014). Contributing to the biodiversity at Issa is the presence of multiple primate species (Table 2.1). For a full list of mammals over 0.5 Kg, please see Appendix 1.

Table 2.1. Primates observed in Issa during the study period. *Not seen in the core study area

Scientific name	**Common name**	**Evidence**
Cercopithecus aethiops	Vervet monkey	Observed
Cercopithecus ascanis	Red-tailed monkey	Observed
Galago senegalensis	Senegal galago	Vocalisations
Otolemur crassicaudatus	Greater galago	Observed
Pan troglodytes	Chimpanzee	Observed
Papio cynocephalus	Yellow baboon	Observed
Procolobus tephrosceles	Red colobus	Observed
Papio anubis *	Olive baboon	Observed
Cercopithecus mitis *	Blue monkey	Observed

Climate and Habitat data

Historically, Ugalla is a predominantly dry habitat with two distinct seasons, the rainy season (October – April), and the dry season (May – September). Dry months have been characterised by having <100mm of rainfall (Hernandez-Aguilar 2006; Stewart 2011). July/August are typically completely dry months, and Ugalla has a mean annual rainfall of <1000mm (Hernandez-Aguilar 2006). The only long-term field research study conducted to date in Issa by Hernandez-Aguilar (2006) reported that August had the highest mean daily maximum temperature (34°C) and November had the lowest (28°C). January was reported as having the highest mean daily minimum temperature (17.2°C) and the lowest was reported in August (14.4°C).

For the current study, I deployed an Onset H8 Pro series Hobo temperature logger in woodland plateau vegetation. This device recorded ambient temperature every 30mins and provided minimum, maximum, and mean temperature readings daily (range: 12.5 – 38.7°C; mean ± Standard Deviation: 20.5°C ± SD 3.8°C: Figure 2.3). Rainfall was recorded using an Onset HOBO data logging rain gauge RG3-M deployed in the woodland plateau near camp. From January to July 2012, rainfall averaged 111 ± SD 93 mm/mo, range: 0–248mm (Figure 2.3). A dry month in this study was, in line with previous work in the area, defined as having <100mm of rainfall (Hernandez-Aguilar 2006; Stewart 2011).

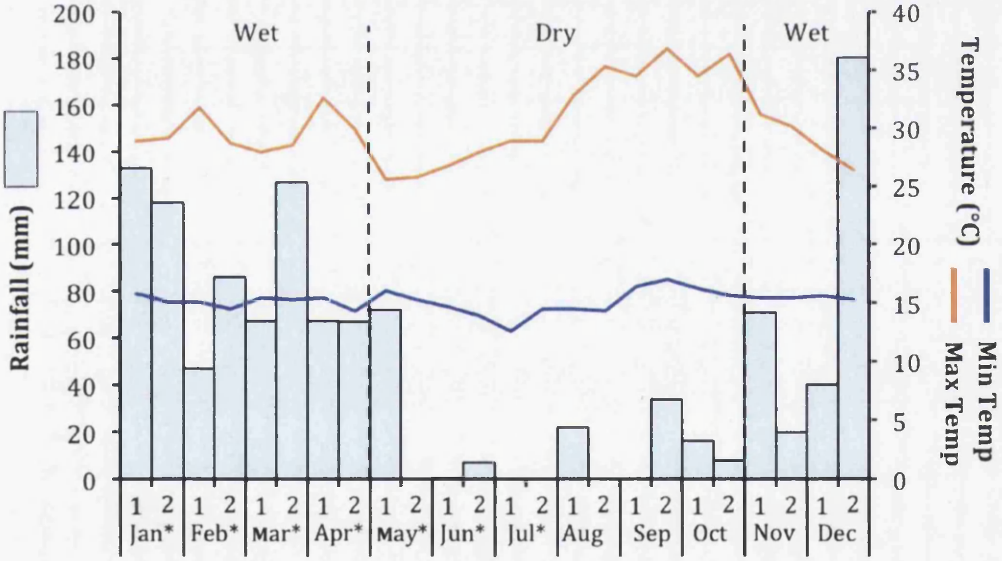

Figure 2.3. Monthly variation in rainfall and temperature at Issa, Ugalla, for the duration of the study period.

Habitat

Ugalla is a vast 3352 km^2 (Hernandez-Aguilar 2006) region comprised of landscape dominated by steep, broad valleys and flat hilltop plateaus that range in altitude from 900 -1800m (Kano 1972; Moore 1994). Two permanent rivers border Ugalla, the

Malagarasi River to the North, and the Ugalla River to the East (Moore 1994; Kano 1972) and the majority of streams in the region are seasonal.

The vegetation of the Issa study area, originally described by Hernandez-Aguilar (2009), is a diverse mixture of habitat types including swamp, dry grassland, wooded grassland, woodland, gallery forest, thicket forest, and hill forest. For the purposes of this thesis, though, I condense these classifications to grassland (wet and dry, Figure 2.4 E and F), woodland (Figure 2.4 C), and forest (Figure 2.4 B) (see Table 2.2 for descriptions). I also introduce an additional habitat type; rocky outcrops, which were included due to their purported importance as baboon refuges from predation risk (Cowlishaw 1997a) (Figure 2.4 F). Forest can be considered as the only habitat type with vegetation dense enough to be considered as "closed" vegetation and covers 1.5% of the study site, whilst the other more "open" habitat types comprise 98.5% of the study site (Hernandez-Aguilar 2006).

Table 2.2. Habitat classifications at Issa.

Habitat categories	Description
Forest	Evergreen forest with open understory, generally beside seasonal water courses.
Woodland	Deciduous trees and shrubs with grass understory and discontinuous canopy.
Dry grassland	Short grasses with some shrubs in valley lowlands or plateaus.
Wet grassland	Tall grasses up to 3m. Seasonally inundated with very low density of trees/shrubs.
Rocky Outcrop	Landscape consisting of exposed bedrock and boulders with low density of trees/shrubs.

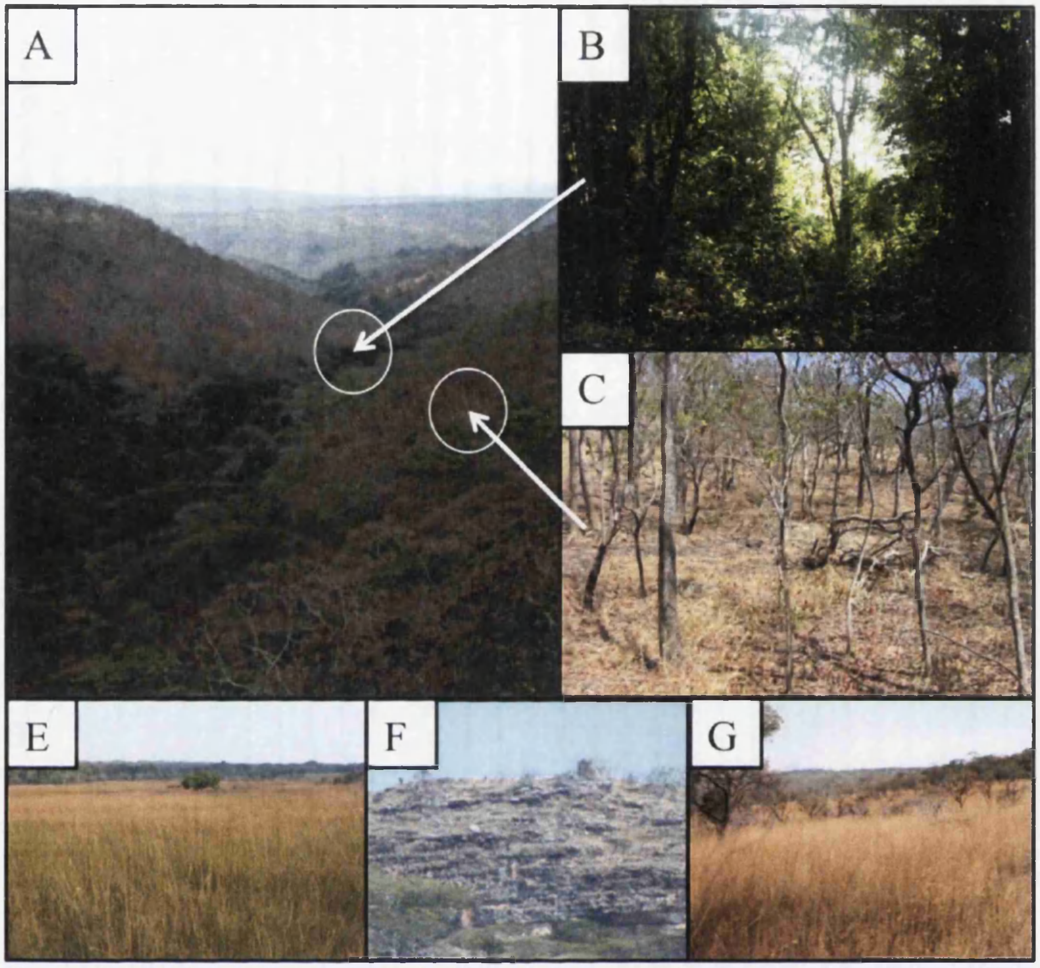

Figure 2.4. Habitat types at Issa. **A**: Gallery forest cutting through miombo woodland. **B**: Forest. **C**: Woodland. **E**: Wet Grassland. **F**: Rocky outcrops. **G**: Dry Grassland.

In order to empirically quantify the relative quantities of vegetation types within the immediate study area I constructed a vegetation classification map. To do this, high-resolution satellite imagery was downloaded from Google Earth (Figure 2.5 A) and geo-referenced into ArcGIS v. 10.1 (ESRI, Redlands, CA, USA) with the WGS 1984 coordinate system. Once completed, the geo-referenced JPEG was then exported as a layer file (.lyr). ArcCatalogue was used to create polygon shape files for each habitat type, which were then added to the ArcMap .mxd file. These shape files were then used to trace polygons around the different habitat types by eye, and in conjunction with an intimate knowledge of the study area, over the base map. Once completed, all veg layers were merged, creating a detailed vegetation map that allowed the easy analysis of distribution according to vegetation type (Figure 2.5 B).

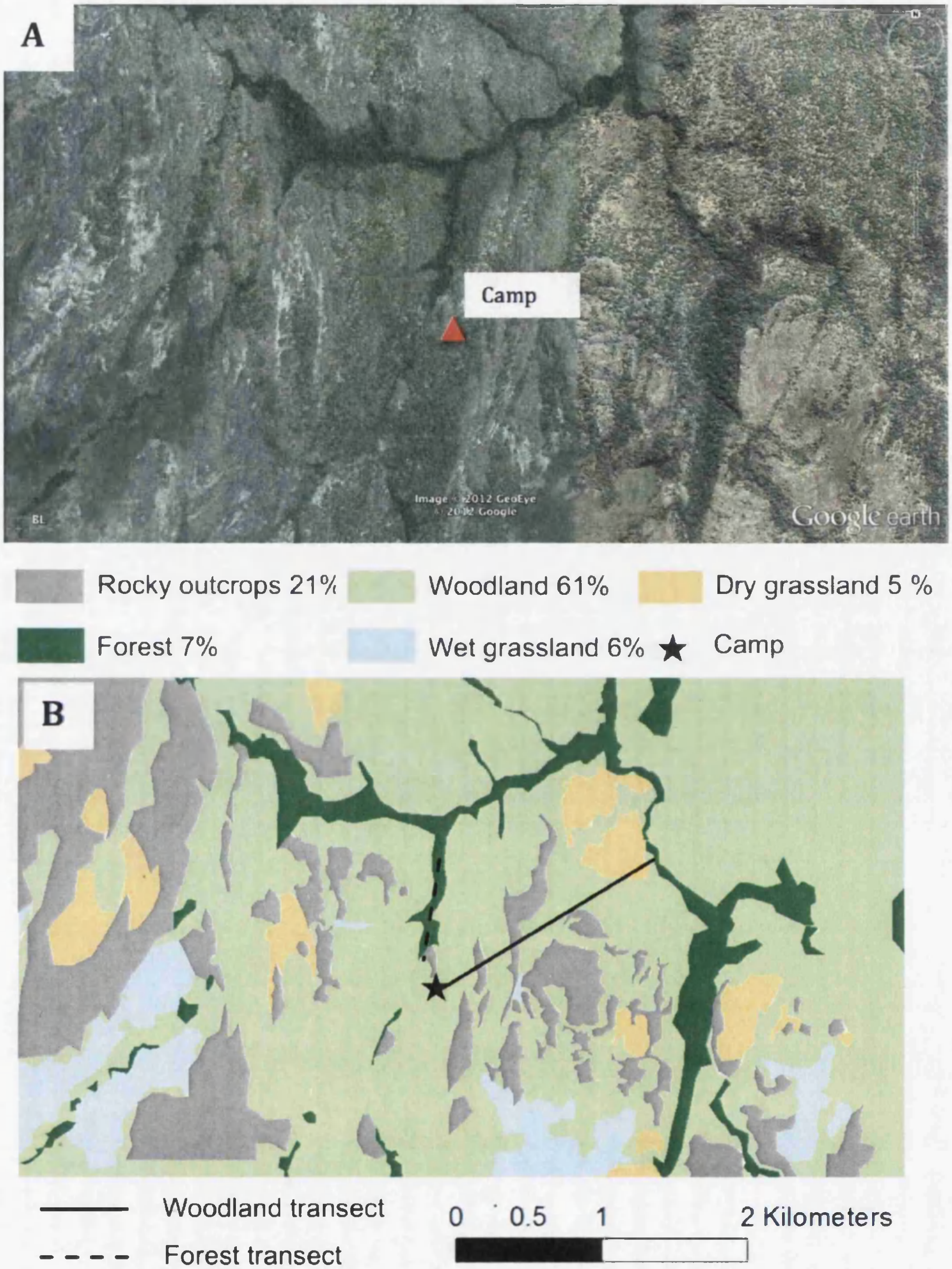

Figure 2.5: **A**: a google map image showing the immediate study area **B**: shows the vegetation classifications post work in ArcGIS and with fruit phenology transects represented by the black lines.

Habitat Productivity

I used two stratified transects placed through miombo woodland (1.7 km; N=383 trees) and the other through the forest (0.6km; N=200 trees) to assess habitat productivity (Figure 2.5 B). Both transects were 10m wide and only included woody plants ≥2m in height and ≥5cm diameter at breast height (DBH). This resulted in a total of 583 shrubs, lianas and trees from 58 different species (mean number of each species = 8.3, SD=12.3, range = 1-64). Transects were walked monthly and the presence/absence of fruit for each plant was recorded (Chapman et al. 1994). The availability of fruit at Issa was then calculated according to the specifications of the relevant chapter, which I describe below:

Monthly fruit availability was subsequently estimated for each habitat type using the fruit availability index (FAI_m) (Figure 2.6), a commonly used method in primate feeding ecology studies (Head et al. 2011; Anderson et al. 2005; Yamagiwa & Basabose 2006; Nkurunungi et al. 2004):

$$A_m = \sum_{k=1}^{n} D_k B_k P_{km}$$

where D_k is the density of species *k* per km^2; B_k is the mean DBH of species *k*, and P_{km} is the percentage of trees of species *k* in a fruiting condition in a month *m*.

During the end of the dry season, beginning of the wet season, both forest and woodland were comparable in the availability of fruit. From December onwards, however, the woodland contained more fruit than the forest (Figure 2.6).

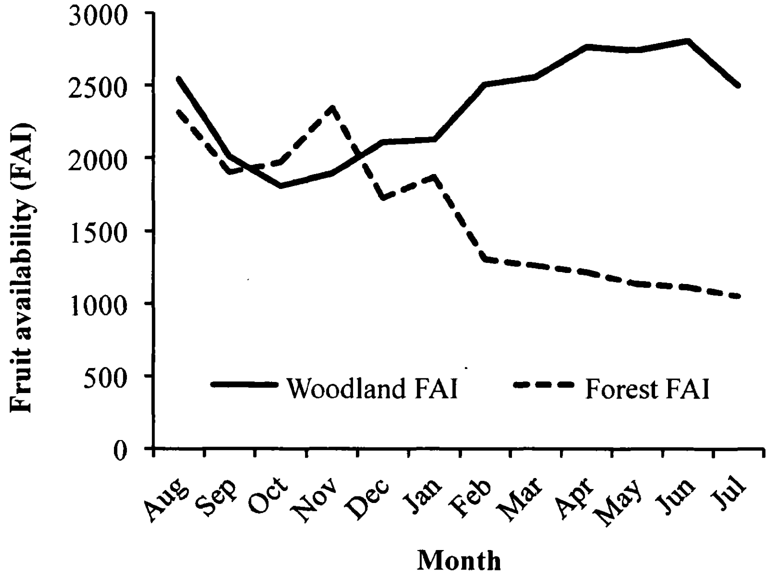

Figure 2.6. Fruit availability indices for the woodland (n= 383 trees) and forest (n= 200 trees) habitats at Issa as estimated by monthly transects

As I am interested in the role of fruit in the Issa baboon diet (Chapter 3) and movements patterns (Chapter 4), I also estimate FAI from a subset of trees known to produce fruit consumed by the baboons. In chapter 5, I explore whether there are more fruiting trees in a fruiting condition in the woodland or in the forest habitats. Therefore, using all trees from both transects (Figure 2.3), I also calculate both the percentage of fruiting trees encountered and the mean distance between fruiting trees for each transect. In chapter 6, I am interested only in the availability of fruits that were known to be consumed by both chimpanzees and baboons. I therefore use the same measure of fruit availability as was estimated in Chapters 3 and 4 for the baboons, and use the same method to calculate fruit availability for the chimpanzees (i.e. only for those trees, which produced fruits identified as being present in the chimpanzee diet).

Baboon Data

Within half an hour walking radius around camp were approximately five troops of yellow baboons ranging from 20 - 55 individuals. The yellow baboon population of the Issa study area had not been previously studied, and were un-habituated to human observers. The initial stages (August-December 2011) of the fieldwork were therefore spent learning to differentiate between the three core troops in the area: Balabala Troop (BT, n = 55), Camp Troop (CT, n = 23) and Matawi Troop (MT, n = 31). As January commenced, I condensed my efforts onto those troops that ranged closest to camp. These were CT and MT. After the initial stages of field work, both troops were relatively accustomed to my presence and I was able to follow them at a distance of 40-50m without any obvious flight response or eliciting alarm barks. This is considerably further than many other studies of baboons at long-term field sites, and whilst this did not allow me to determine gender ratios or demographics for either troop, I could gain accurate observations of their space use by recording their position using a hand-held GPS recorder (see below).

Troop follows

Between January and July 2012, MT and CT were followed for 12 days a month. Follows were normally conducted by me plus a research assistant, but on occasion follows were conducted by a single observer. Once found, the troop was followed until they reached a sleeping grove, typically around 19:00 UTC+03:00. Observers would then return the following morning to the same place at 07:00 UTC+03:00 (before baboons left the grove). This was repeated until they were lost or a full three-day follow was completed. It was attempted to follow each troop for two stints of three days per month (Table 2.3).

The un-habituated nature of both troops, combined with the extensive network of small rocky valleys and thick brush of the landscape often meant that we lost sight of the study troop. On these occasions, we would search in adjacent areas for ± 1.5hrs, and if the troop could not be located after this time, we abandoned the follow, and returned to camp.

Follow days were designated randomly each month, and troops could often be located based upon recent sightings. However, where no prior knowledge of baboon troop whereabouts was known, troops were searched for starting at their previous known location. If that troop could not be located, the other troop would be searched for in the same manner. If neither troop could be located, it was attempted to allocate an additional follow day at a later date that month. As CT troop ranged closest to camp they became the more habituated of the two troops (probably because they were both more familiar with researcher presence, and were closer to camp making ad-hoc sightings more frequent). As a consequence CT was, on average, followed for more days each month (see Chapter 3) (Table 2.3).

Troop Movement

Both CT and MT inhabited sparse, plateau woodland, which did not obstruct satellite signal. This facilitated the accurate (±10m) and consistent use of GPS devices in recording locational fixtures. We used hand held Garmin 520Hcx 2-way radio Global Positioning Systems (GPS) to record baboon movement through space. This was a cost effective and feasible substitute for telemetry tracking and yielded accurate location data.

Using a function of the GPS called 'Tracking' it was possible to have the GPS automatically take a fixture at a custom time interval. I set the function to record a coordinate every five minutes for the duration of the follow of both troops. If the troop was lost for > 10mins, 'Tracking' was turned off and turned back on only when the troop was relocated. Of the fixtures > 98% were within ±10m accuracy but were never more accurate than ± 4m. Fixtures with accuracy poorer than 10m were deleted (Table 2.3). Though fixes were not taken from the centre of the group (see above), they were taken by the observer whilst following the exact path taken by the baboons. Therefore, rather than a lack of locational accuracy, there is instead a lag time in when the baboons were actually located where the fix was subsequently taken. Following the central mass of the group was made easier by troop spread for both troops rarely being >50m.

Table 2.3: This table shows the total number of successful and unsuccessful tracking days by month for each troop and the total number of locational fixtures recorded.

	Camp Troop				Matawi Troop				
Month	**Full follows**	**Part follows**	**Not found**	**GPS Points**	**Full follows**	**Part follows**	**Not found**	**GPS Points**	**Tracking Days**
Jan	4	4	0	660	0	0	5	0	13
Feb	3	2	0	540	2	3	0	374	10
Mar	4	2	3	762	3	1	3	412	16
Apr	1	2	3	296	2	3	0	543	11
May	5	2	1	785	5	1	1	611	15
Jun	3	4	0	632	0	1	3	64	11
Jul	2	0	0	245	1	1	1	177	5
Total	22	16	7	3920	13	10	13	2181	81

Troop Diet

Since foraging behaviour could not be observed at close range, diet was inferred from macroscopic faecal analysis. During the following of the baboons, fresh faeces were encountered on a regular basis. Each fresh faecal sample was collected in an individual, plastic zip lock bag that was secured and labelled according to the date collected and what troop it was from, with a marker pen. The bags were then transported back to camp and processed, within 48 hours.

We collected 351 fresh faecal samples (monthly mean = 24.9, s.d. =18.9, monthly range=3-59) from three troops of baboons at Issa between August 2011 and July 2012 (Table 2.4). All samples were then analysed macroscopically according to the methods detailed by McGrew (2009): samples were weighed then sieved through a 1mm mesh with local river water. The contents of the sieve were then sluiced in the running water allowing faecal matter to be broken up, and the digested material washed away. The undigested parts were then counted or rated (according to a three-point scale: abundant, common, rare, (Yamagiwa et al. 1993)) in relation to the total size of the remaining faecal matter (Table 2.5).

Table 2.4: Fecal samples collected by month in 2011-2012. Note. N = 135 (Camp Troop), N = 65 (Matawi Troop), N= 75 (Balabala Troop), N = 74 (Unknown)

Troop	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
CT	21	18	10	x	25	17	9	8	2	3	6	16
MT	x	x	x	x	x	x	15	20	8	13	5	4
BT	x	x	12	63	x	x	x	x	x	x	x	x
Unknown	x	x	32	24	11	7	x	x	x	x	x	x
Total	**21**	**18**	**54**	**87**	**36**	**24**	**24**	**28**	**10**	**16**	**11**	**20**

Table 2.5. Categorised, undigested food types found in baboon faeces and the recording methods used.

Category	Criteria	Recorded as
Fibre	*Roots and stems*	*%*
Chewed greens	*Leaves and grasses*	*ACR*
Fruit skin		*ACR*
Seed pods		*ACR*
Seeds		*Counted for medium and large seeds. ACR for small seeds.*
Meat/bone/hair		*ACR*
Invertebrates	*Generally ant and termite heads*	*ACR*

Non fruit plant parts are represented in the faecal as partly digested leaf fragments and fibre (stems, pith, roots and bark), which cannot be identified to species level and so were separately rated with respect to the total mass of the faecal sample on the three-point scale. Fruit skins, seedpods, small seeds, animal remains, and invertebrates were also rated and removed and finally, morphologically similar seeds of a medium or large size were counted, recorded and removed from the sieve. A numerical value for the non-fruit plant component of the diet was subsequently calculated by converting the ratings as follows: abundant =3; common =2; rare =1 (Tutin & Fernandez 1993). A foliage score was subsequently achieved for each sample by combining the numerical values for the leaf fragment and fibre content. The frugivorous content of each faecal sample was calculated as the total number of fruit species found in each sample (Tutin et al. 1991; Yamagiwa & Basabose 2006).

Seed box collections were used as a key to identify seeds. Seeds from the faecal were matched to those in the box and the name of the seed consequently recorded. If the seed had not yet been identified, it would have a number in place of a name. If the seed could not be matched to any in the boxes, they would be collected and dried. Once dry, they were placed in their own compartment of a seed box and labelled with a unique number. Care was taken to include numerous numbers of seeds within each compartment to show any variation. The unique number was then used to identify the seed in the records until the species was identified, at which point the number was replaced by a name. This system allowed for unidentified seeds to be recorded and consequently traced back to the date it was found and by which troop it was consumed.

Analysis

Throughout the thesis, I provide a detailed description of the analyses used in the methods section of the relevant chapters. I therefore provide only a brief overview of the spatial analyses and statistics I use here.

Spatial Analysis

All cleaned GPS coordinate data were uploaded into R, and projected into the Universal Transverse Mercator geographic coordinate system (UTM, zone 36S, WGS-1984 ellipsoid), to form a spatial points data frame. This was then used to calculate day path lengths (Chapter 4), home range estimates (Chapters 5 and 6) and movement trajectories (speed and turning angle: Chapters 4 and 5). Only GPS observations from full-day follows (7am-7pm) were used to calculate DPLs. Speed was calculated between all consecutive GPS points and turning angle as the departure of the path from a straight line (i.e. turning angle). Home range estimations were conducted using two separate methods - minimum convex polygons (MCP), and kernel density estimates (KDE), using a 95% isopleth.

In order to calculate the evenness of habitat (Chapters 5 and 6) and range use (Chapter 5), GPS coordinates were uploaded into ArcGIS 10 (UTM, zone 36S, WGS-1984 ellipsoid) and saved as a shape file. This was then (1) merged with the habitat layer file (see page 28 and Figure 2.5 B), to provide a habitat identity for each GPS coordinate, used to calculate evenness of habitat use (Chapters 5 and 6) and (2) merged with a 150x150m grid layer, overlaid within the HR of the relevant troop, to provide a count of observations within each cell, used to calculate evenness of HR use (Chapter 5).

Statistical Analysis

I use Pearson's rank correlations and t-tests for all univariate, normally distributed data, and Spearman's rank correlation and Wilcoxon signed-ranks tests for non- normally distributed data. In order to test the effect of multiple factors on response variables (i.e. DPL in Chapter 4; speed and turning angle in Chapters 4 and 5; and dietetic diversity in Chapter 3), I utilise multivariate statistical modelling. When testing the effect of multiple variables on the response variable, I use a linear model (LM) (Chapter 4). More commonly though, I needed to include nested random effects, to account for any uncertain effect of sampling day and month, for which I use a generalized linear mixed model (GLMM) (Chapters 3 and 6) or a linear mixed model (LMM) (Chapters 4 and 5). Count data was modelled with a Poisson distribution and binary data (presence/absence) with a binomial distribution (Chapters 2 and 6). When the relationship between the fixed terms and response variable was non-linear, I use a generalized additive model (GAM), which is more flexible in detecting non-linear relationships (Chapter 5). Co-linearity between fixed terms in all models were checked using Spearman's rank correlation tests, with a cut-off criterion of $r_s = 0.60$ (Tabachnick & Fidell 2012). I used backward selection of variables for each set of compatible fixed effects and the best model was selected by the lowest Akaike information criterion (AIC) value (Akaike 1998).

Chapter 3 - A preliminary report on the feeding ecology of yellow baboons (*Papio cynocephalus*) in the Issa valley of western Tanzania

Abstract

The survival of primates, like all animals, depends primarily on an adequate supply of consumable resources. Understanding the feeding ecology of primates is therefore of paramount importance in almost every aspect of their biology and ecology. Despite being a largely well-studied primate, the diet of yellow baboons (*Papio cynocephalus*) is described from a limited part of their range. The Issa valley of western Tanzania presents a climatically and ecologically unique setting of previously unstudied population of yellow baboons. In this chapter I present the first description of Issa baboon diet using macroscopic faecal analysis, conducted on 351 samples collected from three separate troops. I subsequently test the variability and content of the diet according to ecological and climatic variables. I found baboons at Issa satisfied their dietary requirements with a wide variety of flora species, and that they supplemented this with the occasional consumption of vertebrates and relatively frequent consumption of invertebrates. The availability of preferred foods (fruits and seeds) did exhibit seasonal variation, but not in synchrony with seasonal patterns of rainfall. The consumption of fruit by baboons at Issa was not correlated with fruit availability, but the presence of foliage and the number of food types present in the samples were inversely correlated with fruit availability. Overall, this chapter finds baboons at Issa selectively exploited their habitat and that, unlike their savannah conspecifics, appear to have sufficient food alternatives during periods of relatively low fruit availability.

Introduction

From a simplistic perspective, the continued survival of primates is dependent on an adequate supply of consumable resources (Hemingway & Bynum 2005). As such, understanding the feeding ecology, and variation in availability of essential foods, is crucial to almost every aspect of primate biology and ecology (Altmann et al. 1977; Hemingway & Bynum 2005; Hamilton 1985). Descriptions of primate diets are consequently commonplace, and can be used to predict species social structure (Janson 1988b), inter-species competition (Schreier et al. 2009), and ranging (Ganas & Robbins 2005; Hoffman & O'Riain 2010; Wieczkowski 2005).

The feeding ecology of baboons is particularly well documented with data on diet food choices existing for at least 19 separate populations across ten different African countries (See Chapter 4, Table 4.1). Among these well studied baboon species, there exists extensive data on the feeding ecology of the yellow baboon (*Papio cynocephalus*) (Mikumi: Norton et al., 1987; Amboseli: Altmann, 1998; Tana River Primate National Reserve (TRPNR): Bentley-Condit, 2009). However, these only represent a limited part of the range of the species. This chapter provides a preliminary report on the feeding ecology of *P. cynocephalus* in a woodland habitat: the Issa valley of western Tanzania, as part of the first study conducted on baboons in this region. The Issa valley (5°23'S, 30°35'E) of western Tanzania, is at a higher elevation and greater annual rainfall compared to the major study sites of yellow baboons; Amboseli (2°40'S, 37°10'E), TRPNR (1°55'S, 40°5'E) and Mikumi (7°12'S, 37°08'E) (i.e. Issa = 1600m, ≈ 1000mm; Amboseli =1,128m, ≈340mm; TRPNR= 55m, ≈644mm; Mikumi = 548m, ≈ 870mm) (Hernandez-Aguilar, 2009; Altmann, 1998; Bentley-Condit, 1995, unpublished data; Norton et al., 1987). These differences suggest that the Issa valley offers a distinct environment from which to gain further insight that broadens our understanding of the feeding ecology of yellow baboons.

The diet of baboons (*Papio spp.*) consists of fruits, flowers, seeds, pods, leaves, gum, and tubers from a variety of plant taxa in addition to any small animal that can be caught (Rowell 1966; Altmann & Altmann 1970; Davidge 1978; Norton, Rhine et al. 1987; Whiten et al. 1987; Whiten et al. 1991; Altmann 1998; Johnson et al. 2013; Okecha & Newton-Fisher 2006; Bentley-Condit 2009; Johnson et al. 2012). As such, they have been attributed with being dietary generalists, eclectic omnivores, and extractive foragers (Altmann 1998), but that also selectively exploit their habitat according to a variety of factors (Norton, Rhine et al. 1987; Hamilton et al. 1978; Whiten et al. 1991). This especially includes the distribution and abundance of plant foods, which vary spatially and temporally (van Schaik et al. 1993). In reflection of this, baboons demonstrate huge dietary flexibility within and across populations (Norton, Rhine, et al. 1987; Whiten et al. 1991).

Fruits and seeds, in particular, are preferred food sources that are selected for by baboons when available (Altmann & Altmann 1970; Barton 1989; Hill & Dunbar 2002). As such, they form an important part of the diet of many baboon populations (Dunbar & Dunbar, 1974; Harding, 1976; Davidge, 1978; Rasmussen, 1978; Sharman, 1981; Sigg & Stolba, 1981; Ransom, 1981; Depew, 1983; Norton et al., 1987; Barton, 1990; Bronikowski & Altmann, 1996). Despite the asynchronous fruiting patterns of different species, the availability of fruits and seeds in the environment inevitably undergo periods of scarcity (van Schaik et al. 1993). During these times baboons must incorporate less nutritious, but more readily available food items into their diet to sustain their dietary demands (Alberts et al. 2005; Post 1981; van Doorn et al. 2010; Hill & Dunbar 2002; Norton, Rhine, et al. 1987; Whiten et al. 1987) often resulting in a reduction in the diversity of their diet (Post, 1982; Norton et al., 1987; van Doorn et al., 2010). These items are known as fallback foods and include items such as grasses and herbs (Hoffman & O'Riain 2010; van Doorn et al. 2010).

In this chapter, I examine the feeding ecology of the Issa valley baboon population, as represented by three troops. My goals are as follows. 1) To provide a quantitative description of baboon food availability at Issa, particularly fruit, and how it varies seasonally. 2) To describe the dietary constituents of Issa baboons and how these change over time. 3) To assess the selective exploitation of the environment, by the baboons, according to the availability of food. Accordingly, I predict the presence of fruit in the diet will be continuous, but will be higher when fruit is more available (Hamilton et al. 1978; Hill & Dunbar 2002; Altmann & Altmann 1970), and in times of relative fruit scarcity, the presence of vegetation (fibre, foliage, roots) will increase (Post 1981; Alberts et al. 2005; Whiten et al. 1987). 4) Lastly, I examine the effect of reduced food availability on the dietetic variability testing the prediction that when food is scarce the baboons will reduce variability of their diet (Post, 1982; Norton et al., 1987).

Methods

Study Site and Subjects

The baboon study-troops ranged within the Ugalla region of western Tanzania (05° 23.34 S 30° 35.04 E), 81km East of Lake Tanganyika (Figure 3.1). The Ugalla region extends over 3352 km^2 and is comprised of steep, broad valleys and flat hilltop plateaus that range in altitude from 900 -1800m. The vegetation of the study area is described is predominantly woodland interspersed with gallery forest and grassland (see Chapter 2, Figure 2.6 B).

Three troops (Camp Troop [CT], n=22; Matawi Troop [MT], n=31; Balabala Troop [BT], n=50 individuals) are studied. All troops were partially habituated to observation and so were tracked on foot by observers for approximately 12 days a month between August 2011 and July 2012. When a troop was found, they were followed at a distance of ~50m, permitting the collection of all fresh faecals found. In total, this resulted in the successful location and following of baboons on 95 days, during which time 351 faecal samples were collected and analysed (mean=3.7/day) (Table 2.4). Faecal samples (from here on referred to as samples) for BT stop after December due to them shifting their range beyond reach from camp. Samples were collected in all months of the study period (monthly mean = 29.2, SD = 21.9, range = 10 – 87).

Phenology

The fruiting phenologies of all trees on two transects were monitored on a monthly basis (n = 583 trees). Please see Chapter 2, pages 30-31 for a more detailed description.

Season classification

Please refer to Chapter 2, pages 25-26 for details on climate and defining seasons.

Fecal analysis

All faecal analysis was conducted according to the method detailed by McGrew et al. (2009). Please refer to Chapter 2, pages 35-36 for a full description.

Variability of Diet

Due to the high number of foods consumed (>50), it is useful to condense these into clustered groups in order to facilitate the testing of temporal variation and diversity in foods eaten. To do this, I remove foods found within <1% of faecals (n=19) and condense the remaining dietary components (species, n=31) found in the faecal samples into categories. This was done using a two-way indicator species analysis (TWINSPAN, Hill, 1979), in in Community Analysis Package 4 (Henderson & Seabym 2007) which uses reciprocal averaging to ordinate dietary components and then subjects them to an iterative, dichotomy procedure that divides the species into similar clusters. Clusters therefore represent food types that are commonly eaten together allowing me to better assess the variation and diversity of the diet over the study period. To do this, I use the number of different food categories observed within each faecal sample. This simple measure was preferred over more common diversity indices, e.g. Shannon Weiner diversity index (e.g. Struhsaker, 1975; Clutton-Brock & Harvey, 1977; Barton et al., 1993), due to the absence of a meaningful measure of abundance in the data.

Analysis

Fruit availability

Out of the 583 trees, shrubs and lianas (58 species from 50 genera) 227 were found to produce fruits that were later identified as being present in the diet of the Issa baboons. Each species was present on the transect in numbers that ranged from 1-64 (mean = 8.3, SD=12.3). In order to estimate a measure of fruit availability for the baboons, I used only those trees that produced fruits found in their diet (n=227, 30 species from 25 genera). This provided a conservative measure of fruit availability. Fruit availability was estimated using the fruit availability index detailed in Chapter 2, pages 30-31 which considers the density of each species on the transect.

Do food types consumed vary?

To examine if diet changed over time, I calculated the proportion of faecal samples containing each of the food categories by month. I subsequently used a Spearman's rank correlation matrix (stats package, R Devlopment Core Team, 2010) to determine whether correlations existed between the categories over time. Negative correlations would indicate that the more one food type is eaten, the less the other one is, and positive correlations indicate that the foods are eaten at the same time.

Factors predicting the content and variability of diet

To assess the variables that influence the presence of fruit or vegetation in the samples, I used a generalized linear mixed model (GLMM) with binomial error structure and a logit link function. For each fruit and vegetation, I used presence or absence as the binary response terms. To investigate the factors predicting the number of categories of food (Table 3.1) present in faecal samples, I used a GLMM with Poisson error structure and a log link function. For all models, I fitted 'day' and 'month' as nested random effects to control for the potential non-independence of samples collected on the same day and/or month. I fitted a series of fixed effects in accordance with my predictions. Continuous variables that were fitted as fixed effects were total monthly rainfall (mm), fruit availability indices (FAIs) and faecal weight (g) (to control for the potential correlation between faecal weight and number of dietary items). Temperature was not included due to the absence of temperature data for four months of the study period. Categorical variables fitted as fixed effects were Troop ID (MT, CT, BT or Unknown; see Table 2.4) and season (wet, dry). Co-linearity between effects was checked using Spearman's rank correlation tests, with a cut-off criterion of $r_s = 0.60$ (Tabachnick & Fidell 2012). Where variables were correlated, I included terms one at a time, and compared models using Akaike's information criterion (AIC) value (Akaike 1998) and backward selection of terms to select the model that had the best fit (Heinänen et al. 2008). The significance of the individual terms was then calculated from the selected model and all dropped terms were put back into the model to obtain level of non-significance (lmerTest package, R: Kuznetsova, 2012). All models were run using lme4 package in R (R Development Core Team 2010).

Results

Fruit availability

Both rainfall and fruit availability varied across the study period. Rainfall averaged 141 ± SD 136 mm/month (range: 0-387mm) (Figure 3.1) and there was a distinct wet (October-April) and dry (May-September) season, defined by months with <100mm rainfall being characterised as dry. The availability of fruit was comparable across the dry season and the wet season (Mann-Whitney U test: $Z = 0.23$, p=0.82). Fruit availability was not correlated with rainfall (n=12, Pearson correlation r^2=-0.51, p=0.091), however if I account for the lag period between rainfall and fruit production offsetting by 1 month (n=11), 2 months (n=10), 3 months (n=9), or 4 moths (n=8), I find the strongest relationship occurs after 4 months (Pearson's correlation r^2=0.82, p=0.012).

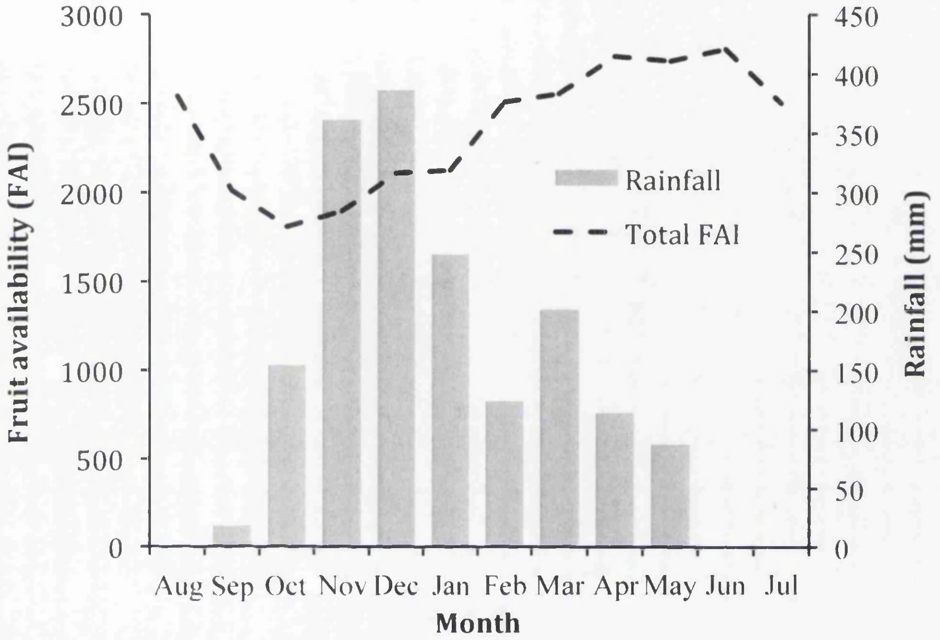

Figure 3.1. Rainfall and fruit availability for duration of study period (Aug-Jul). Fruit availability values displayed are the square root of the actual values as actual values are too large.

Dietary constituents

Fruit remains in baboon samples was common, appearing in 59.4% (monthly SD = 21%, monthly range = 20-82%, monthly mean = 51.9%) of samples. Foliage was also found in samples throughout the study period and was represented in 76% (monthly SD = 21%, monthly range=25-100%, monthly mean = 73%) of all samples. 58.4% of samples contained faunivorous remains, 57% of which were those of invertebrates and 1.4% vertebrates (mammalian and reptilian). On one occasion, an adult male of CT was also observed carrying and periodically eating a dead bush hare (*Lepus* sp.). For a full list of dietary items, please see Table 2 in Appendix 2.

Variability of Diet

TWINSPAN produced a dichotomous hierarchy of clusters in which dietary components within a cluster were more similar than those in other clusters. In this case, all foods that were found in >1% of samples (n=29) were condensed into seven categories (Table 3.1). Consequently, this allowed me to determine which foods were eaten together and cluster them together so that I can more easily interpret whether the foods consumed change through the year. I subsequently found the presence of category A in the diet was relatively stable throughout the study period (Figure 3.2). However, the remaining categories were much more variable (Figure 3.2). I found a positive correlation between the presence of categories F and G (n= 12, Spearman's rank correlation $r_s = 0.65$, p= 0.022) and a negative correlation between categories B and E (n= 12, Spearman's rank correlation $r_s = -0.63$, p= 0.028) suggesting that when baboons consume category G they also consume category F, whilst they consume more of B when they are not eating E and vice versa. This provides some evidence that the baboons are relying on different foods at different times of the year. However, when I apply a Bonferoni correction I find these correlations lose their significance.

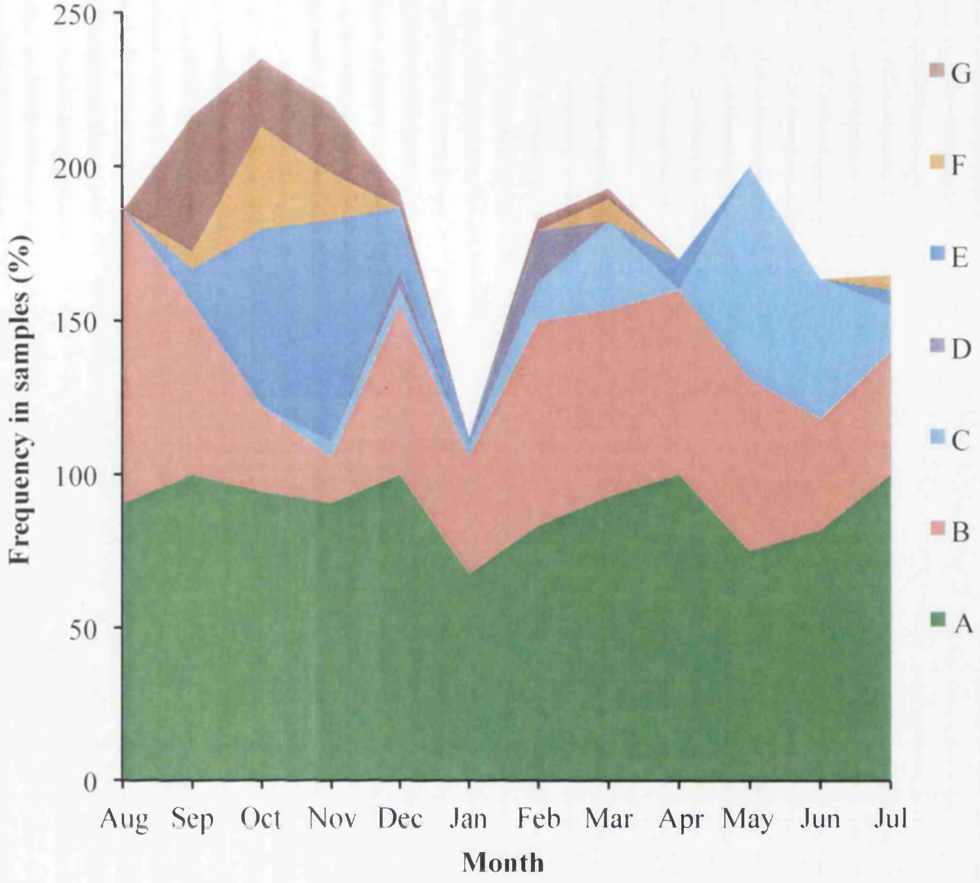

Figure 3.2. The presence of food categories (food components within a cluster were more often found in faecal samples together than those in other clusters), as frequency of occurrence in samples (%), by month.

Table 3.1. Foods consumed and the frequency of occurrence in baboon samples (%), ordered by category. For a full list of fruit species consumed please see the Appendix 2, Table 2.

Foods consumed	Frequency in faecal samples (%)
Category A	
Fibre	53.8
Leaf fragments	42.2
Fauna	58.4
Category B	
Leptactina banguelensis (Sapotaceae)	2.3
Grewia rugosifolia (Tiliaceae)	1.7
Strychnos panganiensis (Loganiaceae)	1.4
Unidentified fruits	8.2
Category C	
*Vitex doniana/mombassae** (Verbenaceae)	2.9
Canthium burtii (Rubiaceae)	2.3
Ximenia caffra (Olacaceae)	1.1
Grass seeds	4.6
Unidentified fruits	3.1
Category D	
Unidentified fruits	1.7
Category E	
Garcinia huillensis (Clusiaceae)	27.9
Uapaca kirkiana (Euphorbiaceae)	4.6
Chrysophylum banguelensis (Sapotaceae)	2.0
Anisophyllea boehmii (Anisophylleaceae)	1.7
Unidentified fruits	2.2
Category F	
Saba comorensis (Apococynaceae)	3.4
Unidentified fruits	8.8
Category G	
Uvaria angolensis (Annonaceae)	1.4
Unidentified fruits	1.1

Names in italics denote the species of the fruit consumed and the name in parentheses is the family to which the species belongs. * These species were grouped together on account of visual differentiation being difficult.

Dietary Responses to Variation in Fruit Availability

The consumption of fruit was continuous throughout the study period, but it did vary. However, I found no evidence to support that this variation was significantly influenced by any of the variables measured (GLMM: FAI: effect (SE) = -0.0007(0.0006), F= 1.15, P= >0.05; Season: F= 1.48, P>0.05; Rainfall: effect (SE) = -0.00003(0.002), F= 0.0004, P>0.05; Sample weight: effect (SE) = 0.011(0.0058), F=3.92, P= 0.054; Troop ID: F=1.02, P= >0.05). As predicted, though, I do find the presence of vegetation in the samples to be negatively influenced by fruit availability (GLMM: effect (SE) = -0.0014(0.00064), F=4.79, P<0.05), but that other factors had no influence (Season: F= 0.47, P >0.05; Sample weight: effect (SE) = 0.0062(0.0068), F= 0.88, P >0.05; Troop ID: F=1.22, P >0.05; Rainfall: effect (SE) = -0.0004(0.002), F= 0.04, P>0.05;).

Food categories consumed

I found the number of food categories recorded in the samples was significantly and negatively influenced by fruit availability (Figure 3.3, GLMM: effect (SE) = -0.00022(0.0001), F=5.63, P<0.05), suggesting that as fruit availability increases, the diversity of foods consumed decreases. Season (GLMM: F=0.82, P>0.05), rainfall (GLMM: effect (SE) = -0.0005(0.0003), F= 2.48, P>0.05), sample weight (GLMM: effect (SE) = 0.0024(0.0017), F= 2.18, P>0.05) and troop ID (GLMM: F=0.11, P>0.05) had no significant effect.

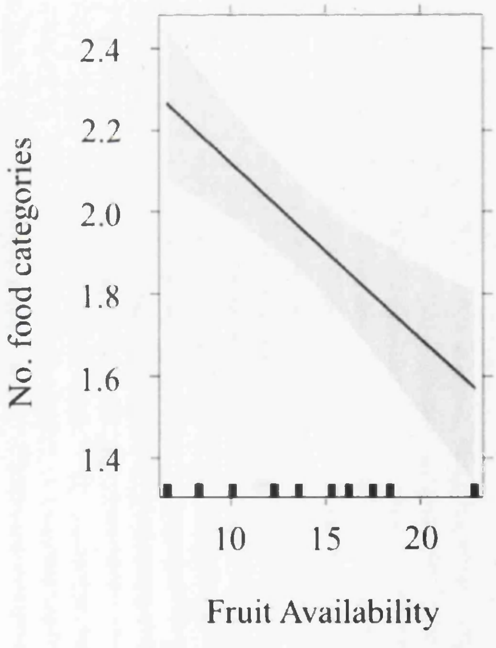

Figure 3.3. Relationship between the numbers of food types eaten and fruit availability. Shaded areas show upper and lower 95% confidence limits of the predicted effect from a GLMM, and the black markers along the x-axis indicate data points.

Discussion

I examined the diet of the Issa valley population of yellow baboons via the faecal analysis of three troops over a one-year study period. I found baboons at Issa consumed a wide variety of flora species (Norton et al., 1987; Dunbar, 1992; Altmann, 1998; Bentley-Condit, 2009), and that they supplemented this with the occasional consumption of vertebrates and relatively frequent consumption of invertebrates (Rhine et al. 1989; Post 1982). The availability of preferred foods (fruits and seeds) did exhibit seasonal variation, but not in synchrony with seasonal patterns of rainfall. The consumption of fruit by baboons at Issa was not correlated with fruit availability; however, I did find that the presence of foliage and the number of food types present in the samples was inversely correlated with fruit availability. I discuss each of these main findings in turn and their robustness according to the methodological challenges faced by this study.

Yellow baboons at Issa, like many other primates, meet their dietary needs through a wide variety of plant species (Bentley-Condit 2009). Fruit is a dominant component of baboon diet (Dunbar & Dunbar 1974; Rasmussen 1978; Sigg & Stolba 1981; Sharman 1981; Davidge 1978; Ransom 1981) that, due to its high nutritional quality, is selected for when available (Altmann 1974). I therefore expected to find fruit remains (seeds) in a high proportion of the samples analysed. Unexpectedly though, the consumption of fruits was not significantly influenced by the availability of fruit in the environment. This could be a result of one of three things: First, macroscopic faecal analysis has well known limitations (Tutin et al. 1991; McGrew et al. 1988), principally of which is that the quantity and caloric content of fruit in faecal samples cannot be reliably estimated, only the presence or absence (Tutin et al. 1991). It is possible then that this is not an accurate reflection of the quantity and even quality of fruits consumed and thus not recognising an existing relationship between fruit availability and fruit consumption. Future work considering the time spent foraging for fruits or a direct measure of quantity of fruits consumed would be required to test whether this is indeed influenced by fruit availability. Similarly, two fruits of different species likely contain different caloric content per unit of mass (Matsumoto-Oda & Hayashi 1999). Revealing this information about each fruit species could then be used to obtain a measure of energy density of foods consumed, and as energy is the primary reason for fruit consumption, this would be a far more robust measurement to test in relation to environmental parameters.

Second, my measure of fruit availability was based upon those trees from transects, that may not be of a sufficient resolution to include all fruit species consumed by the baboons. Therefore, future fruit availability estimations may be improved by monitoring the phenologies of fruiting trees important to the baboons.

Third, the lack of any relationship between fruit consumption and availability of fruit in the environment could be a result of the baboons' successive exploitation of different fruit species throughout the year in accordance to availability (Alberts et al. 2005). This explanation is supported by the finding that fruit is consumed continually (see Figure 3.2) across each month of the study period. Moreover, fruits comprising category B (see Table 3.1) were eaten when fruits in category E were not, and vice versa suggesting the baboons are switching their consumption of fruits in concert with their relative availabilities in the habitat. In this way, baboons at Issa typify the generalist feeding strategy prevalent in their genus, by successive exploitation according to availability to achieve a level of stability in their diet (Alberts et al. 2005). However, it is unlikely that the baboons were able to achieve complete stability as fruit consumption still exhibited heterogeneity across months. In support of this, baboons at Issa eat more foliage (fibres and leaves) when fruit is less available. Foliage and fibre are often fallback foods baboons (Hoffman & O'Riain, 2010; van Doorn et al., 2010) and many other primates (Wrangham et al. 1998; Goldsmith 1999; Lambert et al. 2004) whose preferable food sources (especially fruits) undergo periods of seasonally predictable scarcity (Chapman et al. 1999).

Fruit availability at Issa also predicts the number of food types consumed by baboons at Issa. I find that when fruit is scarcer, baboons at Issa consume significantly more food types. In this chapter, foods are classed together into categories according to apparent similarities and dissimilarities in when they are consumed. These categories are defined by the TWINSPAN procedure, which iteratively partitions the data via one-dimensional ordinations by reciprocal averaging. Accordingly, I assume then that the more categories present in a sample, the more diverse the diet of the baboon was. Consequently, I find that when fruit is less available, the diet of the baboons at Issa becomes more diverse. However, in the face of a seasonally predictable shortage of food, baboon populations occupying savannah or mountainous regions exhibit a reduction in their dietetic diversity, putatively as they have fewer alternative foods available to them (Norton, Rhine, et al. 1987; Post 1982; Byrne et al. 1993). However, despite some seasonal variation in the availability of fruit within the woodland dominated habitat of Issa, it is possible that, unlike their savannah and mountain dwelling conspecifics, there are still sufficient alternatives during periods of low fruit availability. If so, it is likely that as the overall availability of fruit decreases, baboons at Issa, in addition to increasing reliance on fallback foods, are exploiting a wider diversity of less abundant fruits in order to satisfy their dietary requirements. Additionally, the relationship between the number of food types consumed and fruit availability supports my earlier result that Issa baboons are switching between foods and successively exploiting their habitat, most likely in accordance to availability (Alberts et al. 2005).

In this chapter, I have presented my results and interpretations in full consideration of the limitations imposed by macroscopic faecal analysis (Doran et al. 2002; Moreno-Black 1978). Therefore, the diversity and constituents of the diet of Issa baboons, reported here, are likely an underestimate (McGrew et al. 1988). Irrespective of this, though, macroscopic faecal analysis made it possible for me to provide the first description of the diet and its temporal variability and adaptability in a previously unstudied population of yellow baboons. As a novel population, inhabiting an environment that is climatically and attitudinally disparate from other yellow baboon study sites (Mikumi: Norton et al., 1987; Amboseli: Altmann, 1998; TRPNR: Bentley-Condit, 2009), this chapter provides a useful contribution to what is known about their feeding ecology.

Chapter 4 - The ecological determinants of baboon troop movements at local and continental scales

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Version of this Chapter submitted to *Movement Ecology* (see Appendix 5)

Abstract

How an animal moves through its environment directly impacts its survival, reproduction, and thus biological fitness. A basic measure describing how an individual (or group) travels through its environment is Day Path Length (DPL), i.e., the distance travelled in a 24-hour period. Here, I investigate the ecological determinants of baboon (*Papio* spp.) troop DPL and movements at local and continental scales. At the continental scale I explore the ecological determinants of annual mean DPL for 47 baboon troops across 23 different populations, updating a classic study by Dunbar (1992). I find that variation in baboon DPLs is predicted by ecological dissimilarity across the genus range. Troops that experience higher average monthly rainfall and anthropogenic influences have significantly shorter DPL, whilst troops that live in areas with higher average annual temperatures have significantly longer DPL. I then explore DPLs and movement characteristics (the speed and distribution of turning angles) for yellow baboons (*Papio cynocephalus*) at a local scale, in the Issa Valley of western Tanzania. I show that my continental-scale model is a good predictor of DPL in Issa baboons, and that troops move significantly slower, and over shorter distances, on warmer days. I do not find any effect of season or the abundance of fruit resources on the movement characteristics or DPL of Issa baboons, but find that baboons moved less during periods of high fruit availability. Overall, this study emphasises the ability of baboons to adapt their ranging behaviour to a range of ecological conditions and highlights how investigations of movement patterns at different spatial scales can provide a more thorough understanding of the ecological determinants of movement.

Introduction

A simple, but revealing measure of an animal's space use is the distance it moves within a 24-hour period. This distance is described as the Day Path Length (DPL). The simple parameters required to quantify DPL make it easily transferable and applicable to terrestrial and/or arboreal animals (Garland 1983; Jetz et al. 2004), thus affording comparative investigations of DPL across species. For example, DPLs provide the basis of analyses of mammalian day range (Carbone et al. 2005), and some of the most comprehensive studies of what determines how far animals travel have been undertaken on primates (Clutton-Brock & Harvey 1977b). Like most mammals, primate ranging behaviours are primarily influenced by the distribution and abundance of essential resources (Clutton-Brock & Harvey 1977b; Isbell 1983; Li et al. 2000), specifically food (Hemingway & Bynum 2005), but a suite of other factors are also important.

In general, primates tend towards an energy maximising strategy (Gerber et al. 2012) whereby, in response to low food availability, they increase their DPLs in search of higher quality food items (Altmann 1974; Wahungu 2001; Barton 1992; Harding 1976; Pebsworth, MacIntosh, et al. 2012). Since plant biomass and net plant productivity can be reliably inferred from rainfall data (Coe et al. 1976; Deshmukh 1984), especially in seasonal habitats (van Schaik et al. 1993), rainfall can be used as an indirect measure of food resources and predicts primate DPLs (Hemingway & Bynum 2005; Altmann & Altmann 1970). Similarly, recent studies have demonstrated that remotely sensed data, particularly the normalized difference vegetation index (NDVI), provides an adequate measure of photosynthetic activity and, therefore, vegetation structure (Myneni et al. 1995), which can hence be used to further understand primate movement ecology (Willems et al. 2009). Increasing primate group sizes also results in longer DPLs (Clutton-Brock & Harvey 1979) since larger groups experience greater intragroup feeding competition (Isbell 1991) and exhaust food patches quicker, forcing more frequent travel between patches (Isbell 1991; Hoffman & O'Riain 2012; Chapman et al. 1995). Note, however, that primates with a more leaf-based and herbaceous diet lessens the effect of group-size on DPLs because the spatial-temporal distribution of leaves is more homogenous (e.g. *Brachyteles arachnoides hypoxanthus* (Chapman et al. 1995);

Colobus badius tephrosceles, (Isbell 1983); *Gorilla* spp., (Doran - Sheehy et al. 2004; Ganas & Robbins 2005)).

Baboons (*Papio* spp.) range throughout sub-Saharan Africa, across a multitude of habitat types making them the most widespread African primate genus (Kingdon 2003) and perhaps coincidentally, are one of the best studied primates, particularly with respect to DPL. Numerous studies have shown that baboon DPLs respond to extrinsic changes in biotic and abiotic factors, attributed to the highly seasonal environments in which they live (Altmann 1974; Wahungu 2001; Barton 1992; Harding 1976; Pebsworth, MacIntosh, et al. 2012), and also to intrinsic social factors (Stacey 1986; Barton 1992). Accordingly, baboon troop DPLs across their range can be reliably predicted by group size and rainfall, as shown by a classic study by Dunbar in 1992 (Dunbar 1992).

Since Dunbar's original study (Dunbar 1992) there have been further studies of the climatic determinants of foraging and ranging behaviour in baboons (Hill & Dunbar 2002; Bettridge et al. 2010; Korstjens et al. 2010), and new data on baboon DPL and ecology now exist. I therefore revisit the question of what determines baboon troop DPLs at a continental scale with the addition of 29 data points (DPLs) taken from recent literature, whilst considering additional ecological variables. I adopt a mixed modelling/model selection approach instead of the stepwise linear regression approach used originally (Dunbar 1992), and also consider the potential impact of anthropogenic influence, primate species number, and NDVI. I consider anthropogenic influence because where baboons rely on predictable and high-quality food sources (e.g. crops or food/waste) that occur in human modified habitats (e.g. Hoffman & O'Riain 2012; Isbell 1991), DPLs are found to be reduced and not predicted well by models that include rainfall and group size as predictors (Bronikowski & Altmann 1996). I consider primate species number on the basis that a high number of primate species may result in increased levels of inter-specific competition, which is known to drive longer DPLs, especially in frugivorous primates (e.g. Isbell 1991; Clutton-Brock & Harvey 1977b; Hill & Dunbar 2002). Additionally, as a more recent technological development, not available to Dunbar in his 1992 study, I also consider NDVI data as it provides a good proxy for photosynthetic activity and vegetation structure for study sites (Pettorelli et al. 2005; Willems et al. 2009).

Our understanding of the ecological determinants of baboon day path lengths at a finer (local) scale comes primarily from arid savannah habitats (Altmann 1974; Post 1981; Sigg & Stolba 1981; Sharman 1981; Davidge 1978; Norton, R. Rhine, et al. 1987), even when considering more recent studies on the topic (Whiten et al. 1991; Gaynor 1994; Bronikowski & Altmann 1996; Swedell 2002; King 2008; Schreier & Grove 2010; Hoffman & O'Riain 2012; Markham 2012; Pebsworth, MacIntosh, et al. 2012). To provide a fuller analysis of the ecological determinants of movement at a local scale, and to complement my continental scale analyse (see above), I investigated the daily movements of two troops of yellow baboons, *Papio cynocephalus*, inhabiting the primate-rich, seasonal, and predominantly woodland habitat of the Issa Valley in Ugalla, western Tanzania. This represents the first study of baboons in this region. I begin by exploring how well my inter-population model predicts DPLs for the Issa baboons, and then go on to consider what local ecological factors predict variation in DPLs and movement characteristics.

Variation in food resources are predicted to have a large effect on baboon space use. The proportion of fruit-based versus leaf-based forage in the diet, in particular, can have a large effect upon day ranges, with DPL increasing with the quantity of fruit in the diet (Clutton-Brock & Harvey 1977b). Since fruit tends to grow ephemerally in small, finite patches, which are distributed heterogeneously, it is quickly exhaustible (Chapman & Chapman 2000; Chapman et al. 1995) and necessitates longer DPLs. Reliance on high-quality fruit can also drastically alter movement characteristics to maximise efficiency (Isbell 1991) and primates foraging on fruit show faster (Pochron 2001), straighter and more goal-directed movement characteristics (Garber 1989; Menzel 1997; Janson 1998). In contrast, leaf-based and herbaceous foods have a more homogeneous distribution in space and time (Ganas & Robbins 2005) affording shorter DPLs and slower, more tortuous movement (Pochron 2000b; Sueur 2011). Regardless of food type, food abundance is dependent upon local, temporal variation in climate (van Schaik et al. 1993; Marshall & Wrangham 2007), and when food is scarce, individuals typically increase their DPLs in search of these food items (e.g. *Papio hamadryas*, (Swedell 2002); *Papio anubis*, (Harding 1976); *Eulemur rubriventer* and *Eulemur fulvus rufus*, (Overdorff 1993); *Gorilla gorilla*, (Cipolletta 2004); *Rhinopithecus* sp., (Grueter et al. 2009); *Colobus satanas*, (McKey & Waterman 1982); *Cercocebus galeritus*, (Wieczkowski 2005)). I therefore expected the baboons at Issa to demonstrate slower, less direct travel, and an increased DPL in times of reduced fruit availability (Altmann 1974; Wahungu 2001; Barton 1992; Harding 1976; Pebsworth, MacIntosh, et al. 2012).

Other climatic variables can also directly influence primate, and specifically baboon, ranging behaviour. If temperatures are too low, or too high, for example, primates reduce time spent travelling in order to conserve energy (e.g. *Rhinopithecus bieti*, (Baoping et al. 2009); *Papio ursinus*, (Stoltz & Saayman 1970)). Thus, ambient temperature can be an important climatic constraint on primate ranging behaviour, and I therefore tested the prediction that the baboons DPLs will be constrained by maximum daily temperatures in the warm Tanzanian climate, resulting in slower movement (Korstjens et al. 2010) and reduced DPL (Stoltz & Saayman 1970). Finally, given that Issa's baboons experience distinct wet and dry seasons, I also tested for any effect of season that might have additional and independent effects upon DPLs and movement characteristics because, for example, the availability of water sources change (Altmann 1974).

Methods

Continental scale

Data collection: For my continental scale analysis I used data provided in Dunbar's (1992) study (Dunbar 1992) and updated this with DPLs of 29 more recent studies from the literature (see Table 4.1). If data were available for more than one group at a study site, I use each troop's DPL, and I collected information on the rate at which troop locations were taken throughout the day, i.e. sampling frequency, and whether annual mean DPL was calculated from >12 months study, <12 months, or if this was unknown, i.e. sample size. This enabled us to test for/control for any potential effect of differences in how annual mean DPL were estimated across studies in my analyses. I also collected information on troop size, anthropogenic influence (whether or not the diet of the troop was supplemented by human derived foods [yes/no]) and the number of primate species occurring at each study site. Nocturnal primates were included in the primate species count so as to account for any indirect competition that may result from their spatial overlap with the baboons. These ecological data for each study site are summarised in Table 4.2, and troop specific data on group sizes and DPLs are summarised in Table 4.1.

In keeping with previous comparative studies (e.g. Bettridge et al. 2010; Korstjens et al. 2010; Dunbar 1992; Hill & Dunbar 2002) I investigated the effect of the following climate variables on mean annual DPL: mean annual temperature (Tann), mean annual rainfall (Pann), variation (standard deviation) in monthly temperature (TmoSD), variation (standard deviation) in monthly rainfall (PmoSD), the number of months per year with less than 100mm of rainfall (P<100), and the primary productivity index (PPI: the number of months in the year where rainfall was more than twice the average annual temperature). PPI is a useful measure of productivity during the growing season in tropical habitats and is therefore a useful index of seasonality (Houerou 1984). These climate data were taken from the original studies and/or (Dunbar 1992); where this information was not available, I followed the methods provided in Bettridge et al. (Bettridge et al. 2010) and used data from the Willmott & Matsuura (Willmott & Matsuura 2001) meteorological database. This database provides a global dataset of annual and monthly temperatures and rainfall in grids of 0.5° latitude by longitude, which are derived from a combination of Legate and Willmott's (D. R. Legates & Willmott 1990; David R. Legates & Willmott 1990) weather station records and the Global Historical Climatology Network (version 2). I calculated average values across all data points in the Willmott & Matsuura dataset that fell within 0.5° latitude and longitude to the relevant site. All temperatures are provided in °C, and rainfall in mm. I also collected remotely sensed information on NDVI, since it is a well-established measure of photosynthetic activity and vegetation structure (Myneni et al. 1995) with proven applications in understanding species' ecology (Pettorelli et al. 2005; Willems et al. 2009). NDVI data was retrieved for an area of 10.25km^2 for each study site from the Oak Ridge National Laboratory Distributed Active Archive Centre (http://daac.ornl.gov/MODIS/modis.html) and a 14-year average for each site was calculated from the available MOD 13Q1 data set (2000-2014). All climate data for each specific baboon study site are summarised in Table 4.3.

Table 4.1. Ecological data for each of the n=47 troops used in the DPL continental comparison model.

Study Site & (Troop)	Troop size	Mean Annual DPL	GPS Sample Interval (mins)	DPL Sample Size	Reference
Amboseli, Kenya (1)	59	6.10	60	>12months	(Post 1978)
Amboseli, Kenya (2)	40	4.20	60	>12months	(Altmann & Altmann 1970)
Amboseli, Kenya (3)	63	4.66	60	>12months	(Bronikowski & Altmann 1996)
Amboseli, Kenya (4)	55	5.43	60	>12months	(Bronikowski & Altmann 1996)
Amboseli, Kenya (5)	55	4.00	60	>12months	(Bronikowski & Altmann 1996)
Amboseli, Kenya (6)	53	5.00	60	>12months	(Markham 2012)
Awash, Ethiopia (1)	160	7.50	NA	>12months	(Swedell 2002)
Awash, Ethiopia (2)	210	8.30	15	>12months	(Schreier & Grove 2010)
Awash, Ethiopia (3)	81	5.30	30	<12months	(Nagel 1973)
Awash, Ethiopia (4)	51	6.50	30	<12months	(Nagel 1973)
Awash, Ethiopia (5)	57	5.40	30	<12months	(Nagel 1973)
Blouberg, SA	25	7.70	5	>12months	(Noser, pers comm)
Bole Valley, Ethiopia	19	1.20	15	<12months	(Dunbar & Dunbar 1974)
Budongo, Uganda	38	3.80	NA	Unknown	(Patterson 1976)
Cape Peninsula, South Africa (1)	49	5.64	20	>12months	(Hoffman 2011)
Cape Peninsula, South Africa (2)	36	4.85	20	>12months	(Hoffman 2011)
Cape Peninsula, South Africa (3)	22	6.61	20	>12months	(Hoffman 2011)
Cape Peninsula, South Africa (4)	16	1.80	20	>12months	(Hoffman 2011)
Cape Peninsula, South Africa (5)	26	3.17	20	>12months	(Hoffman 2011)
Cape Peninsula, South Africa (6)	16	3.92	20	>12months	(Hoffman 2011)
Cape Peninsula, South Africa (7)	35	4.13	20	>12months	(Hoffman 2011)
Cape Peninsula, South Africa (8)	24	2.89	20	>12months	(Hoffman 2011)
Cape Peninsula, South Africa (9)	115	2.96	20	>12months	(Hoffman 2011)
Cape Peninsula, South Africa (10)	85	7.90	30	>12months	(Davidge 1978)
CholOlo, Kenya	102	5.60	15	Unknown	(Barton 1989)
Drakensberg, SA (1)	9	4.30	30	<12months	(Whiten et al. 1987)
Drakensberg, SA (2)	14	3.80	30	>12months	(Whiten et al. 1987)
Erer-Gota, Ethiopia	72	9.50	NA	>12months	(Kummer 1968)
Gashaka Gumti, Nigeria (1)	19	3.10	30	>12months	(Warren et al. 2011)

Table 4.1. Continued

Study Site & (Troop)	Troop size	Mean Annual DPL	GPS Sample Interval (mins)	DPL Sample Size	Reference
Gashaka Gumti, Nigeria (2)	28	2.40	30	>12months	(Warren et al. 2011)
Gilgil, Kenya	57	4.60	NA	<12months	(Harding 1976)
Honnet, SA (1)	77	4.00	NA	>12months	(Stoltz & Saayman 1970)
Honnet, SA (2)	59	6.50	NA	>12months	(Stoltz & Saayman 1970)
Ishasha, Uganda	45	2.40	60	>12months	(Rowell 1966)
Metahara, Ethiopia	87	5.80	NA	<12months	(Aldrich-Blake & Bunn 1971)
Mikumi, Tanzania	120	3.40	NA	>12months	(Rasmussen 1978)
Mkuzi, SA	71	6.04	10	Unknown	(Gaynor 1994)
Mt. Assirik, Senegal (1)	250	8.10	30	>12months	(Sharman 1981)
Mt. Assirik, Senegal (2)	135	7.60	30	>12months	(Sharman 1981)
Mulu, Ethiopia	22	1.10	NA	Unknown	(Dunbar, pers comm)
Suikersbosrand, South Africa	78	4.10	NA	>12months	(Anderson 1981)
Tana, Kenya	75	5.30	15		(Wahungu 1998)
Tsaobis, Namibia (1)	57	6.00	30	>12months	(King 2008)
Tsaobis, Namibia (2)	32	6.00	30	>12months	(King 2008)
DeHoop, South Africa (1)	40	5.65	30	<12months	(Hill 1999)
DeHoop, South Africa (2)	17	4.86	30	<12months	(Hill 1999)
Mt. Zebra, South Africa	28	2.50	NA	Unknown	(Seyfarth 1976)
Issa, Tanzania	24	4.70	5	<12months	Current study
Issa, Tanzania	32	3.70	5	<12months	Current study

Table 4.2: Ecological data for the 23 baboon populations used in the DPL continental comparison model.

Species & Study Site	Latitude	Longitude	Altitude	#Study Troops	#Pr[1]	Ant?[2]	References[3]
Papio anubis							
Bole, Ethiopia	9.42	38.00	1700	1	4	No	(Dunbar & Dunbar 1974)
Budongo, Uganda	1.93	31.67	700	1	7	No	(Patterson 1976)
Chololo, Kenya	0.40	36.95	1660	1	2	No	(Barton 1989)
Gashaka Gumti, Nigeria	7.51	11.61	320	2	9	Yes (1/2)	(Warren et al. 2011)
Gilgil, Kenya	-0.49	36.32	1770	1	1	No	(Harding 1976)
Ishasha, Uganda	-0.62	29.66	950	1	4	No	(Rowell 1966)
Metahara, Ethiopia	8.91	39.93	950	1	2	No	(Aldrich-Blake & Bunn 1971)
Mulu, Ethiopia	9.30	40.83	1275	1	2	No	(Dunbar, *unpublished*)
Papio cynocephalus							
Amboseli, Kenya	-2.64	37.25	1130	6	3	Yes (1/6)	(Post 1978; Altmann & Altmann 1970; Bronikowski & Altmann 1996)
Mikumi, Tanzania	-7.09	37.42	550	1	5	No	(Rasmussen 1978)
Tana, Kenya	-1.93	40.14	30	1	6	No	(Wahungu 1998)
Issa, Tanzania*	-5.51	30.56	1600	2	6	No	This study
Papio hamadryas							
Awash, Ethiopia	8.84	40.01	950	5	2	No	(Swedell 2002; Schreier & Grove 2010; Nagel 1973)
Erer-Gota, Ethiopia	9.56	41.38	1200	1	1	No	(Kummer 1968)
Papio papio							
Mt. Assirik, Senegal	12.87	-12.80	150	2	6	No	(Sharman 1981)
Papio ursinus							
Blouberg, SA	-23.03	29.06	900	1	3	No	(Noser, *unpublished*)
Cape Point, SA	-34.27	18.43	50	10	1	Yes (7/10)	(Hoffman & O'Riain 2010; Pebsworth, MacIntosh, et al. 2012; Davidge 1978)
Drakensberg, SA	-29.47	29.26	2250	2	1	No	(Whiten et al. 1987; Whiten et al. 1991)

Table 4.2: Continued

Species & Study Site	Lat-itude	Long-itude	Alti-tude	#Study Troops	#Pr[1]	Ant?[2]	References[3]
Honnet, SA	22.63	30.18	310	2	2	Yes (1/2)	(Stoltz & Saayman 1970)
Mkuzi, SA	-27.60	32.05	125	1	2	No	(Gaynor 1994) from (Hill 1999)
Suikersbosrand, SA	-26.50	28.22	1600	1	2	No	(Anderson 1981)
Tsaobis, Namibia	-22.55	15.73	1000	1	1	No	(King 2008)
DeHoop, SA	-34.43	20.57	10	2	1	No	(Hill, *unpublished*)
Mt. Zebra, SA	-32.20	25.39	1500	1	1	No	(Seyfarth 1976) from (Hill 1999)

[1] Pr, number of primate species. [2] Ant, Indicates whether baboons studied experience anthropogenic influences, and if so, how many troops. [3]Unpublished data are acquired from authors listed.

Statistical Analyses:

I fitted annual mean DPL as the response variable in a linear mixed model (LMM) in R (lme4 package (R Development Core Team 2010), R version 3.1.0) to determine which of the aforementioned ecological and climatic variables best explained variation in mean baboon troop DPLs. I fitted 'population' as a random effect to control for the potential non-independence of data from multiple troops within the same population. Co-linearity between all effects was checked using Spearman's rank correlation tests, with a cut-off criterion of $r_s = 0.60$ (Tabachnick & Fidell 2012) for including effects in the same model. I then fitted a series of models entering combinations of ecological and climate variables as continuous fixed and/or categorical fixed effects. Table 4.4 provides the top ten candidate models used to predict variation in annual mean DPL at a continental scale. To choose among models, I adopted a minimum adequate model selection procedure that considered all biologically meaningful combinations of the fixed effects described. Candidate models with the lowest Akaike information criterion (AIC) value (Akaike 1998) were consequently selected. Where models had AIC scores within two points of each other, both models were considered to be plausible alternatives and the model that was the most parsimonious (i.e. the model with the fewest fixed effects) was selected preferentially (Burnham & Anderson 2002). The significance of individual terms were then calculated from the selected model and terms not included in the selected model were put back into the model to obtain level of non-significance (lmerTest package, R: (Kuznetsova 2012)).

Table 4.3: Climate and environmental data for the 23 baboon study populations used in the DPL continental comparison model.

Species & Study Site	Pann	PmoSD	Tann	TmoSD	PPI	P<100	NDVI
Papio anubis							
Bole, Ethiopia	1105	85.75	19.50	1.30	8.0	8.0	0.47
Budongo, Uganda	1679	68.18	22.10	0.75	10.0	4.5	0.84
Chololo, Kenya	549	40.31	22.90	1.03	5.0	9.5	0.29
Gashaka Gumti, Nigeria	1800	109.90	26.60	1.00	8.0	5.0	0.38
Gilgil, Kenya	595	20.95	18.10	0.69	5.0	11.0	0.46
Ishasha, Uganda	1292	37.87	22.00	0.93	10.0	6.0	0.68
Metahara, Ethiopia	639	58.99	24.50	1.56	6.0	9.0	0.26
Mulu, Ethiopia	1105	64.00	15.90	1.61	8.0	7.0	0.42
Papio cynocephalus							
Amboseli, Kenya	336	23.44	22.86	1.43	3.0	11.0	0.26
Mikumi, Tanzania	832	63.27	25.21	2.72	6.0	6.0	0.6
Tana, Kenya	803	49.57	28.00	1.12	5.0	9.0	0.72
Issa, Tanzania*	1200	79.69	20.00	0.32	7.0	5.0	0.6
Papio hamadryas							
Awash, Ethiopia	639	49.28	24.62	1.68	6.0	8.8	0.28
Erer-Gota, Ethiopia	665	59.12	24.20	1.61	5.0	9.0	0.32
Papio papio							
Mt. Assirik, Senegal	953.9	97.90	30.50	2.45	5.0	7.7	0.47
Papio ursinus							
Blouberg, SA	343	35.42	20.75	3.67	7.0	12.0	0.50
Cape Point, SA	743	36.86	17.90	3.47	6.9	10.0	0.42
Drakensberg, SA	1197	82.57	14.60	4.18	8.3	6.0	0.45
Honnet, SA	307	45.01	21.33	3.58	3.0	10.3	0.29
Mkuzi, SA	630	37.77	22.40	2.92	6.0	9.8	0.68
Suikersbosrand, SA	700	44.42	15.95	4.50	7.0	9.0	0.56
Tsaobis, Namibia	122	16.45	13.80	2.33	3.0	12.0	0.12
DeHoop, SA	428	9.23	16.50	3.07	7.0	12.0	0.58
Mt. Zebra, SA	343	16.11	15.00	4.57	6.0	12.0	0.32

Pann average annual rainfall, *PmoSD* standard deviation for average monthly rainfall (mm), *Tann* average annual temperature (°C), *TmoSD* standard deviation for average monthly temperature (°C), *PPI* primary productivity index (number of months in the year in which rainfall was twice the average annual temperature), *P<100* number of months with less than 100mm rainfall, *NDVI* normalised difference vegetation index retrieved from remote sensing data. * Current study; not included in continental analysis.

Table 4.4: Akaike Information Criteria (AIC) values for the top ten candidate models that predict variation in annual mean DPL at a continental scale. Candidate models are based on compatible effects, in ascending order of AIC value. The model in bold indicates the final model selected.

Candidate models	**df**	**AIC**
Tann + Pann + Ant + Samp	8	168.6
Tann + P<100 + Samp + Ant	7	169.0
Tann + P<100 + Samp + Ant + GS	8	169.1
Tann + Pann + Ant + Samp + Alt	9	169.2
Tann + Pann + Ant	**6**	**169.5**
GS + Pann + Ant + Samp + Alt	8	169.9
GS + PPI + Ant + Samp + Alt + Pr	9	170.0
Ant + Samp + NDVI + P<100 + Tann	8	170.6
Ant + Samp + Alt + P<100 + Tann	8	170.6
Ant + Samp + NDVI + PmoSD + Tann + TmoSD	9	171.4

Alt altitude (meters above sea level), *Pr* primate species count at study site, *Ant* troops exposed to anthropogenic influence, *Pann* average annual rainfall, *PmoSD* standard deviation for average monthly rainfall (mm), *Tann* average annual temperature (°C), *TmoSD* standard deviation for average monthly temperature (°C), *PPI* primary productivity index (number of months in the year in which rainfall was twice the average annual temperature), *P<100* number of months with less than 100mm rainfall, *NDVI* normalised difference vegetation index retrieved from remote sensing data, *Samp* sample size (>12 months, <12 months or unknown).

Local scale

Study site: Local scale data was collected in the Issa valley of western Tanzania (05° 23 S 30° 35 E), 81km East of Lake Tanganyika. The Ugalla region extends over 3352 km^2 and is comprised of steep, broad valleys and flat hilltop plateaus that range in altitude from 900 -1800m. The habitat of the study area is described as being a diverse mixture of vegetation types including swamp, dry grassland, wooded grassland, woodland, gallery forest, thicket forest, and hill forest (Stewart et al. 2011).

Movement data: Movement data were collected by CJ and field assistants from January to August 2012 in accordance with the regulations of the Tanzanian Wildlife Research Institute. In total 81 days were spent tracking two troops of yellow baboons over the study period. These were Matawi Troop (MT, N = 31 group members) and Camp Troop (CT, N = 22 group members). The baboons were successfully located on 61 of these tracking days. Once found, the troop was followed until they reached a sleeping site, typically around 19:00. Observers would then return the following morning to the same place at 07:00 (before baboons left the sleeping site). This was repeated until they were lost, or a full three days of follows were completed. In total this yielded a total observation time of 546 hrs (CT: 349 hrs, MT: 197 hrs). Due to the unhabituated nature of the baboons, and my reliance on opportunistic sightings required to start a follow, follow days are distributed randomly across study months. On all occasions the troops were followed, troop movement was recorded at 5-minute intervals, at a distance of 20-50m behind the troop, using hand-held Garmin 520Hcx 2-way radio Global Positioning Systems (GPS). These GPS data were used to record the distance troops travelled from sunrise (07:00 ± 15 mins) to sunset (19:00 ± 30mins).

To calculate DPLs, distances between consecutive GPS points were calculated using the Great-Circle Equation (Dunlap et al. 1972). DPL's were only calculated from full-day follows, or where the baboon locations were unknown for a period of less than 60 minutes representing a mean of 4.8 full day follows per month (CT: 3.1 days per month, MT: 1.7 days per month). Movement characteristics, as described by speed and turning angle distributions can provide information on orientation and searching behaviour (Benhamou 2004). Speed (m/min) and turning angle (θ) were calculated for successive GPS locations using the adehabitatLT package, R (Calenge 2006).

Temperature and season: Please refer to Chapter 2, pages 25-26 and Figure 2.4 for a full description of the local climate and seasonality during the study period.

Food availability: Whilst baboons rely on a variety of food sources (Norton, R. Rhine, et al. 1987), fruit comprises a large portion of their diet (Ransom 1981b; Davidge 1978; Sharman 1981; Sigg & Stolba 1981; Rasmussen 1978; Bronikowski & Altmann 1996; Depew 1983; Harding 1976; Barton 1989; Dunbar & Dunbar 1974; Norton, R. Rhine, et al. 1987) and is selected for when available (Altmann 1974). I therefore utilised a pre-established phenology transect, that intersected the miombo woodland habitat, that was 1.7km in length and 10m in width and was fully contained within the home range of CT. Only woody plants known to produce fruits or seed pods that were consumed by the baboons and that were ≥ 2m in height with a diameter at breast height ≥ 5cm were monitored. This resulted in a total of 288 shrubs, lianas and trees from 17 species. The transect was walked every month for the duration of the study period, and the presence/absence of fruit or seed pods for each plant was noted (Chapman et al. 1994). Fruit abundance (I use this as a proxy for fruits and seed pods combined) was then estimated with a commonly used measure, the monthly fruit abundance index (FAI_m) (Head et al. 2011; Anderson et al. 2005; Yamagiwa & Basabose 2006; Nkurunungi et al. 2004):

$$FAI_m = \sum_{k=1}^{n} D_k B_k P_{km}$$

where D_k is the density of species k per km2, B_k is the mean DBH of species k, and P_{km} is the percentage of trees of species k in a fruiting condition in a month m (Figure 4.1).

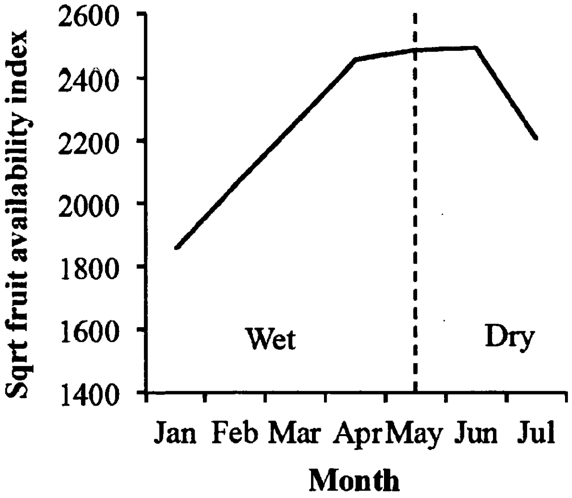

Figure 4.1: Fruit abundance. Fruit abundance at Issa for duration of study period. The dashed line represents the division between seasons.

Statistical analyses: To test for differences in DPLs of the two Issa troops, a Mann Whitney U-test was used. To investigate what factors predicted variation DPL I used a linear model (LM) (lme4 package, R: (R Development Core Team 2010)), with normal error structure. I fitted a series of fixed effects in accordance with my predictions. My two continuous effects were maximum temperature (^{o}C) and FAI, and I fit season (wet, dry), and troop ID as categorical effects. I used maximum temperature as a reflection of the hottest part of the day, which is most likely to constrain baboon DPL. Table 4.5 provides the top ten candidate models used to predict variation in DPL at the local scale.

Table 4.5: Akaike Information Criteria (AIC) values for the top ten candidate models that predict variation in DPL at a local scale. Candidate models are based on compatible effects, in ascending order of AIC value. The model in bold indicates the final model selected.

Candidate models	df	AIC
Max Temp	**1**	**418.4**
Max Temp + Se	2	418.7
Max Temp + FAI	2	419.2
Max Temp + Tr	2	419.9
Max Temp + Tr + Se	3	420.1
Max Temp + Tr + FAI	3	420.9
Max Temp + Se + Tr + FAI	4	422.1
Tr + Se	2	430.6
Se + FAI	2	431.1
Tr + Se + FAI	3	432.6

FAI fruit availability index, *Max Temp* maximum temperature, *Se* season, *FAI* fruit abundance index, *Tr* troop ID

To test what factors predicted variation in speed and/or distribution of turning angles I implemented generalised additive models (GAM) (mgcv package, R: (R Development Core Team 2010)). I only analysed speed and turning angle data where baboons were not stationary (i.e. speed > 1 m/min), and randomly sub-sampled n=10 data points from each observation day to remove any temporal auto-correlation in my data. I then fitted maximum temperature, FAI and season (wet, dry) as fixed effects, whilst controlling for any effect of day (of study period) and troop (CT, MT). I used a GAM here rather than a standard linear model because GAMs are more capable of recognising nonlinear temporal variation (Hastie & Tibshirani 1986). The smoothed effect of time (day of study period) was based on penalized regression splines, to take into consideration the cyclic pattern of patterns of space-use.

For both my LMM (DPL analyses) and GAMs (speed, turning angle analyses) minimum adequate model selection was based on a procedure that considered all biologically meaningful combinations of fixed effects. The best model was subsequently selected by the lowest AIC value (Akaike 1998), but models within two AIC points were considered to be plausible alternatives and the model that was the most parsimonious (i.e. the model with the fewest fixed effects) was selected preferentially (Burnham & Anderson 2002). The significance of the individual terms was then calculated from the selected model and all dropped terms were put back into the model to obtain the level of non-significance (lmerTest package, R (Kuznetsova 2012)).

Results And Discussion

Continental scale

My analysis of the effects of ecological and biological variables on DPLs at a continental scale indicates that mean DPLs for 47 baboon troops across 23 different populations were best explained by a model that considered the independent effects of mean monthly rainfall, mean annual temperature, and anthropogenic influence (Table 4.6; Figure 4.2 and see Table 4.4 for best candidate models). All other fixed effects tested did not significantly predict variation in annual mean DPL (Table 4.6). I discuss each of the main effects in turn.

Table 4.6: Estimates, standard error, test statistics and P-value for compatible predictors of annual mean DPL at a continental scale from a Linear Mixed Model. The best fitting model included those terms shown in bold text; for AIC values of the best candidate models tested see Table 3.

Model term	Estimate	Standard error	*t*-value	*df*	*p*
Temperature (mean annual)	**0.24**	**0.07**	**3.61**	**1**	**0.002**
Rainfall (mean annual)	**-0.003**	**0.0007**	**-4.14**	**1**	**0.0005**
Anthropogenic influence[1]	**-2.04**	**0.46**	**-4.39**	**1**	**0.0001**
Sample size (months)[2]	0.34	0.79	0.44	2	0.08
Temperature (monthly SD)[3]	0.41	0.27	1.51	1	0.14
Troop size	0.005	0.005	0.92	1	0.36
Altitude	-0.0006	0.0005	-1.25	1	0.22
Sample frequency (GPS)[4]	-0.03	0.02	-1.65	1	0.14
NDVI	-0.84	1.89	-0.44	1	0.66

[1] Categorical effect (yes, no); reference category was no anthropogenic influence. [2] Categorical effect representing whether the mean DPL was calculated from >12 months study, <12 months, unknown. [3] Standard deviation in rainfall across months. [4] The frequency of GPS fixes taken per hour to calculate DPL.

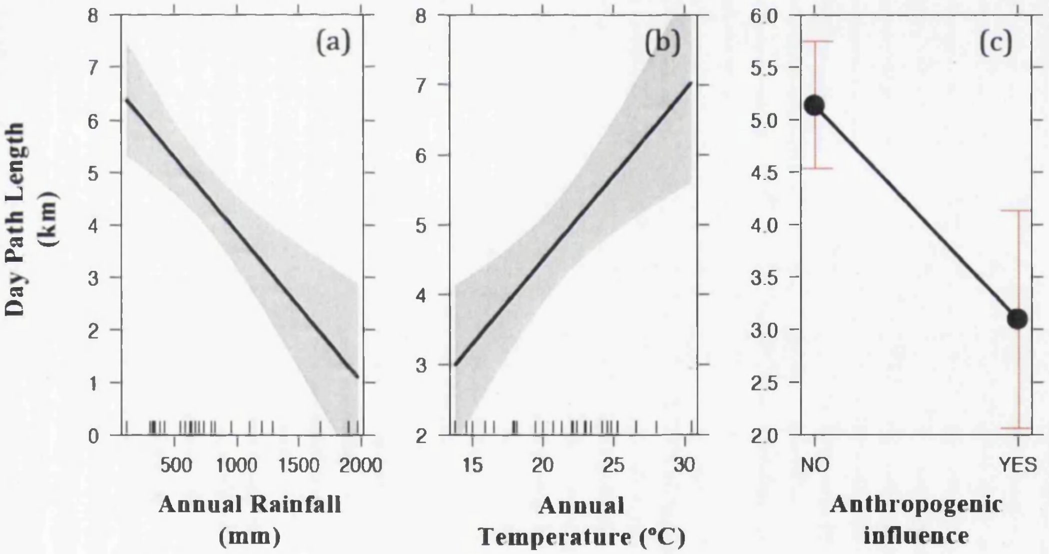

Figure 4.2: Predictors of DPL for N=47 baboon troops across Africa. Significant effects of (a) average monthly rainfall (effect[SE] = 0.04[0.01]; df =1; p=<0.0003); (b) average annual temperature (effect[SE] = -0.23[0.06]; df =1; p=0.001); (c) Anthropogenic influence (effect[SE] = -2.01[0.42]; df =1; p=0.0001). Effects shown are predictions from our LMM (see Table 7) and upper and lower 95% confidence limits are indicated by shaded areas for (a) and (b) and whiskers for (c).

With higher mean monthly rainfall I found shorter baboon DPLs. As higher levels of precipitation typically result in more productive habitats and therefore more food (van Schaik et al. 1993; Deshmukh 1984), troops should encounter food more frequently and thus travel shorter distances at sites that experience high rainfall (Altmann 1974). A more direct measure of vegetation (NDVI) did not, however, predict annual mean DPL. One possible reason for this might be because of baboons reliance on surface water, that they require on a daily basis (Altmann & Altmann 1970), and whilst NDVI may represent "better" quality habitat, it does not necessarily reflect water availability, which might act as a constraint on baboon movement. I also found that baboons in hotter habitats travel further than those in cooler habitats. If the relationship between temperature and DPL in this case were causal, we would expect baboons to travel less far in hotter habitats, due to enforced rest as a result of thermal loading (Hill 2006). Instead, it is likely that higher ambient temperatures reflect more arid and therefore less productive environments with less surface water (Fischer & Turner 1978). I therefore interpret the positive effect of hotter environments on annual mean DPL to be a consequence of variance in productivity and surface water across sites. Given the significance of annual temperature and monthly rainfall at this scale, it would be instructive to gather information on the availability of drinking sites/surface water in future work to quantify directly the importance of this resource in determining baboon DPL. The last effect to predict annual mean DPL at the continental scale was "anthropogenic influence" (yes, no). Anthropogenic influence was not considered by Dunbar (1992) in his original model, but has since been highlighted as an important factor mediating DPLs (Bronikowski & Altmann 1996; Hoffman & O'Riain 2012). This is because baboons in human-modified habitats typically have access to high quality and predictable food resources meaning baboons are able to sate their nutritional requirements within a smaller daily ranging distance, e.g. by crop-raiding and/or scavenging human foods (Brennan et al. 1985; Hill 2005; Siemers 2000; Altmann 1988; Saj et al. 1999; Strum 2010; Hoffman & O'Riain 2012).

Contrary to Dunbar (1992) and my own expectations, I did not find that group size predicts variation in annual mean DPL. The negative effect of increasing group size on ranging behaviour has been well documented across the primate order (Chapman 1990;

Clutton-Brock & Harvey 1977b) and within the baboon genus (Barton 1992; Stacey 1986; Dunbar 1992). The lack of any group size effect here might be explained by the importance of the key ecological variables retained in my final model; these appear to be far more important, perhaps reflecting the changing environments and associated increase in exposure to human-modified habitats that baboons are experiencing. The effect of human-modified habitat use has also been reported to negate the effect of group size at a local scale. In the Cape Peninsula, South Africa, Hoffman & O'Riain (Hoffman & O'Riain 2012) found that the largest group in the population (N=115) had a DPL that did not differ significantly from the two smallest troops (both troops N=16), which was explained by their near 100% use of human-modified habitat.

Local scale

At a local scale, I found that the median DPL for CT and MT were 4.7 km (range: 3.1–8.5) and 4.3 km (range: 1.5–6.0) respectively (Figure 4.3), and there was not a statistical difference between the DPLs of the two troops (Mann Whitney U-test: n_{CT}= 22, n_{MT}= 12, P = 0.725). Comparison of these observed DPLs and those DPLs predicted by the best continental-level model (see above) that considers monthly rainfall, annual temperature, and anthropogenic influence, whilst accounting for population, revealed that the actual DPL of Issa baboons was similar to the predicted DPL (Figure 4.4). Therefore, it appears that yellow baboons at Issa are not atypical and the same ecological factors that impact on baboon troop DPLs throughout their range are also good predictors of Issa troops DPLs.

Consideration of local ecological factors revealed that Issa baboon troops travelled significantly further (Table 6; Figure 4.5) and faster (Table 8) on cooler days. Due to the sensitivity of the vertebrate brain to even slight changes in temperature, the need for primates to regulate their internal temperature is vital (Precht & Brück 1973). In order to cool the brain, baboons dissipate heat through panting (Hiley 1976), however, they lack more typical mechanisms for the effective cooling of the brain (i.e. carotid rete) that are present in other similar sized, sympatric mammals (Brain & Mitchell 1999). This likely makes high radiant temperatures a greater challenge to their thermoregulation (Brain & Mitchell 1999). To avoid overheating, baboons have been observed to adjust their activity according to their thermoregulatory needs, with temperature being a negative function of activity in hot environments (Bronikowski & Altmann 1996; Stoltz & Saayman 1970; Hill 2006; Stelzner 1988). During periods of intense thermal loading, baboons are found to respond by seeking shade and engaging in more sedentary behaviours such as resting and grooming (Korstjens et al. 2010; Hill 2006; Pochron 2000a). Similarly, Stelzner (Stelzner 1988) found that travel rate in Amboseli baboons was dependent on ambient temperature at a microhabitat type level, and on hot days the baboons would slow down when traversing more shaded areas. It is plausible then, that as heat stress increases, baboons at Issa are forced into more sedentary activities, which could result in the reduced DPLs and speeds I observed. Concurrent direct observations of individual and troop level behaviours would be required to confirm that Issa baboons move less on hotter days due to enforced resting.

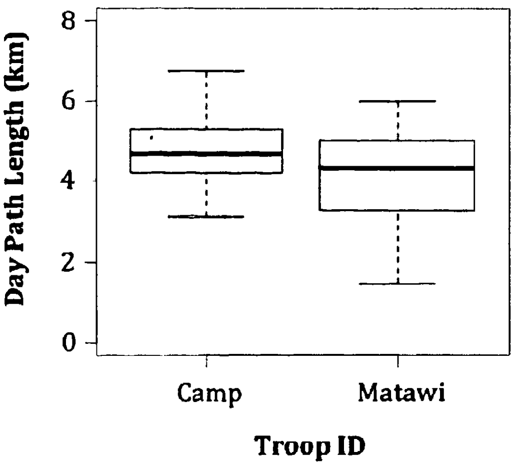

Figure 4.3: DPL of Issa baboon troops. Median DPLs of CT and MT troops during the study period. The upper and lower quartiles are shown by the range of the 'box', median value by the horizontal line within the box, and the full extent of the data given by the 'whiskers'.

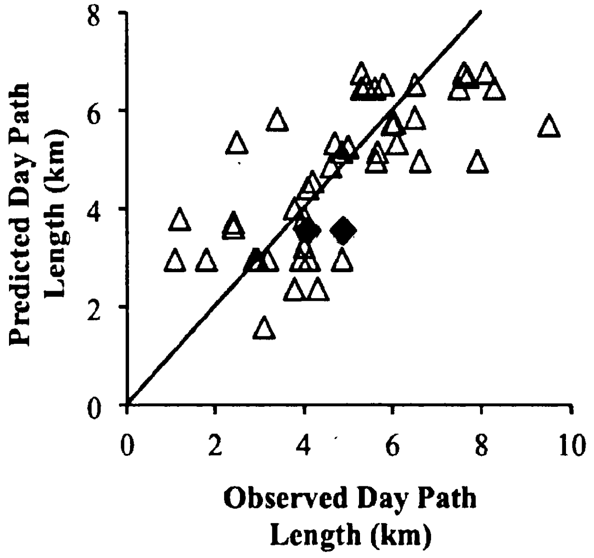

Figure 4.4: Predicted DPL against observed DPL for baboons on a continental scale. Predicted DPL calculated from a best fitting model model considering the effects of average monthly rainfall, average annual temperature, and anthropogenic influence, for troops listed in Table 4.1. The straight line passing through (0,0) is a hypothetical perfect 1:1 fit between the model and data. Predictions from the model are for N=47 troops with data for the Issa troops (Ugalla, current study) omitted; observed DPLs for the Issa troops are shown by filled diamonds.

Table 4.7: Estimates, standard error, test statistics and P-value for predictors of DPL at a local scale from a Linear Model. The best fitting model included those terms shown in bold text; for AIC values of the best candidate models tested see Table 4.5.

Model term	Estimate	Standard error	*t*-value	*df*	*p*
Max. temperature	-261.8	75.2	-3.48	1	0.0017
Fruit Abundance Index	27.6	204.7	0.14	1	0.89
Season (dry, wet) [1]	-512.61	408.24	-1.26	1	0.22
Troop ID (CT, MT) [2]	-276.18	405.24	-0.68	1	0.50

[1] Reference category was wet season. [2] CT = Camp Troop. MT = Matawi Troop; reference category was Camp Troop

Table 4.8: Estimates, standard error, test statistics and P-value for predictors of speed in the selected General Additive Model at a local scale. The best fitting model included those terms shown in bold text. Effect of smoothing factor is also shown with estimated degrees of freedom (edf), reference degrees of freedom (rdf), test statistic (*F*) and *p* value.

Model term	**Estimate**	**Standard error**	***t*-value**	***df***	***p***
Max. temperature	-0.04	0.01	-2.79	1	0.005
Fruit Abundance Index	-0.003	0.03	-0.09	1	0.93
Season (dry, wet)[1]	0.004	0.14	0.027	1	0.98
Rainfall	0.007	0.005	1.43	1	0.16
Smoothing factor		***F***	**edf**	**rdf**	***p***
Day		0.16	1	1	0.69

[1] Reference category was wet season.

Contrary to my expectations, I did not find FAI to significantly affect either DPL (Table 4.7) or the movement characteristics of baboons at Issa (Table 4.8; Table 4.9). A critical influence on ranging patterns of *P. cynocephalus* is the distribution of foods (Altmann 1974). In contrast with other studies (Altmann 1974; Wahungu 2001) local fruit abundance (here, FAI) did not significantly predict DPL (Table 4.7). My finer resolution analysis of the baboon's movement characteristic similarly found no effect of FAI on speed or turning angles. This is surprising, as primates have been consistently shown to use the space in their habitats according to the learned locations of particular resources and consequently move efficiently between them (Janson 1998; Menzel 1997; Garber 1989; Pochron 2001). This is especially true of fruiting trees, a core food group for baboons (Ransom 1981b; Davidge 1978; Sharman 1981; Sigg & Stolba 1981; Rasmussen 1978; Bronikowski & Altmann 1996; Depew 1983; Harding 1976; Barton 1989; Dunbar & Dunbar 1974; Norton, R. Rhine, et al. 1987). In support of this, Noser & Byrne (Noser & Byrne 2007) found baboons demonstrated increased route linearity and speed when travelling to sparse, out of site, fruit patches indicating the tendency for baboons to use their space in an efficient, goal-directed way. For this reason, I expected Issa baboons to demonstrate more direct travel movements when fruit availability increases. The difference between the two studies is instructive, and highlights the need for combining behavioural (or at least basic activity data) with movement information, so that it is possible to analyse segments of travel between known resources (Noser &

Byrne 2007). I therefore proceeded to explore whether FAI and/or season predicted the time troops spent moving (i.e. <1m/min versus >1 m/min) (see Appendix 3). I reasoned that time spent feeding should decrease with proportion of carbohydrate-rich fruits (Noser & Byrne 2007; Lehmann et al. 2008) in the diet (Hill & Dunbar 2002) resulting in decreased moving time as compared to other time budget variables (Lehmann et al. 2008). Therefore, I expected to see less time spent moving during periods of high FAI, and my model (Appendix 3, Table 3) confirmed this to be the case. Thus, whilst fine-scale movement of Issa baboons was not predicted by the availability of fruit resources, fruit availability did fundamentally alter the time they spent moving (Figure 4.6) (Clutton-Brock & Harvey 1977b; Isbell 1983; Altmann & Altmann 1970).

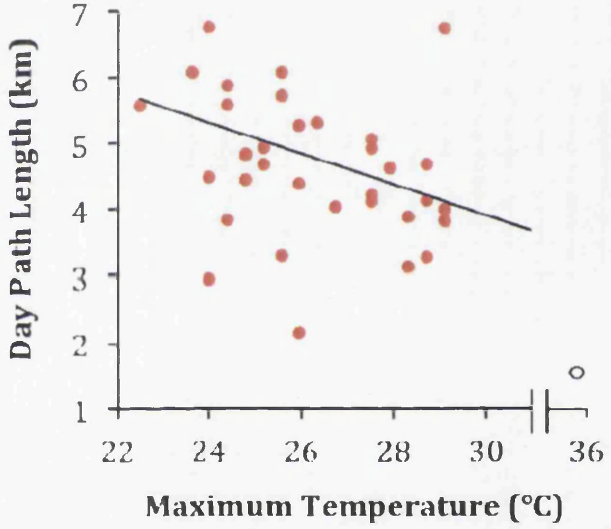

Figure 4.5. Relationship between maximum daily temperature and DPL in Issa baboons. The fitted line represents DPL as predicted by temperature (LMM: effect[SE] = -235.8[104.8]; df = 1; p = 0.025; see Table 6 for full model results). The empty circle to the right hand side represents the highest daily temperature and lowest DPL reading recorded; removing this data point does not quantitatively change the model results.

Table 4.9: Estimates, standard error, test statistics and P-value for predictors of the distribution of turning angles in the selected General Additive Model at a local scale. Effect of smoothing factor is also shown with estimated degrees of freedom (edf), reference degrees of freedom (rdf), test statistic (*F*) and *p* value.

Model term	**Estimate**	**Standard error**	***t*-value**	***df***	***p***
Max. temperature	-0.008	0.009	-0.98	1	0.33
Fruit Abundance Index	-0.0006	0.03	-0.19	1	0.98
Season (dry, wet) [1]	-0.14	0.072	-1.93	1	0.055
Rainfall	-0.00009	0.003	-0.04	1	0.97
Smoothing factor		***F***	**edf**	**rdf**	***p***
Day		1.98	1	1	0.16

[1] Reference category was dry season.

I found no significant effect of season (wet, dry) on baboon DPLs or movement characteristics (Table 4.7; Table 4.8; Table 4.9), although the effect of season on the distribution of turning angles was P = 0.055 (Table 4.9), indicating a trend for troops' movements to become more direct during the dry season in line with my original predictions. It may be possible that the lack of any strong seasonal patterns on movement characteristics may be due to the availability of water. Baboons are obligate drinkers (Altmann 1974) relying heavily on surface water, the availability of which is subject to large variation in sub-Saharan Africa. Surface water is therefore an important determinant of baboon ranging patterns (Sigg & Stolba 1981), and its availability is ultimately determined by seasonal rainfall (Norton, R. Rhine, et al. 1987) (also see above continental model). During my study period, surface water was readily available to the baboons, and so was unlikely to constrain movement paths. However, my study period did not extend through the driest months at the end of the dry season when running water at Issa becomes stagnant and gradually more confined to water holes (Hernandez-Aguilar 2006). Thus, the influence of surface water availability on ranging patterns cannot be fully determined without further study.

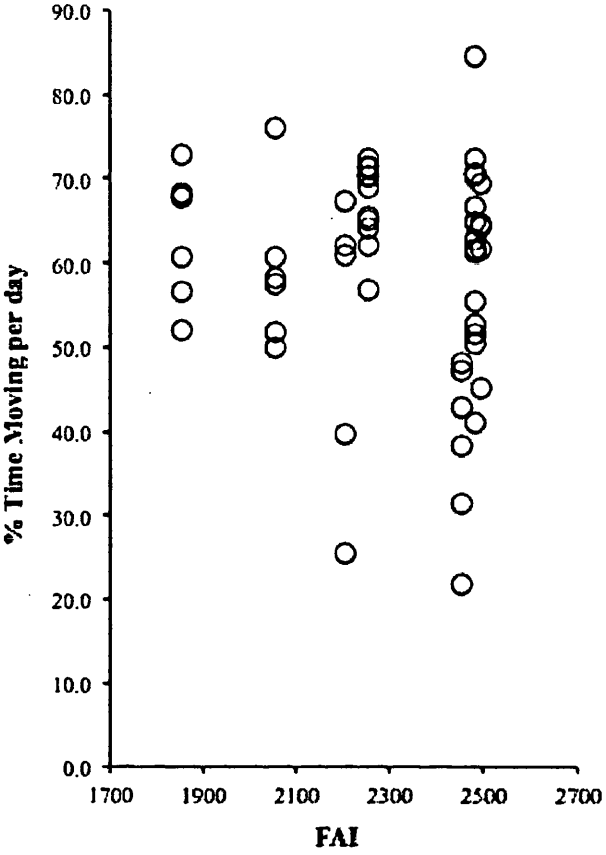

Figure 4.6: The proportion of time spent moving vs. not moving plotted against the Fruit Abundance Index. Fruit abundance values on x-axis are the square root of the actual value.

There may well be other key ecological factors that are important drivers of Issa baboon movements that I did not measure. For example, baboons mitigate the serious threat of nocturnal predation by utilising sleeping sites (i.e. specific sleeping trees or cliffs) (Altmann & Altmann 1970; Cowlishaw 1997b), and it is possible that the lower limit of DPL is set by the troops having to reach or travel between these sleeping sites (Hall 1962; Anderson 1984; Pebsworth, MacIntosh, et al. 2012). Also relevant is the capacity of predation, especially by ambush predators, to influence ranging behaviour of primates (Willems & Hill 2009). Areas perceived to be 'high-risk' (vegetation allowing predators to conceal their approach) are commonly avoided by baboons (Cowlishaw 1997a), and leopards (*Panthera pardus*), the primary predator of baboons (Cowlishaw 1994), were encountered frequently at Issa (Stewart & Pruetz 2013). Their impact on the movement ecology of Issa baboons may be significant (Willems & Hill 2009), and for this to be true, I would expect the baboons to underuse the forest habitat (the habitat with the lowest visibility, thus favouring leopards ambush hunting (Bothma & Riche 1986; Bertram 1982)), which is something I test for in chapter 5.

Overall, this study emphasises the ability of baboons to adapt their ranging behaviour to extrinsic variables (Swedell 2011), and provides much needed data on baboon space-use from a woodland context. This adaptability is reflected, at least in part, by the ubiquity of baboons across a multitude of ecological and climatological contexts throughout sub-Saharan Africa (e.g. from the forests of Gombe in Tanzania, to the deserts of Tsaobis in Namibia). At a continental scale, I demonstrate the importance of including the role of human derived food sources in predicting the ranging patterns of baboons (Hoffman & O'Riain 2012). Human-derived foods are becoming increasingly available to baboons as the distinction between "wild" and "human" landscapes becomes blurred (Kaplan et al. 2011), and this factor, it seems, has a stronger effect upon variance in DPLs than group size, for example (Dunbar 1992). Moreover, this study highlights how investigations of movement patterns at different spatial and temporal scales can provide a fuller analysis of the ecological determinants of movement. Site-specific considerations in particular are important, for example, temperature. At a continental scale, baboons in hotter places travel further, whilst baboons on a local scale travel less far on hotter days. In this instance, I find the role of temperature changes depending on the spatial scale at which it is investigated.

Chapter 5 - Habitat selection and movement patterns of yellow baboons in the Issa valley, western Tanzania

Abstract

Home ranges (HR) are the areas of the environment that animals utilise for the purposes of foraging, mating and rearing their young. Their size, location, and utilisation are determined by the availability and distribution of key resources. The examination of HR and how it changes over time, therefore allows us to better understand the ecology of the animal. I investigated the HR use and habitat selection of two troops of baboons in the Issa valley, Tanzania. GPS data collected over a 7-month period revealed mean HR sizes of 2.47km^2 and 6.01km^2 for the two troops, and these did not vary significantly across seasons. Both troops also demonstrated differential patterns of space-use within their ranges. The intensity of space use decreased significantly as distance from sleep site increased for both troops. The baboons utilized wet grassland, forests and woodland habitats less than expected, and used rocky outcrop habitat significantly more, based on the proportions of available habitat. I suggest rocky outcrops may be used as refuges from predation due to the greater visibility afforded; therefore their proportional over-use may be a result of predator avoidance. Woodland comprises the majority of available habitat, therefore despite using woodland less than expected both troops spent the majority of their time in this habitat. Forest comprises <2% of available habitat, thus by under-utilizing this habitat baboons showed a stark avoidance of forest habitat. Since both woodland and forest habitats provide baboon food resources, I hypothesise the avoidance of forest habitat may, at least in part, be due competition avoidance with sympatric primate species that rely on it more heavily, and/or reduced visibility in this habitat type that leaves them vulnerable to predation. Additionally, with the use of Generalised Additive Models, I show that the movement trajectories of both troops varied significantly over the period of the study. Speed and turning angle of troop travel varied predictably according to habitat type, with baboons moving faster and taking straighter routes through habitats they tended to avoid. Overall, these findings highlight the value of examining habitat selection and movement patterns within an

animal's selected home-range to better understand the drivers of patterns of space use, which can then be used to inform conservation and management of primate habitats.

Introduction

Animal movements are typically confined to specific home ranges, which I define here as "the area occupied by an adult animal [group] in its search of food and mates and caring for offspring but does not include seasonal migrations or occasional sallies outside the usual area" (Burt 1943). The location, size, and utilisation of these home ranges is primarily determined by the availability and distribution of key resources (Clutton-Brock & Harvey 1977b; Milton & May 1976; Perry & Garland 2002). Investigations of animal space use, and their use of resources therein, can therefore provide us with fundamental understanding of species ecology (Li et al. 2000; Morales et al. 2010) and is important for applied conservation efforts (Hoffman 2011; Wartmann et al. 2010; Douglas-Hamilton et al. 2005).

Primates are an excellent model for exploring patterns of space-use. They display a diversity of life-history and ecological strategies attributable to the ecological niches they exploit (e.g. arboreal, terrestrial, diurnal, nocturnal) and their diversity in dietary preferences (e.g. frugivory or folivory). Across primate species, patterns of space-use are in the most determined by ecological factors including the distribution and availability of food (Hemingway & Bynum 2005), surface water (Altmann 1974), sleep sites (Anderson 1998), predation risk (Boinski et al. 2000; Cowlishaw 1997b), and competitive intra- (Isbell 1983; Goodall 1986; Clutton-Brock & Harvey 1979) and inter-specific (Holenweg et al. 1996) interactions. All of these factors are, however, interdependent, and it is difficult to disentangle their relative importance. For example sleep sites are often located close to important resources to minimise travel time and increase potential foraging time (e.g. spider monkey, *Ateles geoffroyi*: Chapman et al., 1989), but at the same time will not be located in areas of especially high predation risk (*Papio cynocephalus*: Rasmussen 1978; *Hylobates klossii*: Tenaza 1975; *Trachypithecus poliocephalus*: Huang et al. 2003), and change over time to avoid local resource depletion (Chapman 1988). This has led researchers to focus on primate exploitation of different habitat types, which differ with respect to one or more of the ecological factors described. For example, dense forest habitats can be both productive (because they exhibit high food availability), and dangerous (as a consequence of the ambush hunting tactics that some primate predators employ: e.g. baboons by lion, *Panthera leo,* and leopard, *Panthera pardus*: Cowlishaw, 1994). Consequently, primates differentially exploit habitat types in accordance with such trade-offs, for example between food productivity (Stevenson et al. 2000; Albernaz 1997; Hill 1999), and perceived predation risk (e.g. chacma baboons, *Papio cynocephalus*: Cowlishaw, 1997 a; vervet monkey, *Cercopithecus aethiops*: Willems & Hill, 2013).

Examining space use in terms of habitat selection can therefore be particularly informative, but one must consider carefully how relative benefits associated with any particular habitat can vary over time, especially in highly seasonal environments. Food availability (and specifically fruit), which explains much variation in primate ranging patterns (Clutton-Brock & Harvey 1977b; Milton & May 1976), is rarely consistent, and instead undergoes seasonally predictable periods of scarcity (van Schaik et al. 1993; Chapman et al. 1994). As such, in frugivorous primates dietary switching is a common adaptation, whereby fallback foods are relied on in order to meet nutritional requirements (Conklin-brittain et al. 1998; Grueter et al. 2009) resulting in changes to patterns of habitat use (Cipolletta 2004; Ganas & Robbins 2005; Singleton & van Schaik 2001; Volampeno et al. 2011; Kim et al. 2011; Albernaz 1997). For example, home range size (HRS) can be reduced when species fall back on leaf forage (western chimpanzee (*Pan troglodytes*), Doran 1997; woolly monkeys (*Lagothrix lagotricha poeppigii*), Fiore 2003; Gorilla (*Gorilla gorilla*), Ganas & Robbins 2005), or increase when primates are required to travel further in order to incorporate higher better fall-back foods such as tubers, roots, insects or seeds in their diet (Blue-eyed black lemur (*Eulemur flavifrons),* Volampeno et al. 2011; Chacma baboon (*Papio ursinus),* Pebsworth et al. 2012); see Hemingway & Bynum (2005) for a review.

Even where HRS and habitat preferences remain relatively stable over time and in space, movement trajectories may alter if an animal's movements are flexible with respect to local changes in resource availability and distribution (Sueur 2011; Bartumeus et al. 2002; Sims et al. 2008). For instance, the speed or distance travelled between any given points within a day, or the distribution of turning angles (relative straightness) of travel, might change where resources become more or less patchy in space and time (Sueur 2011), but this does not necessitate a change in space use, only a change in *how* the space is used. Examination of movement trajectories can therefore provide insight into subtle, but important differences in the way in which primates use their space (Ramos-Fernández & Mateos 2004), that may not be captured by examining habitat preferences or by estimating home-ranges alone, and consequently better elucidating their adaptability in foraging strategies.

Here, I investigate habitat selection and movement patterns of yellow baboons (*Papio cynocephalus*) in Ugalla, western Tanzania. Baboons are a very successful genus that are ubiquitous in a multitude of habitat types across the majority of sub-Saharan Africa (Kingdon 2003). They are consequently well studied with descriptions of home range use from a number of long-term studies (Amboseli: Altmann & Altmann 1970; Post 1981; Cape Point: Davidge 1978; Gilgil: Harding 1976; De Hoop: Hill 1999; Cape Peninsula: Hoffman & O'Riain 2010; Chololo: Barton 1992; Mikumi: Rasmussen 1979; Okavango: Hamilton et al. 1976; Mkuzi: Gaynor 1994; Mt Assirik: Sharman 1981; Tsaobis: Cowlishaw 1997; Suikerbosrand: Anderson 1981). These extensive studies provide support for a relationship between the distribution and availability of preferred foods and differential patterns of space use (Altmann 1974; Wahungu 2001; Barton 1992; Harding 1976; Pebsworth, MacIntosh, et al. 2012). Fruits and seeds, in particular, are preferred food sources that are selected for by baboons when available (Altmann & Altmann 1970; Barton 1989; Hill & Dunbar 2002). As such, they form an important part of the diet of many baboon populations (Dunbar & Dunbar, 1974; Harding, 1976; Davidge, 1978; Rasmussen, 1978; Sharman, 1981; Sigg & Stolba, 1981; Ransom, 1981; Depew, 1983; Norton et al., 1987; Barton, 1990; Bronikowski & Altmann, 1996).

The majority of our understanding of baboon space use comes from East Africa, where baboons inhabit arid savanna habitats (Altmann 1974; Norton, R. Rhine, et al. 1987; Post 1981; Sigg & Stolba 1981; Sharman 1981) but see Ransom (1981) Wahungu (2001). In this study, I describe patterns of space use for two troops of yellow baboons (*P. cynocephalus*) within a predominantly forest and woodland habitat in the Issa Valley of western Tanzania.

I begin by describing baboon troop HR using two commonly used methods: minimum convex polygon (MCP: Hayne, 1949) and kernel density estimate (KDE: Worton, 1989), considering the differences between these methods and any potential effects of sampling periods upon HRS estimates. I then proceed to test the hypothesis that Issa baboons exhibit differential patterns of space-use within home ranges. I expected the baboons to preferentially utilise habitat types within their home-range with a higher encounter rate of fruit and areas close to sleeping sites in order to maximise foraging efficiency (Schoener 1971; Milton & May 1976; Stephens & Krebs 1986; Chapman et al. 1989), respectively. However, if the baboons experience increased risk of encounter with potential predators and/or competition from other primates in such food-rich, vegetation dense habitats, the baboons may leave these food rich areas as rapidly as possible (Cowlishaw 1997). Although I expect the baboons to make rational choices about how they use their environment (above) I assume that these decisions take place through an evolutionary process, resulting in variation in speed and turning angle of troop movement trajectories that reflect the decision-making processes underlying differential patterns of space use (Sueur 2011). I therefore also compare troop movement trajectories for the space/time periods I find to be different (see above).

Methods

Study Subjects

Troop movement data were collected for two yellow baboon troops, Camp Troop (CT, n= 22 individuals) and Matawi Troop (MT, n=31) from January to August 2012. Troops were followed at a distance of 20-50m, with particular effort paid in following the centre mass of the troop, and GPS locations were recorded every five minutes (accuracy <±10m). Though not formally measured, troop spread was rarely large (<40m), which made following the centre mass of the troops easier. The speed of the baboons was matched as best as possible by maintaining a 20-50m gap between the baboons and observer. Troops were followed from dawn until dusk whenever possible, resulting in an average of 9 hours and 108 GPS locations per day, over 38 days (CT) and 23 days (MT) respectively, totalling 546 hours and 6102 GPS fixes.

Home Range Estimation

All GPS coordinates were read into R and projected into the geographic coordinate system Universal Transverse Mercator, zone 36 S, WGS-1984 ellipsoid, to form a spatial points data frame. Two different methods – minimum convex polygons (MCP), and kernel density estimates (KDE) – were then used to estimate the home range size in R (package adehabitatHR, Calenge, 2006). I briefly describe each method in turn. The MCP (Hayne 1949) considers the area encompassed by the outermost observations of the animal, which unless the HR is perfectly convex, will produce an overestimation of the HR. The MCP was ubiquitous in the field of HR studies (Ostro et al. 1999) and I therefore use this method here, to allow comparisons of my study troops with earlier work, but due to the coarseness of this method, care must be taken in the interpretation, and I give preference to the KDE. The 95 percent KDE describes the space in which 95 percent of the animals movement is predicted to occur, and is used here to estimate home range sizes as they produce realistic ranges using probabilistic modelling (Worton 1989). A 95% contour was used to exclude outlying data points and exploratory areas (Howell & Chapman, 1997; Pebsworth et al., 2012), and to calculate the KDE, I used the smallest smoothing parameter that resulted in a contiguous area (Berger & Gese 2007; Jacques et al. 2009) using several proportions of the h_{ref} bandwidth (ad hoc technique) (Pebsworth, Morgan, et al. 2012). I define the core area here as the region within the home range that receives the highest density of utilisation (Burt 1943). I adhere to the methods outlined in analogous studies by calculating the core range as the area which includes 50% of the data points (i.e. 50% KDE) (Pebsworth, MacIntosh, et al. 2012; Cimino & Lovari 2003; Howell & Chapman 1997).

To delimit the minimum period of time a HR could be quantified, I plotted an estimate of HR as a function of number GPS location fixes. I did this for each HR estimator and each troop. I then conducted a change point test to provide an indication of where a significant shift in the mean HR (over successive samples) is detected. I did this in R v. 1:1.2 (Changepoint package, Jammalamadaka & Sengupta, 2001). This approach provides a broad indication of the minimum number of location points required before a stable HR estimation is reached, and thus a time-window over which I can reliably make comparisons of HR.

Environmental Factors

Please refer to Chapter 2, pages 25-26 and for a full description of rainfall, temperature and seasonality at Issa.

Habitat classification

In this thesis, habitats are classified as being either wet grassland, dry grassland, woodland, forest and rocky outcrops. Rocky outcrops were not included in the original description of the study site (Hernandez-Aguilar 2006), but are included here due to their purported importance as baboon refuges from predation risk (Cowlishaw 1997a). Please refer to Chapter 2, pages 27-28 (Figure 2.6 B) for a detailed description of how these habitats were defined, quantified and analysed in accordance with baboon troop movements.

To provide an indication of productivity of potential baboon foods between habitats, I used the presence/absence of seed pods and fleshy fruits (referred to from here collectively as fruit) once per month on two stratified transects for the two dominant habitat types at Issa (woodland and forest, Figure 2.7). Of course, seeds and pods and fruits are available in other habitats (e.g. Grassland and rocky outcrop habitats), but these are the habitats primarily used by the baboons and fruits and seeds are the primary foods consumed by them (see Chapter 3). Please refer to Chapter 2 pages 30-31 for full description phenology monitoring at Issa. These transects suggested the availability of fruit was higher in the woodland compared to forest habitat, whether I consider the percentage of fruiting trees encountered on the transect (Figure 5.1A; Wilcoxon signed ranks test: $z=3.13$, $df=6$, $p=0.0017$), or the mean distance between fruiting trees on the transect (Figure 5.1B; Wilcoxon signed ranks test: $z=3.0$, $df=6$, $p=0.0027$). Moreover, the difference in the availability of fruits in woodland and forest habitats became greater over the study period, regardless if I used the percentage fruiting trees available (Pearson's correlation: $r=0.81$, $df=5$, $t=3.08$, $p=0.027$), or the mean distance between fruiting trees ($r=0.94$, $df=5$, $t=6.43$, $p=0.0013$), emphasising the increasing disparity in fruit availability between habitat types suggesting that major differences were only present in the dry season.

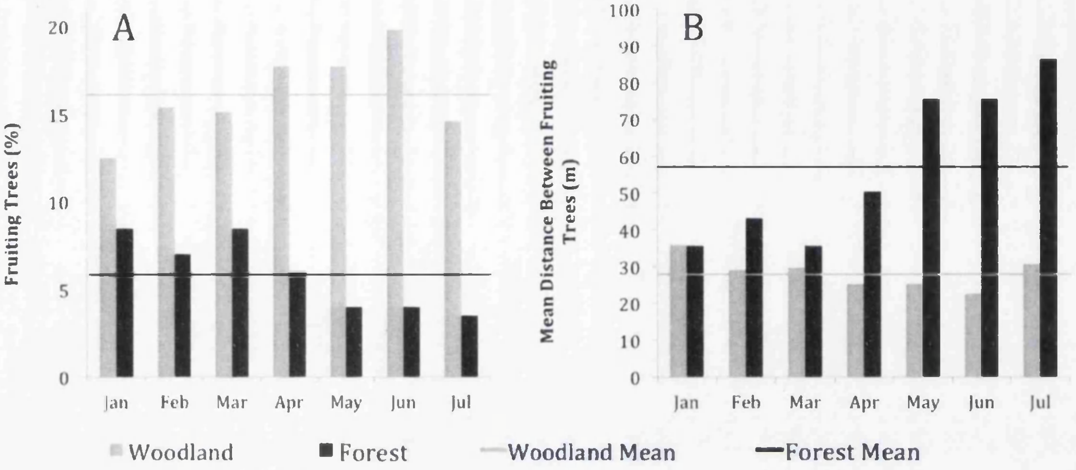

Figure 5.1. **A**: The percentage of fruiting trees in woodland and forest habitat by month, with lines depicting the mean over the study period **B**: The mean distance between fruiting trees (m) in woodland and forest habitats by month, with the lines depicting the mean over duration of study period.

Statistical Analyses

All statistical analyses were conducted on KDE home ranges, following preliminary comparisons with MCP, which show KDE to be superior (Pebsworth, Morgan, et al. 2012). To determine evenness of home range use, home ranges of both troops, as estimated by KDE, were divided into 150x150m grids cells (GeoWizards plugin for ArcGIS 10). The number of observations in each cell was then compared with a theoretical count for each cell (calculated as the number of observations if they used each cell evenly). The difference between these two distributions was then tested using a Kolmogorov-Smirnov 2-sample test.

To examine the troop's evenness of habitat use, a Wilcoxon signed ranks test was used, and to determine relative preference for each habitat type, Krebs' (1989) Electivity Index (EI) was calculated, by month for each habitat type and each troop. However, as baboons must depart from and return to sleeping sites, it is possible that habitat preference may be biased towards those that contain the sleeping sites. To assess, therefore, whether sleeping site location biases habitat preference, data from the first hour in the morning and the final hour in the evening were excluded (i.e. only data collected from 8am-6pm) and the EI was run again. A Wilcoxon signed ranks test was then employed to determine if the EI after the removal of the first and last hour of the day were significantly different to EI before their removal. The EI ranges from +1 (strongly preferred) to -1 (strongly avoided), and is calculated as follows:

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

Where h_i is observed proportion of time spent in habitat i, and p_i is the relative availability of habitat i in the home range of the troop.

A Spearman's rank correlation was used to test for a relationship between the distance of a grid cell from the closest sleeping site and intensity of use within that cell. However, because two adjacent cells on the grid are not statistically (spatially) independent of each other, and are therefore likely to share a common set of characteristics, analyses were also run using a subset of the cells so that no one grid cell adjoins another on any side (50% of total cells) (Hill & Weingrill 2007).

To provide information on orientation and searching behaviours of Issa baboons I calculated their movement characteristics (speed and turning angle). These were calculated in R (adehabitatLT package, Calenge et al., 2009) and are described by turning angle distributions and speed, which can provide information on orientation and searching behaviour (Benhamou 2004). Speed (m/min) and turning angle (θ) were calculated for successive GPS locations using the adehabitatLT package, R (Calenge 2006). Two generalised additive models (GAM) were subsequently used to test the effect of habitat type on turning angle and speed whilst controlling for any effect of day (of study period). Prior to testing, though, I first filtered out those steps where the baboons were essentially stationary (<5 meters/minute). This allowed a more refined analysis of whether the baboons are moving faster in less preferred habitats, rather than the baboons simply spending more time stationary in preferred habitats. I utilised GAM modelling here as opposed to a standard linear model to allow more flexibility in the recognition of nonlinear temporal variation. Accordingly I fitted 'day' as a smoothed effect, with troop and habitat type as linear predictors. Models were run in R (mgcv package, R Devlopment Core Team, 2010).

Results

Home Range Estimation

Statistics suggest HR is reliably estimated after approximately 1000 fixes for CT, and 500 fixes for MT, which equates to approximately 1.75 and 1.7 months of data collection respectively (Figure 5.2).

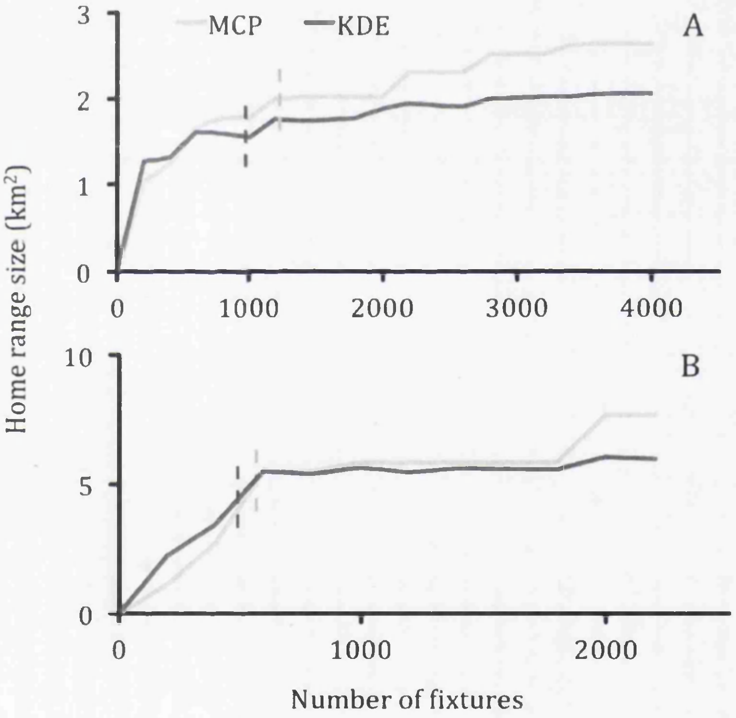

Figure 5.2: Estimated home range size for CT (A) and MT (B) as a function of the number of GPS location fixes collected

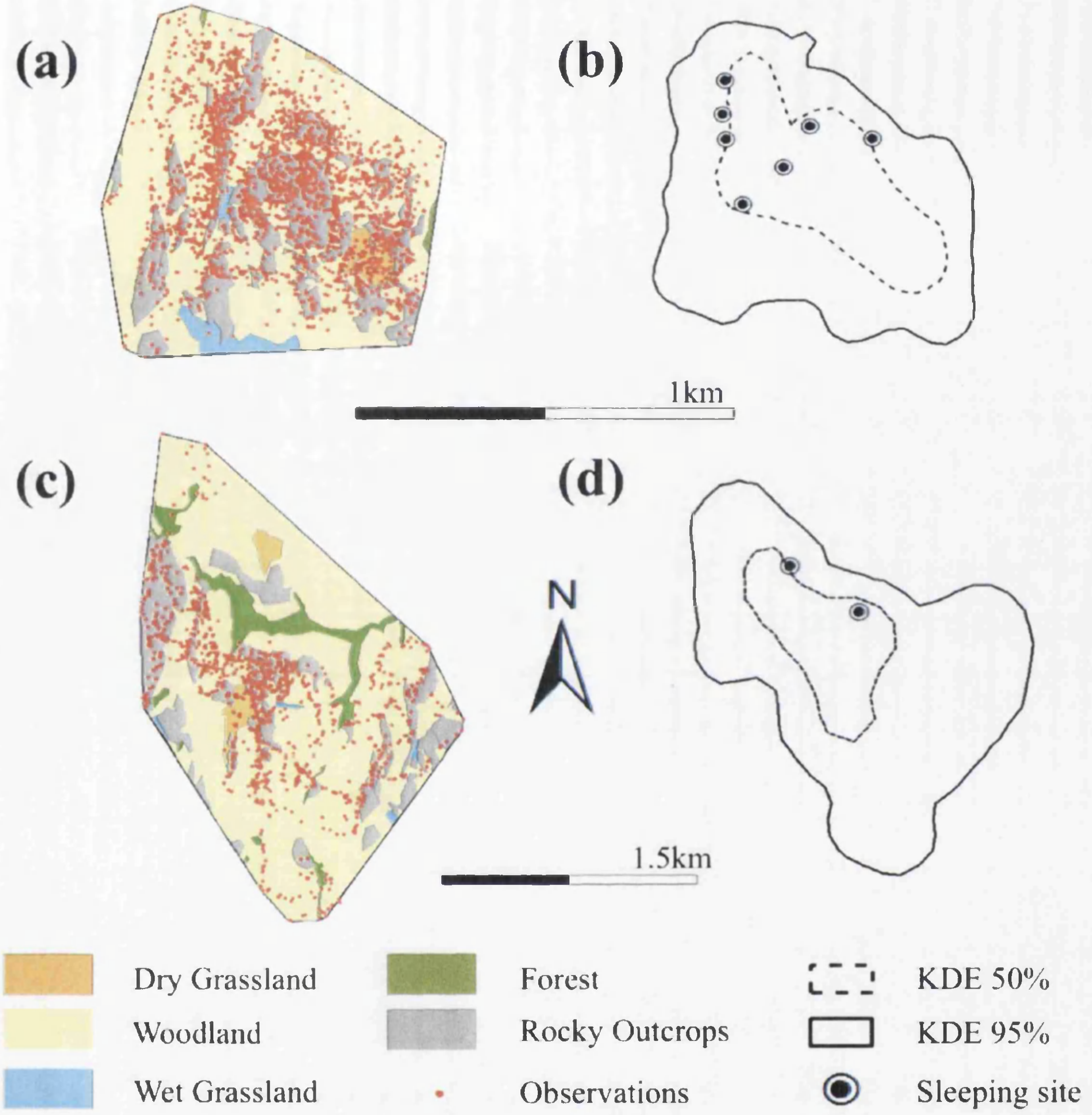

Figure 5.3: Home ranges as calculated by the two methods of estimation. (a): Camp Troop MCP with habitat map overlaid with observations, (b) Camp Troop 95% and 50% KDE with sleeping sites, (c) Matawi Troop MCP with habitat map overlaid with observations, (d) Matawi Troop 95% and 50% KDE with sleeping sites.

Table 5.1. Habitat composition within home ranges of MT and CT.

Habitat type	MT Home Range (%)	CT Home Range (%)
Woodland	69	65
Rocky Outcrop	25	29
Dry Grassland	3	3
Forest	3	1
Wet Grassland	0	2

HR sizes for each troop, using MCP and KD methods for the full datasets are shown in Figure 5.3, and indicate the HR of MT was larger than CT for both estimation methods with overlapping space comprising 49% of CT's, and 17 % of MT's HR, as calculated from the KDEs (Figure 5.3). Despite the obvious difference in HR size between the two troops, the HR compositions in terms of habitat type were strikingly similar (Table 5.1). The size of each troops HR and core HR varied very little between the seasons (Table 5.2), irrespective of the home range estimator used, however, I did observe a shift in the location of the core HR for both troops (Figure 5.4).

Table 5.2. Home range sizes (km^2) by season according to the 95% KDE, core KDE (50%) and MCP estimation methods. Numbers in parentheses refer to the number of recorded observations.

	Camp Troop		Matawi Troop	
Estimator	Dry (n=1662)	Wet (n=2257)	Dry (n=551)	Wet (n=1625)
KDE 95%	2.18	1.97	5.58	5.66
KDE 50%	0.65	0.56	1.41	1.17
MCP	2.30	2.31	4.97	5.84

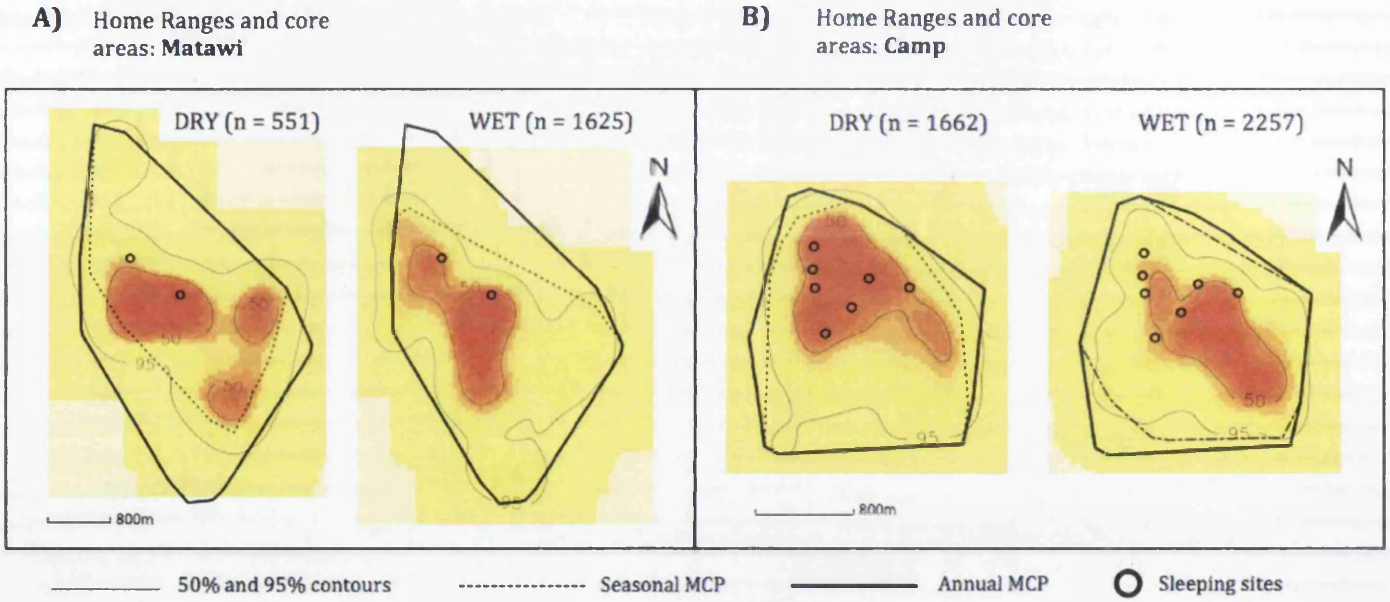

Figure 5.4. Seasonal variation in home range size, shape and core use for Camp Troop and Matawi Troop from January-July 2012

Patterns of Space-use

Both troops spent the most time in woodland and rocky outcrops, with a relatively minor amount of time spent in grassland (wet and dry) and forest (Figure 5.5), in line with their respective abundance within the HRs (Table 5.1), and these were not seasonally variable (see Appendix 3). Neither troop used the full extent of their home range evenly (CT: $D = 0.44$, $n = 110$, $p < 0.001$; MT: $D = 0.72$, $n = 318$, $p <0.001$) and both troops demonstrated similar avoidances and preferences of habitats (Figure 5.6 A) in relation to their relative abundances within their respective HRs. Furthermore, when I control for the potential bias of sleeping site location by removing the first and last hour of the day from the data set, I show that patterns of habitat use were not significantly different (Wilcoxon signed ranks test: $W=2270$, $n= 65$, $p=0.45$). Both CT and MT appear to underuse the forest habitat and overuse rocky outcrops, however these were significant only for CT, with MT's use of them being much more variable (Figure 5.6 A). This variability for MT is likely a result of the lower sample size. To consolidate this, I calculate a Kreb's EI for both troops combined (Figure 5.6 B, Table 5.3). When merged, Issa baboons demonstrate a preferential use of rocky outcrops, the deviation of which was statistically significant (Table 5.3). Issa baboons use the woodland and dry grassland habitats in proportion to their availability whilst significantly underusing the wet grassland and forest habitats. However, if I apply a Bonferoni correction, none of the habitat preferences remain significant.

In total, CT were followed to a sleep site on 24 occasions (n=7 sleep sites, density=3.38/km^2) and MT on 14 occasions (n=7 sleep sites, density=1.01/km^2). CT re-used all sleep sites (mean=3.42, SD=1.72, range = 2-7), whilst MT re-used only three sleep sites (mean=2.5, SD=2.35, range=1-7). As distance from sleeping sites increased, the intensity of grid cell-use decreased significantly for CT (Spearman's rank correlation: $r_s =-0.44$, $p < 0.001$, $n=118$) but not significantly for MT ($r_s=-0.12$, $p >0.05$, $n=202$). However, on repeating the analysis with the exclusion of the sleep sites that were used on just one occasion by MT, the relationship became stronger and significant ($r_s=-0.47$, $p <0.001$, $n=202$). Moreover, repeating the analysis with a subset of cells (50% of total) to control for spatial non-independence of adjacent grid-cells, I found the result remained consistent (CT: $r_s = -0.39$, $p <0.005$, $n = 58$; MT: $r_s = -0.44$, $p <0.001$, $n = 98$).

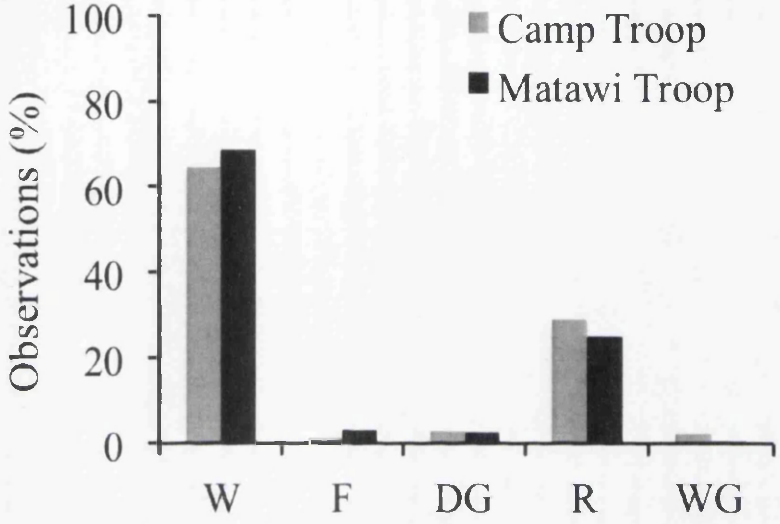

Figure 5.5: Percentage of observations (%) in each habitat for both troops. (**W**: woodland, **F**: Forest, **DG**: D ry Grassland, **R**: Rocky Outcrop, **WG**: Wet Grassland).

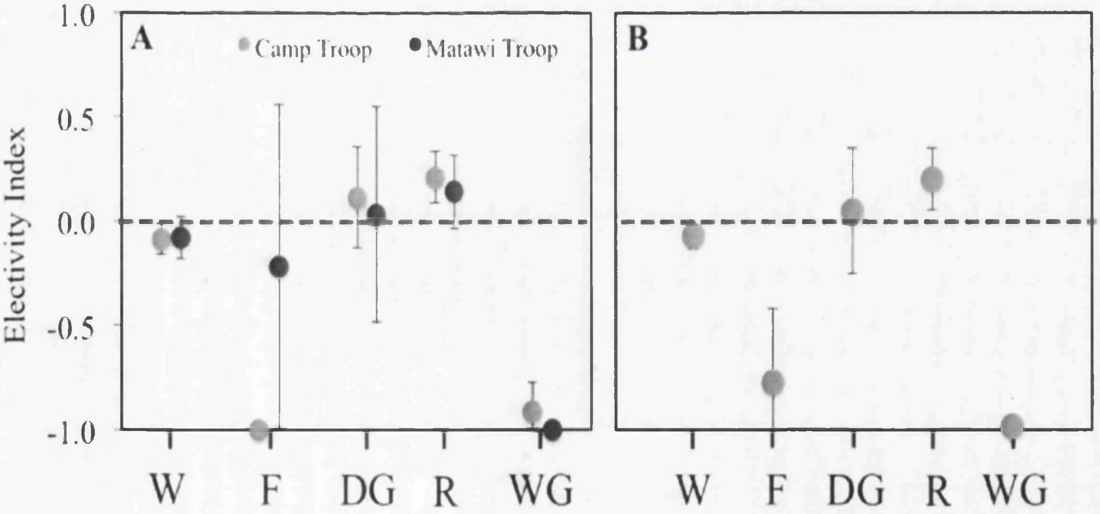

Figure 5.6. Average monthly Kreb's habitat Electivity Index (*EI*) illustrating baboon habitat preferences (**W**: woodland, **F**: Forest, **DG**: Grassland, **R**: Rocky Outcrops, **WG**: Wet Grassland) during the study period for **A**: Both troops separately and **B**: Both troops combined.

	Camp Troop (n=7 months)			**Matawi Troop** (n=6 months)			**Troops Combined** (n=7 months)		
Habitat type	**W**	**P**	**Direction**	**W**	**P**	**Direction**	**W**	**P**	**Direction**
Woodland	2	<0.05	-ve*	4	>0.05	-ve	6	>0.05	-ve
Rocky outcrops	28	<0.05	+ve*	18	>0.05	+ve	28	<0.05	+ve*
Dry grassland	20	>0.05	+ve	20	>0.05	+ve	19	>0.05	+ve
Wet grassland	0	<0.05	-ve*	0	<0.05	-ve*	0	<0.05	-ve*
Forest	0	<0.05	-ve*	11	>0.05	-ve	0	<0.05	-ve*

Table 5.3. Wilcoxin signed ranks tests on proportion of time spent in each habitat type each month against predicted time spent in each habitat if they are used randomly in proportion to their availability. **+ve** indicates baboons are using habitats more than expected and **–ve** shows the opposite. Directions with an asterix represent significant differences between observed and predicted.

Troop Movement Characteristics

Movement trajectories varied little between troops (Figure 5.7). In the case of habitat effects, both baboon troops demonstrated clear and significant differences in their movement trajectories between different habitat types (Figure 5.8; Tables 5.4, 5.5). Most obviously, the baboons appeared to travel faster and more directly through the dry grassland habitat (Figure 5.8). The effect of troop was significant for turning angle, but not speed, with MT travelling significantly less directly than CT (Table 5.4).

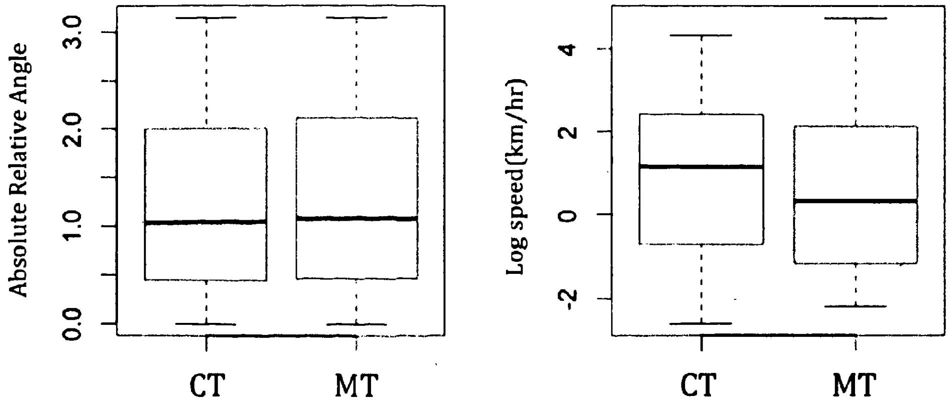

Figure 5.7: Median absolute relative turning angles and log speeds by troop (CT: n=2652, MT: n=1453), with 1st and 3rd Quartiles shown by extent of box, minimum and maximum values given by whiskers.

Table 5.4: Coefficients for the effect of habitat type on **turning angle** in the selected generalized additive model, fitted with Gaussian errors. The table shows parameter estimates (Estimate), standard errors (SE), associated test statistic (F value) and p values. Effect of smoothing factor is also shown with estimated degrees of freedom (edf), reference df, test statistic (F) and p value. Reference categories were woodland for habitat, and CT for troop.

	Estimate	**SE**	**df**	**F**	**p**
Habitat			4	3.58	0.0064
Woodland	0.00	0.00	1		
Dry Grassland	-0.23	0.08	1		
Rocky Outcrop	-0.07	0.03	1		
Forest	-1.28	0.94	1		
Wet Grassland	-0.75	0.47	1		
Troop			1	6.17	0.013
CT	0.00	0.00	1		
MT	0.11	0.04	1		
		Edf	**Ref.df**		
Day		6.79	7.92	2.94	<0.0001

Table 5.5: Coefficients for the effect of habitat type on **speed** in the selected generalized additive model, fitted with Gaussian errors. The table shows parameter estimates (Estimate), standard errors (SE), associated test statistic (F value) and p values. Effect of smoothing factor is also shown with estimated degrees of freedom (edf), reference df, test statistic (F) and p value. Reference categories were woodland for habitat, and CT for troop. * There were no observations from within the forest post removal of data points <5 m/min.

	Estimate	**SE**	**df**	**F**	**p**
Habitat			3	3.51	0.012
Woodland	0.00	0.00	1		
Dry Grassland	-0.74	1.12	1		
Rocky Outcrop	-0.13	0.42	1		
Forest*	NA	NA	1		
Wet Grassland	15.57	4.85	1		
Troop			1	0.89	0.087
CT	0.00	0.00	1		
MT	-0.40	0.42	1		
		edf	**Ref.df**		
Day		7.71	8.59	3.12	<0.01

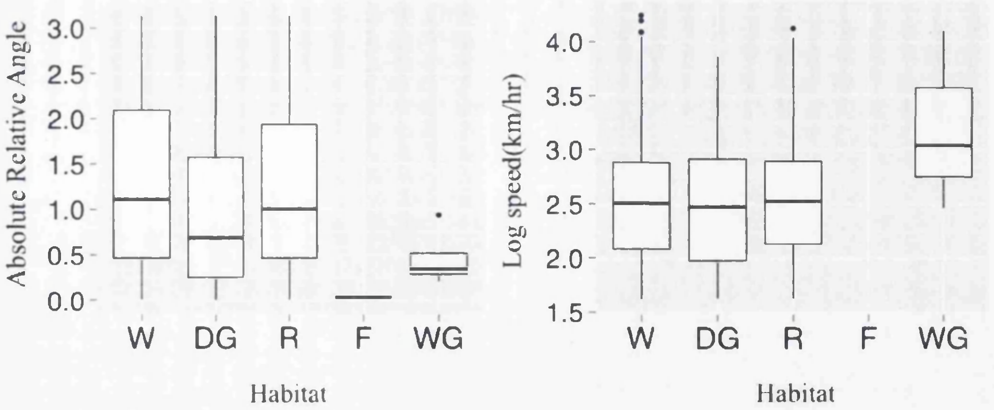

Figure 5.8: Median absolute relative turning angles and log speeds by habitat types (n=4105), with 1st and 3rd Quartiles shown by extent of box, minimum and maximum values given by whiskers (**W**: woodland, **R**: Rocky, **DG**: Dry Grassland, **WG**: Wet Grassland, **F**: Forest). Insufficient observations within forest resulted in lack of box and whisker.

Discussion

I investigated the home range use and habitat type selection of two troops of baboons in the Issa valley over a seven-month study period. After comparing different HRS estimation methods, and the validity of my estimations, I have shown that baboons at Issa, like those elsewhere across their distribution (Cowlishaw 1997b; Hill 1999), do not use their home range evenly. Instead they use their environment preferentially according to habitat type (Cowlishaw 1997b) and sleeping site availability (Barton et al. 1992; Sigg & Stolba 1981). Moreover, I find that habitat preferences significantly affect the movement characteristics of the baboons; with the baboons moving faster and straighter in habitat types they tend to avoid. Though I will discuss the causality of this relationship in the paragraphs to come.

The results suggest that my sample period was sufficiently long to investigate patterns of space use in my population. Between troops, I found differences in HRS and shape (Figure 5.3), but the habitat types of which they were comprised were very similar.

These differences in size and structure are therefore unlikely to be a result of different preferences for habitat type of resources between the two troops, but rather a possible consequence of group size and/or sleeping site availability. Group size of MT was a third larger than CT, and correspondingly had a 188% larger HRS, supporting data from previous studies that report HRS positively correlates with group size (Barton 1992; Hoffman 2011; Stacey 1986). However, with a sample size of just two, I must be cautious with this interpretation and other factors, such as availability of sleeping sites must be considered. For example CT used a higher number of sleeping sites over the course of the study, which may also indicate a higher density of potential sleep sites, and thus negate the need to range further in order to encompass the required number. Baboons, like many other animals, are limited in where they can range, by the need to depart from and return to a sleeping site each day (Barton 1992). Due to this, and the multiplicity of sleeping sites used by baboons, they can be considered multiple central place foragers, reducing overall travel costs by selecting a sleeping site close to a current feeding area (Chapman et al. 1989). Obviously though, baboons alternate the use of sleeping sites as a result of other factors, including as a strategy of parasite avoidance (Hausfater & Meade 1982) and perceived predation risk (Hamilton 1982). Therefore, the characteristics of baboon HR at Issa, and their utilisation of the space within it, are likely to be at least partly defined by the availability and distribution of appropriate sleeping sites.

A primary underlying determinant of habitat use, by any baboon troop, is food availability and distribution (Altmann & Altmann 1970; Post 1978; Barton et al. 1992). Different habitat types have varying degrees of productivity, thus I expected baboons to exhibit a preference for habitats that provide a higher return of food in return for effort (Schoener 1971). Despite the baboon diet being broad and varied (Norton, R. Rhine, et al. 1987) fruit is a coveted food source that is selected for when available. Therefore, I assume fruit availability is a reliable proxy for baboon food availability. Accordingly, I find both forest and woodland habitats at Issa produced fruit (Figure 5.1a), and whilst the baboons use the woodland habitat in proportion to its availability, they almost entirely avoid the available forest habitat. Assuming baboons at Issa conform to conspecifics in selecting for fruit during periods of availability, then why are baboons at Issa completely avoiding a potentially rich food source? I suggest two potential reasons are (1) to mitigate competition with other primate species, and (2) to reduce predation risk. In the case of inter-species competition, the forest habitat is used by the majority of the other diurnal primates at Issa, especially *Pan troglodytes* and *Cercopithecus ascanius* (Stewart & Pruetz 2013; Tapper et al. 2014). It is therefore possible that baboons at Issa avoid the forests to reduce competition with sympatric primate species (Wahungu 1998). As such, in Chapter 6 I continue by investigating this as a working hypothesis using ranging and dietary data for *P. troglodytes* at Issa. From this I aim to test whether species' spatiotemporal movements are unrelated, show evidence of attraction, or of avoidance, and to what degree they overlap in the species they consume.

In the case of predator avoidance, a number of studies have shown mammals to avoid or increase their vigilance in areas where the perceived risk of predation is high. This behavioural manifestation of trophic interaction has been termed 'landscapes of fear' (Brown et al. 1999), and they have been observed in elk (*Cervus elaphus,* Kittle et al. 2008; Laundré et al. 2011), squirrels (*Xerus inauris,* van der Merwe & Brown 2008), dugongs (*Dugong dugon,* Wirsing et al. 2007; Wirsing et al. 2008), vervet monkeys (*Cercopithecus aethiops pygerythrus,* Willems & Hill 2009) and samango monkeys (*Cercopithecus mitis erythrarchus,* Coleman & Hill 2014). Baboons are at risk from an array of carnivores including the leopard (*Panthera pardus*) (Altmann 1974), which poses the largest threat at Issa and is likely to be most abundant at Issa, with sightings, tracks and vocalisations being relatively common (Stewart & Pruetz 2013). Since leopards are predominantly ambush predators (Bothma & Riche 1986; Bertram 1982) risk of predation is likely to increase as visibility decreases, as leopards may better able to conceal their approach (Hill 1999). Therefore, baboons may avoid low visibility forest habitats at Issa to maximise detection of leopards, and reduce the risk of an encounter. The fact that the baboons used rocky outcrops more than they would if they used them in proportion to their availability supports this idea since rocky outcrops may offer refuges, providing safety from terrestrial predators (Berger 1991). Indeed, the availability of these refuges have been found to be influential in determining patterns of habitat use in baboons (Cowlishaw 1997b), especially for those belonging to smaller troops (Cowlishaw 1997a). Whilst I did not quantify fruit availability on these rocky outcrops, vegetation was comparatively sparse compared to the forest and woodland. Therefore it is plausible that the greater than expected use of rocky outcrops, compared to forest, by both troops, likely serves an anti-predatory function.

I also found that the intensity of quadrat cell use within HRs decreased significantly as distance from sleep sites increased. Sleeping site availability has been suggested as being as limiting as food and water in savannah and grassland habitats of yellow baboons (Washburn & DeVore 1961). Areas abundant in food but lacking availability of sleep sites are found to be completely void of baboons in areas of Amboseli (Altmann 1974) and the Namib desert (Hamilton et al. 1976). Nocturnal predation has been suggested as a major selective force in baboons (Rasmussen 1979), therefore to mitigate this risk, baboons utilise specific sleeping sites, which offer valuable protection (Kummer 1968; Altmann & Altmann 1970). Daily ranging patterns and habitat-use in baboons is consequently dictated by the need to leave from, and return to, a sleeping site (Barton 1992), and I find strong evidence of this here. Therefore, whilst it is apparent that sleeping sites are important, the approach I used here is very basic (Hill & Weingrill 2007). Future investigations would benefit from employing the use of spatial correlations in order to determine other important factors, including location of water sources, which dictate space use within the home range (Willems & Hill 2009; Coleman & Hill 2014).

Contrary to other studies, I found very little difference in the size or location of HRS (Table 5.2) (Altmann 1974; Wahungu 1998), or the intensity of use per habitat, for either troop between seasons (wet, dry). However, finer grain analysis on movement trajectories did reveal a significant temporal effect on movement trajectories. The effect of day on both speed and turning angle was significant when fitted to a GAM suggesting the troops are demonstrating behavioural flexibility in how they move, and importantly, I found this to differ according to habitat type across days. When searching for spatially predictable, patchy resources such as fruits, it is more efficient to travel faster and more directly between patches (Pochron 2001). In contrast however, when fruit is less available, and less nutritious fall-back foods must be relied on that are not spatially predictable, direct and faster movement is inefficient. Therefore, the sensitivity of movement trajectories can offer great insight into the environment. Here, I find a significant effect of habitat type on movement trajectories (i.e. both speed and turning angle). For example, I find baboon troops at Issa move faster and straighter through wet grassland (and possibly forest, though there are insufficient observations in this habitat to confirm this), regardless of whether I remove all data where baboons are essentially stationary. This is likely caused by the lack of foods in the wet grassland and the potentially higher perceived risk of the forest, which despite having a high number of refuges in the tall trees, has poor visibility which would favour the ambush hunting of leopards (Bothma & Riche 1986). Conversely, the Issa baboons move slower and turn more in habitats with more resources and are relatively less risky such as woodland and rocky outcrops. I infer from this that the baboons are identifying less preferable habitat types, for whatever reason, and are choosing to move straight and quickly as to pass through in minimal time – perhaps using them only as through-roads to reach more preferred foraging habitats. However, it is important to consider that speed and turning angles recorded are not directly recorded from the baboons. Instead they come from an observer who is following the baboons and whilst ever effort was made to maintain pace and follow the centre of mass of the group, there will undoubtedly be a loss of resolution as the movement characteristics are translated through the observer. Therefore, to verify these results, baboon attached GPS devices would be required.

Baboons at Issa are a previously un-studied population, which unlike the majority of baboon studies to date, inhabit a seasonal, woodland-dominated habitat. Coupled with the diversity of habitat types and the richness of sympatric primate species, this has permitted us to contribute to the overall understanding of an already well-studied primate's ecology. Overall, I have shown that baboons at Issa, like those elsewhere (Cowlishaw 1997b; Hill 1999), do not use their home range evenly. Instead they use their environment preferentially according habitat type (Cowlishaw 1997b) and sleeping site availability (Barton et al. 1992; Sigg & Stolba 1981). I suggest that the preferential use of different habitat types is most likely a reflection of their relative productivity and their relative risk with regards to predation and inter-species competition. I find no effect of season on the size and characteristics of baboon HR at Issa, but I do find the way they use the space that they select from the environment changes over time (Wahungu 1998; Altmann 1974) and between habitat types (Cowlishaw 1997b). In the absence of behavioural data, these differences in movement trajectories support my inference that different habitats are used for different purposes, emphasising the significance of decision-making processes that underlie the patterns of space-use (Sueur 2011).

Chapter 6 - Living together: differential utilisation of niche components by sympatric yellow baboons and chimpanzees in the Issa valley of Ugalla, western Tanzania

Abstract

Due to commonalities in diet, and high levels of sympatry, interspecific competition between primates is common. Within and between competing primate species, the differential utilisation of niche components, such as diet and habitat use, is essential in facilitating coexistence. Chimpanzees (*Pan troglodytes*) for example are commonly found existing in sympatry with baboons (*Papio sp.*) and both these species are described as having large overlaps in diet. This overlap in turn has been hypothesised to be causing inter-specific competition. In this chapter, I explored the potential for competition between chimpanzees (*Pan troglodytes schweinfurthii*) and yellow baboons (*Papio cynocephalus*) in the Issa valley of Ugalla, western Tanzania. I did this by comparing the diet and space-use of an un-habituated chimpanzee community, and three partially habituated baboon troops. Diet was inferred through macroscopic faecal analysis of 299 chimpanzee faecals and 351 baboon faecal samples between August 2011 – July 2012 and space-use was analysed using GPS observations (chimpanzees=1297, baboons=4138) collected between January-July 2012. Fruit consumption was continuous but variable in both species, and it was not found to be influenced by fruit availability in either primate. Chimpanzees consistently consumed higher numbers of fruit species throughout each month of the study. Foliage consumption was high in both species, but was influenced by fruit availability only in baboons. Foliage consumption was comparable between species across months. Qualitative diet overlap was found to be high, with baboons consuming eight of the ten most important chimpanzee fruits. However, quantitative analysis indicated overlap was high only during the late dry season/early wet season but was otherwise low. Chimpanzees and baboons at Issa overlapped substantially in their respective ranges but habitat-use within ranges differed significantly between species. Most notably, chimpanzees seemed to overuse the forest, whilst baboons seemed to underuse in proportion to its availability. In conclusion, I found that despite periods of high overlap

in fruits consumed, the differential utilisation of niche components reported in the chapter suggest competition is unlikely to be an important constraint for chimpanzees and baboons at Issa.

Introduction

Ecological communities are often comprised of many species, each one with its own specific requirements. When two or more species overlap in these requirements, the issue of coexistence becomes convoluted (Gause 1932). If species exist in the same geographic area regularly encounter one another, they can be considered sympatric, and then, species-specific ecological adaptations putatively decrease competition to make coexistence possible (Begon et al. 2006; Dew 2005; Eccard & Ylönen 2003). The mechanisms behind these adaptations often include differential utilisation of three primary niche components: diet, habitat and activity time (Schoener 1974).

Evidence for interspecific competition between sympatric species, however, is often circumstantial due to multitude of habitat types across which it can exist. Care must, therefore, be employed when hoping to generalise beyond a single study. The occurrence of competition is difficult to detect unless direct observations of inter-specific aggression (Houle 1997; Stevenson et al. 2000) or competitive dominance (French & Smith 2005) are made. More commonly, competition is inferred according to: a limited food supply to demand ratio (Janson & Emmons 1990), dietary similarities (Terborgh & van Schaik 1987; Ganzhorn 1999), similarities in mass (Ganzhorn 1999), species richness saturation (Lawes & Eeley 2000) and limited social group sizes (Janson 1988a). As primates often have commonalities in dietary requirements (Ganzhorn 1999) and frequently occur sympatrically, with more than ten species being found at some locations, they permit a rare opportunity through which to consider dietary overlap, niche separation, and interspecific competition in mammals (Head et al. 2011).

Overlap in the consumption of food species is thought to be the most pertinent causation of competition in primates, particularly in times of low food availability (Ganzhorn 1999). Fruit in particular comprises a substantial component of the diet in many primate species (Wrangham et al. 1998) and invariably undergoes periods of scarcity in accordance with regional seasonality (van Schaik et al. 1993). Consequently, dietary overlap in sympatric primate species, at its most severe, can lead to the presence of one species being limited by the presence of another by competitive exclusion (e.g. *Cercopithecus nictitans stampflii* and *Cercopithecus diana diana*: Eckardt 2004). More commonly however, this is avoided by physiological mechanisms such as differences in digestive ability between primates to switch to foliage (e.g. *Gorilla sp.* and *Pan troglodytes*: Tutin et al. 1991; Tutin & Fernandez, 1993; Head et al. 2011: *Cercopithecus* sp.: Lambert 2002; *Alouatta palliate* and *Atelese geoffroyi*: Milton 1993), and behavioural mechanisms such as partitioning use of habitat type and location, and the timing and ranging of activities (Schreier et al. 2009).

Two primates that are often found living sympatrically along the equatorial zone between Senegal and western Tanzania include the chimpanzee (*Pan troglodytes*) and the baboon (*Papio* spp.) (Matsumoto-Oda & Kasagula 2000). Chimpanzees are endangered species (IUCN 2014) whose range is confined primarily to equatorial Africa between Senegal and Tanzania with baboons being of least concern (IUCN 2014), and widespread across Africa (Kingdon 2003). The two genera are found sympatrically at numerous African sites including: Gombe (Goodall 1986) and Mahale (Nishida 1990) in Tanzania; Budongo (Sugiyama 1968), Bwindi (Nkurunungi et al. 2004), Kalinzu (Hashimoto 1995) and Kibale (Wrangham et al. 1991) in Uganda; Gashaka (Sommer & Ross 2007) in Nigeria; and Kahuzi-Biega in the Democratic Republic of Congo (Yamigawa et al. 1988). To date, most studies offer, at most, a qualitative overview on dietary overlap (Wrangham 1991). More commonly, however, diet is reported separately. These reveal chimpanzees to be predominantly frugivorous (McGrew et al. 1988) and baboons, despite a preference for fruit (Altmann & Altmann 1970), to have a much more varied diet and are accordingly considered to be frugivore-folivores (Norton, Rhine, et al. 1987). Currently, despite both species being commonly studied at a number of study sites (see above), only a single study by Matsumoto-Oda & Kasagula (2000) provides a direct comparison of the diets between these species from a habitat where they are both found. A large overlap in species diets was reported, and consequently, Matsumoto-oda & Kasagula (2000) stress that competition between the two species during the fruit-scarce season could have profound and negative consequences for the chimpanzee population. When the two species share a common fruit species, baboons may have the advantage as they are better able to digest unripe fruit (Wrangham et al. 1998; Lambert 2005) compared to chimpanzees, which specialise primarily on ripe fruits (Goodall 1986; Newton-Fisher 1999; Wrangham et al. 1998). As such, further advancements in elucidating the ecological relationship between these two species may help to better conserve the endangered chimpanzee, especially in light of increased encroachment of people on the forests (Matsumoto-Oda & Kasagula 2000).

In this study, I compare the diet and space-use of an un-habituated chimpanzee community (*Pan troglodytes schweinfurthii*), and three partially habituated yellow baboon (*Papio cynocephalus*) troops in the Issa valley of Ugalla, western Tanzania. The Issa study site is comprised of a mosaic of habitat types but mostly consists of miombo woodland interspersed with gallery forest. Issa is home to seven primate species: red colobus (*Procolobus tephrosceles*), vervet monkey (*Chlorocebus aethiops*), redtail monkey (*Cercopithecus ascanius*), greater galago (*Otolemur crassicaudatus*), lesser galago (*Galago senegalensis*), and the chimpanzee (*Pan troglodytes schweinfurthii*) and yellow baboon (*Papio cynocephalus*). Of these, it is the yellow baboons that exist in the greatest densities and that are closest in size to the chimpanzees. Ugalla has been described as one of the driest (Moore 1994), more marginal habitats in which chimpanzees are known to live (Kano, 1972; Ogawa et al., 2007), with population densities being far lower than nearby forested areas such as Gombe (Goodall 1968; Ogawa et al. 2007). With this in mind, if the chimpanzees at Issa are competing for food with the sympatric baboons, it could exacerbate the already marginal conditions in which they exist. In other words, even if the two species have been coexisting sympatrically for many years, this does not obviate the possibility that the presence of baboons can make it harder for the chimpanzees. It is therefore useful to examine the space-use and dietary overlap in these species at this site.

In Chapter 5, I showed baboons to exhibit avoidance of the gallery forest habitat, despite the availability of fruit within it. I therefore hypothesised that this differential pattern of habitat use by the baboons could result from competition mitigation via niche separation (Schreier et al. 2009; Chapter 5). In order to test this hypothesis I first quantify food (specifically fruit) availability for the two species by estimating fruit abundance along transects within the species ranges. Second, I determine what food species are being consumed by each species from macroscopic faecal analysis. This allows me to describe the food species that are important to both species and examine the degree of dietary overlap, and how this varies over time. Following other studies

(Matsumoto-Oda & Kasagula 2000), I expect to see a reasonable overlap in foods consumed, and that this overlap will vary seasonally. Accordingly, I predict that fruit availability will correlate positively with fruit consumption by both chimpanzees (Wrangham et al. 1998) and baboons (Altmann 1974; Barton 1989), and that overlap in fruit species consumed will be greatest during times of fruit scarcity. To determine the extent of the overlap in habitat utilisation between the chimpanzees and the baboons, I compare the relative preferences for different habitat types using Electivity Index (Krebs 1989). Together, the degree of overlap in diet and space used will allow me to assess the potential for interspecific competition between the chimpanzees and baboons at Ugalla, an important first step in understanding coexistence between the two species in this unique habitat.

Methods

Study site and subjects

Baboon diet data were collected from three troops comprising of 50, 22 and 33 individuals from August 2011- July 2012. Chimpanzee diet data were collected on the entire community at Issa, which genetic analysis identifies as being comprised of at least 67 individuals (Rudicell et al. 2011) from August 2011-July 2012. Baboon spatial data were collected on two troops comprising 22 and 33 individuals from January-July 2012 (see Chapter 2). Chimpanzee spatial data was collected on the entire Issa community from January-July 2012.

Seasonality

Please refer to Chapter 2, pages 25-26 (Figure 2.4) for details on defining seasons.

DIET

Measures of fruit availability

Fruit availability indices (FAI) were calculated according to the methods outlined in Chapter 2, pages 30-31, and incorporates both fleshy and non-fleshy (i.e. seed pods), which are from here collectively referred to as fruit. Because neither chimpanzees nor baboons were found to consume all species of fruit on the transect, I estimate fruit availability indices (FAI) specific to each species (see Chapter 2, page 31 for detailed methods of how FAI is calculated), based on trees of the transect known to produce consumed fruits. Consequently, I produce a FAI for both chimpanzees and baboons, based only on the fruits known to be consumed by that particular species (Figure 6.2). However, as not all fruits consumed were found on the transects, FAI for each species was based only on the proportion of fruits from the transects that were found in their diet. Therefore, whilst not all consumed fruits are represented in the FAI, I must assume that this is an accurate reflection of FAI as a whole. In support of this, I find no significant difference in the inter-month variability between the total FAI, chimpanzee FAI and baboon FAI (Levene's test: F=0.43, p=0.65).

Faecal collection and macroscopic analysis

Field assistants and I collected 299 fresh faecal samples (monthly mean = 24.9, s.d. =18.9, monthly range=3-59) from chimpanzees and 351 (monthly mean=29.1, s.d.=21.7, monthly range=10-87) from baboons (Table 6.1). Baboon samples were collected during baboon specific follows that were conducted up to 12 days a month. Chimpanzee faecal samples were collected opportunistically and were reliably identified to the species by the distinct odour, size and location (e.g. under a nest or on a chimpanzee path).

All samples were then analysed macroscopically according to the methods detailed by McGrew et al. (2009), Chapter 2, pages 35-36: samples were weighed then sieved through a 1mm mesh with local river water. The contents of the sieve were then sluiced in the running water allowing faecal matter to be broken up, and the digested material washed away. The undigested parts were then counted or rated (according to a three-point scale: abundant, common and rare (Yamagiwa et al. 1993)) in relation to the total size of the remaining faecal matter.

Non fruit plant parts were represented in the faecals as partly digested leaf fragments and fibre (stems, pith and roots), which cannot be identified to species level and so were separately rated with respect to the total mass of the undigested material on the three-point scale. Small seeds, and animal remains were also rated and removed and finally, morphologically similar seeds of a medium or large size were counted, recorded and removed from the sieve. For most seeds, morphological disparities were sufficient to identify them easily to a species level (e.g. *Garcinia hulliensis*) but for some it was only possible to identify them to a genus level (e.g. *Ficus* sp.). Please refer Chapter 2, page 36 to see procedure for unidentified seeds.

A numerical value for the non-fruit plant component of the diet was subsequently calculated by converting the ratings as follows: abundant =3; common =2; rare =1 (Tutin & Fernandez 1993). I subsequently calculated a foliage score for each sample by combining the numerical values for the leaf fragment and fibre content (Tutin & Fernandez 1993). A fruit score was obtained for each sample by totalling the number of fruit species found (Tutin et al. 1991; Yamagiwa & Basabose 2006). These scores are used in subsequent analyses in this chapter.

Seed identification was conducted according to the methods specified in Chapter 2, pages 35-36.

Table 6.1. The number of faecal samples collected and analysed over each month of the study period for both primate species.

	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
Baboon	21	18	54	87	36	24	24	28	10	16	11	20
Chimpanzee	3	50	15	59	19	12	27	24	53	21	9	7

Dietary overlap and fruit availability

I present qualitative data on dietary overlap by identifying fruit species that were shared between the two species during the study period. However, as this can exaggerate the level of overlap by not considering the relative importance of each item in the diets, I also measure dietary overlap between the baboons and chimpanzees using the Renkonen method (Eckardt 2004; Head et al. 2011):

$$P_{jk} = \left[\sum_{i=1}^{n} \left(\min p_{ij} p_{ik} \right) \right] 100$$

where P*jk* is the monthly percentage overlap between species *j* and species *k*, p*ij* is the proportion of faecals containing resource *i* of the total number of faecals belonging to species *j*, p*ik* is the proportion of faecals containing resource *i* of the total number of faecals belonging to species *k*, and *n* is the total number of resource states. I subsequently use a Spearman's rank correlation to determine if there is a relationship between overlap in fruits consumed and fruit availability (FAI calculated from all fruit species consumed by both species).

Diet analysis

To determine if chimpanzees and baboons differed in the fruit or foliage consumed, I used generalized linear mixed models (GLMM) with Poisson error structure. I ran two models, one with fruit score as my response, and one with foliage score as my response variable. In both models, I fitted 'day' and 'month' as random effects to control for potential non-independence of samples collected on the same day/month. Sample weight was fitted as a continuous fixed effect, and primate species was fitted as a categorical fixed effect (baboon or chimpanzee).

To examine what factors influence the presence of foliage and/or fruit in the diet of each species, I used mixed models for each species. Because foliage and fruit scores for baboons cannot be predicted by a model with Gaussian or Poisson error distribution due to a high number of zero values (see also Chapter 3), I convert the foliage and fruits scores to a simple presence and absence data (binomial model). The distribution of fruit and foliage scores for chimpanzees, however, were suited to a model with Poisson error structure. In both my baboon and chimpanzee model, I fitted both fruit and foliage as response terms and 'day' and 'month' as nested random effects to control for the potential non-independence of samples collected on the same day/month. Mean monthly temperature (^{o}C), total monthly rainfall (mm), fruit availability indices (FAIs) and faecal weight (g) (to control for the potential correlation between faecal weight and number of dietary items) were fitted as continuous fixed effects. Season was fitted as a categorical variable (wet, dry).

In all models, co-linearity between fixed effects was checked using Spearman's rank correlation tests, with a cut-off criterion of $r_s = 0.60$ (Tabachnick & Fidell 2012). Where variables were correlated, I included terms one at a time, and compared models using Akaike's information criterion (AIC) value (Akaike 1998) and backward selection of terms to select the model that had the best fit (Heinänen et al. 2008). The significance of the individual terms was then calculated from the selected model and all dropped terms were put back into the model to obtain level of non-significance (lmerTest package, R: Kuznetsova 2012). All models were run using lme4 package in R (R Development Core Team 2010).

SPACE-USE

Habitat classification

Habitat types at Issa were classified according to the methods outlined in Chapter 2 pages 27-28 (Figure 2.6 B), and primate ranging data was collected using species-specific methodology.

Location data

In the case of baboons, focal troop follows were conducted on two troops of partially habituated baboons from 07:00 to 19:00 h up to 12 days/month and GPS fixtures recorded at 5 minute intervals (see Chapter 4 for more details). The ranging behaviour of the unhabituated chimpanzee community at Issa, by necessity, was more opportunistic. Evidence of chimpanzee presence was obtained during reconnaissance walks (where no habitat bias was associated search effort), or from following fresh tracks and/or vocalisations within the Issa study site (~85km^2). GPS fixtures were taken when any signs of chimpanzee presence was identified. These included direct sightings (n=33), faecals (n=183) or nests (n=1070). If a direct sighting of a chimpanzee (or chimpanzees) was made, and they did not flee immediately, they were tracked until they were lost from sight.

Habitat preferences

Using all locational fixtures, I delineated a separate range for each primate using a kernel density estimate (KDE). This method produces a realistic range using probabilistic modelling (Worton 1989). This was done for both chimpanzees and baboons, using all locational fixtures, which although not being directly comparable with each other, do allow us to calculate quantities of each habitat type present within their respective ranges. However, due to >80% of chimpanzee observations belonging to nests, it is possible that the data is biased to habitats where nests can be made. I therefore take three subsets of the data: 1) Just direct sightings and faecals (n=216) and 2) nests only (n=1070) and 3) direct sightings, faecals and nests (n=1286). I then test the preference or avoidance of each habitat type in relation to its availability for each subset using Krebs' (1989) Electivity Index. I then use a Wilcoxon signed ranks test to determine if nest locations are biasing habitat electivity's. The Electivity Index (*EI*) ranges from +1 (strongly preferred) to -1 (strongly avoided), and is calculated as follows:

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

Where h_i is the number of GPS fixes from within habitat i, and p_i is the relative availability of habitat i in the MCP of that species.

Results

DIET

Fruit Availability and Seasonality

For a description of seasonality see Chapter 2 pages 25-26, and for overall fruit availability in the forest and in the woodland see Chapter 2, pages 30-31 and Figure 2.7.

Composition of Diet

Macroscopic faecal analysis revealed the chimpanzees consumed 50 unique species of fruit and the baboons consumed 53 between August 2011 and July 2012. I found 40% of chimpanzee fruits and 38% of baboon fruits were shared. Fruit was found in a much higher percentage of chimpanzee samples than in baboons, and was the most frequently found food type (Table 6.2). Foliage was common to both chimpanzee and baboon samples, and was found in similar frequencies (Table 6.2). Invertebrate and vertebrate remains were found more frequently in baboon samples than in chimpanzee samples (Table 6.2). *Garcinia huillensis* (fleshy fruit) was the fruit that was found in the highest proportion of samples in both primate species (Table 6.3), and *Ficus* (fleshy fruit) was found in a large proportion of chimpanzee samples during almost every month of the study period.

Table 6.2. Percentage of all samples, by species, that contain each of the major food types followed by a monthly mean and standard deviation.

Food type	**Chimpanzee** **% Total (monthly mean ± SD)**	**Baboon** **% Total (monthly mean ± SD)**
Fruit	96.32 (96.96 ± 6.39)	59.26 (51.9 ± 20.73)
Foliage	77.59 (78.77 ± 16.95)	76.35 (73.24 ± 20.5)
Invertebrates	7.36 (11.87 ± 13.24)	56.7 (55.81 ± 21.25)
Vertebrates	0.33 (0.93 ± 3.21)	1.4 (1.39 ± 3.7)

Inter-specific diet comparison

Overall, 40% of chimpanzee fruits were also eaten by baboons and 39% of baboon foods were also eaten by the chimpanzees. Renkonen's method to estimate overlap in diet revealed an overlap range of 0% – 63% (mean=15.29%) according to month (Figure 6.1). The degree of overlap fluctuated over the duration of the study and peaked during the late dry season/early wet season (Figure 6.1). Overlap did not vary seasonally (Wilcoxon signed ranks test: n=5, v=12, p=0.31), and did not correlate to FAI (n=12, Spearman's correlation r_s= -0.46, p=0.13). I also found that eight out of the ten most frequently consumed chimpanzee fruits were eaten by the baboons, and the chimpanzees ate six out of the ten fruits most frequently consumed by the baboons (Table 6.3). *Garcinia huillensis*, when in season was highly prevalent in the diets of both species suggesting it is a preferred dietary item at this time. As a result, it is during the period of fruiting of *Garcinia huillensis* that I observed the highest overlap in the diet between baboons and chimpanzees.

Table 6.3: The ten most consumed species of fruit by baboons and chimpanzees based on the frequency in faecal samples (%)

Species	**Life form**	**Frequency in *Papio* diet (%) and rank (x)**	**Frequency in *Pan* diet (%) and rank (x)**
Garcinia huillensis	Tree	27.9 (1)	27.4 (1)
Unknown species	?	6 (2)	0
Uapaca kirkiana	Tree	4.6 (3)	1 (28)
Unknown species	?	3.7 (4)	8.7 (9)
Saba comorensis	Liana	3.4 (5)	22.7 (2)
Vitex sp.	Tree	2.9 (6)	12.7 (5)
Canthium burtii	Shrub	2.3 (7)	4.7 (16)
Leptactina banguelensis	Shrub	2.3 (7)	0
Unknown species	?	2.3 (9)	0
Chrysophylum banguelensis	Shrub	2 (10)	0
Ficus sp.	Tree	1.8 (14)	18.1 (3)
Oxyanthus speciosus	Shrub	0	15.4 (4)
Anisophyllea boehmii	Tree	1.7 (18)	11.4 (6)
Afromomum mala	Herb	0.9 (29)	11 (7)
Unknown species	?	0.00	11 (7)
Grewia sp.	Shrub	1.7 (19)	8.4 (10)

Numbers in parentheses refer to the rank

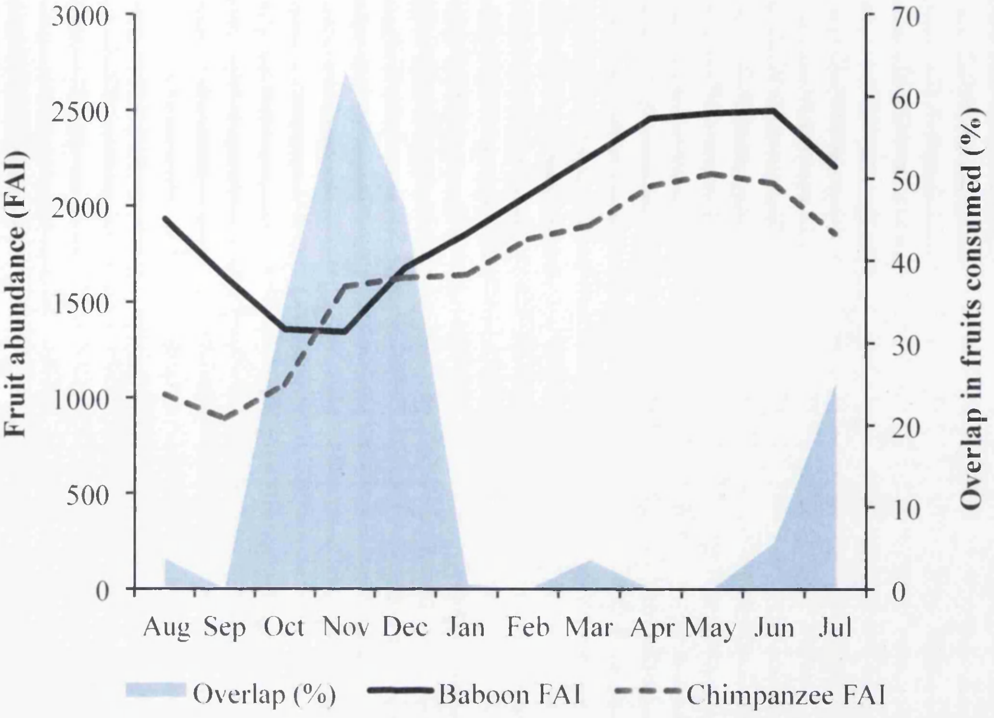

Figure 6.1. Dietary overlap between chimpanzees and baboons per month, and abundance of fruit. Fruit abundance values on y-axis are the square root of the actual value.

Chimpanzees consumed significantly more fruit species per sample than baboons (Figure 6.2B; LMM: estimate(SE)= 1.45(0.12) , t value= 12.42, p =<0.0001) when controlling for weight of the sample (estimate(SE)= 0.0018(0.00048) , t value= 3.81, p =<0.001), and this was consistent across month of study (mean [chimpanzees] = 15.25, SD= 6.61, range= 8-28; mean [baboons] = 7.58, SD= 4.52, range=2-18) (Figure 6.2D). Despite the absence of data on the volume of fruit consumed by either primate, the results support the prediction that the chimpanzees are more frugivorous than the baboons.

Foliage scores were comparable between the two primate species (Figure 6.2A; LMM: estimate(SE)= 0.025(0.13), t value= 0.20, p =0.85) controlling for weight of the sample (estimate(SE)= 0.0052(0.00054), t value= 0.4.69, p =0.<0.0001), and this pattern was consistent across the study period (Figure 6.2C).

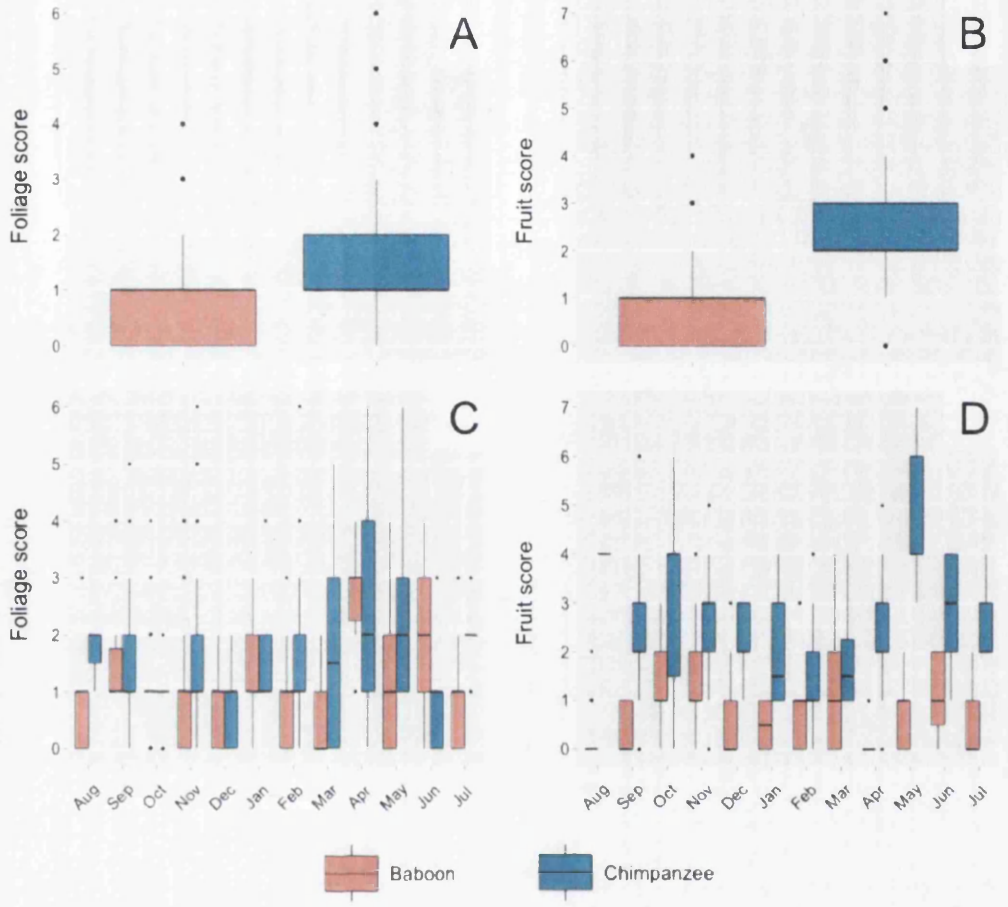

Figure 6.2: (A) Median foliage score in faecal samples for baboons (n=351) and chimpanzees (n=299). (B) Median number of fruit species (fruit score) in faecal samples for baboons (n=351) and chimpanzees (n=299). (C) Median foliage score in faecal samples for baboons and chimpanzees per month (n=12). (D) Median number of fruit species in faecal samples for baboons and chimpanzees per month (n=12). In all boxplots, upper and lower quartiles are shown by the range of the 'box', median value by the horizontal line within the box and the full extent of the data shown by the 'whiskers', with black dots representing outliers.

Species diet and fruit availability

Foliage score in chimpanzee samples was a positive function of sample weight (GLMM: Foliage estimate (SE) = 0.0011(0.00036), F= 8.41, $p < 0.01$), but none of the other factors measured had a significant effect (GLMM: FAI: effect (SE) =

0.0004(0.0003), F= 1.27, P >0.05; Season: F= 1.42, P>0.05; Rainfall: effect (SE) = 0.0005(0.0009), F= 0.31, P>0.05). To determine if chimpanzees consumed less foliage when fruit was present in the diet, I also included fruit score as a continuous fixed effect in the GLMM model. However, this does not influence the result of the model (GLMM: effect (SE) = -0.21(0.11), F = 3.72, P>0.05). Fruit score was not influenced by any of the factors measured (GLMM: FAI: effect (SE) = -0.0001(0.0003), F= 0.21, P >0.05; Season: F= 0.50, P>0.05; Rainfall: effect (SE) = -0.0006(0.0007), F= 0.83, P>0.05; Sample weight: effect (SE) = 0.0005(0.0003), F= 3.35, P>0.05). I consequently find no evidence that the variability in chimpanzee diet is influenced by the availability or consumption of fruit as measured by faecal samples.

The presence of fruit in baboon samples was not significantly influenced by any of the variables measured (GLMM: FAI: effect (SE) = -0.0007(0.0006), F= 1.15, P >0.05; Season: F= 1.48, P>0.05; Rainfall: effect (SE) = -0.00003(0.002), F= 0.0004, P>0.05; Sample weight: effect (SE) = 0.011(0.0058), F=3.92, P= 0.054). The presence of foliage in the samples, however, was negatively influenced by fruit availability (GLMM: effect (SE) = -0.0014(0.00064), F=4.79, P<0.05), but other factors had no influence (Season: F= 0.47, P >0.05; Sample weight: effect (SE) = 0.0062(0.0068), F= 0.88, P >0.05; Rainfall: effect (SE) = -0.0004(0.002), F= 0.04, P>0.05).

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Habitat composition

Figure 6.3 shows the availability and use of the different habitat types within the range of each species (Figure 6.4). Despite the majority of observations for chimpanzees being recorded in the woodland, the Electivity Index and paired statistical comparisons of availability vs. observed use suggest chimpanzees underuse this habitat in proportion to its availability (Figure 6.5; Table 6.4). Dry grassland, wet grassland and rocky outcrops were also under-used, suggesting avoidance of these by the chimpanzees (Figure 6.5; Table 6.4). Conversely, the forest habitat was substantially over-utilised suggesting a strong preference (Figure 6.5; Table 6.4). These deviations from the expected values were statistically significant (Table 6.4). From comparing the Electivity Indices calculated from faecal, sightings and nest observations with just faecal and sighting observations. I determined that habitat preferences were unbiased by nests (Wilcoxon signed ranks test: W=98, n=35, p>0.05). Furthermore, the utilisation distribution of habitats between observations of just nests compared to faecal, and direct sightings revealed no significant difference (Wilcoxon signed ranks test: W=529, n= 35, p >0.05).

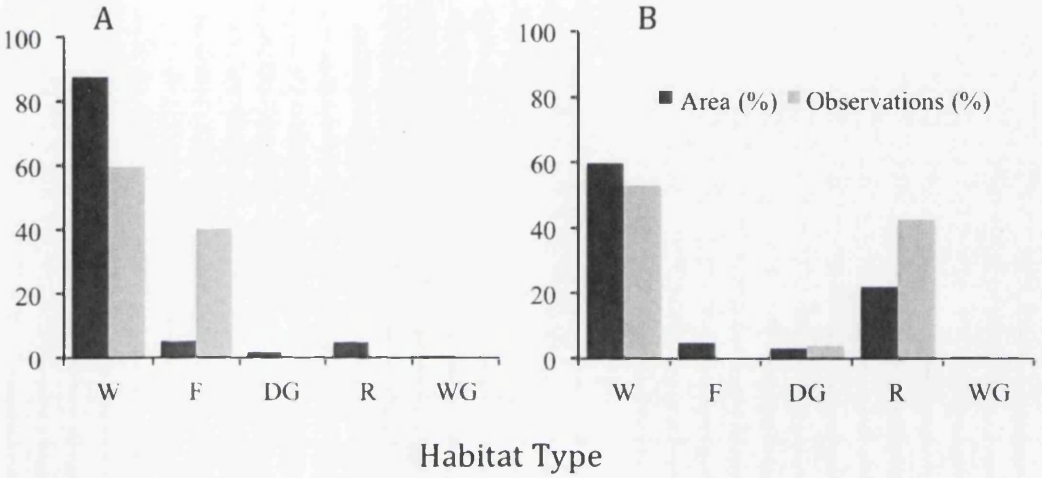

Figure 6.3: Percentage coverage of each habitat type, and percentage of observations from within each habitat. (**W**: woodland, **F**: Forest, **DG**: Dry Grassland, **R**: Rocky outcrops, **WG**: Wet Grassland.).within the estimated range of (A) chimpanzees and (B) baboons.

Electivity indices and paired statistical comparisons of availability vs. use for baboons show wet grassland and forest habitats are under-used, suggesting avoidance of these by the baboons (Figure 6.5; Table 6.4). Conversely, rocky outcrops are slightly over-used, suggesting a preference for this habitat type (Figure 6.5). These deviations from the expected values were statistically significant for these habitat types (Table 6.4). Woodland and grassland were not significantly preferred or avoided and therefore likely used in proportion to their availability (Figure 6.5; Table 6.4).

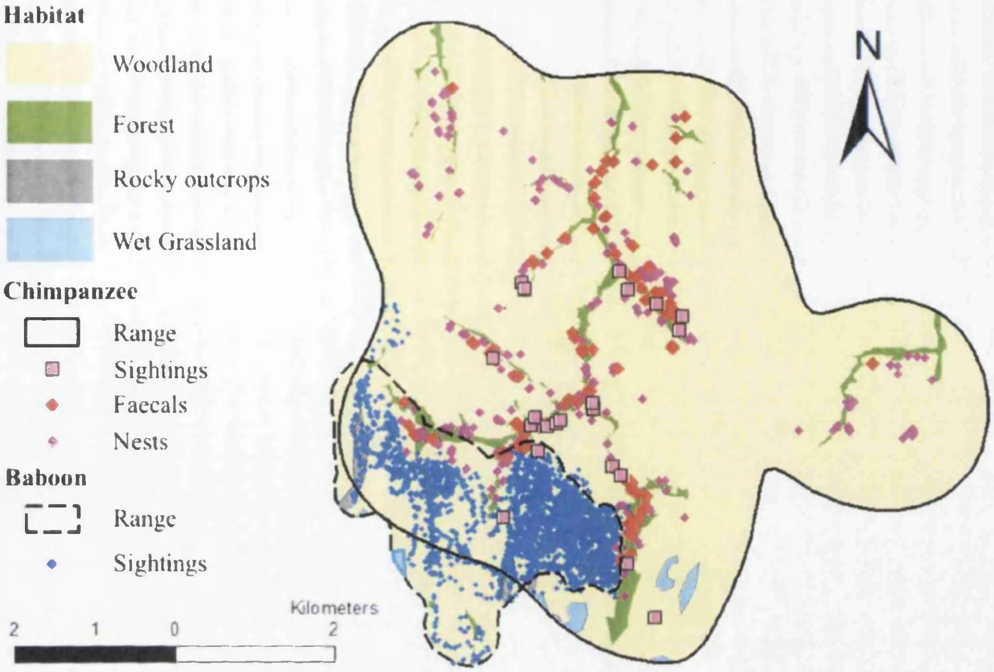

Figure 6.4. The ranges, as estimated by kernel densities, of the chimpanzee community (n= 1297 observations), and baboon troops (as estimated from two troops: CT and MT, n= 4138 observations (See Chapter 5)) at Issa.

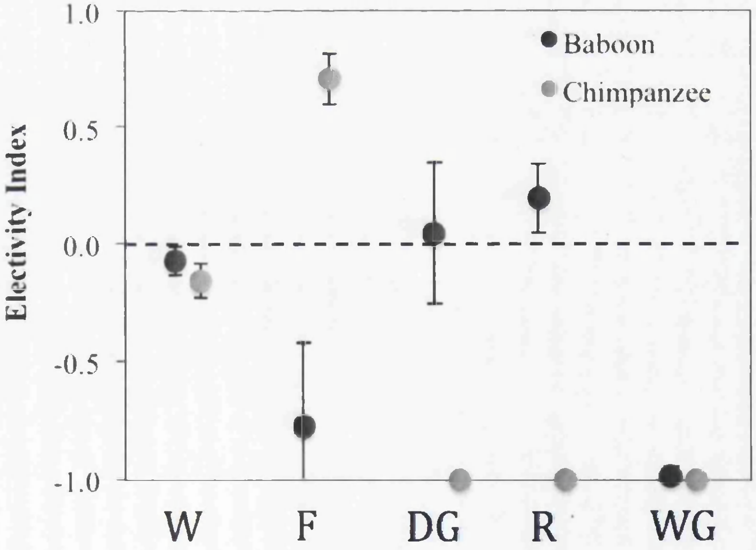

Figure 6.5: Krebs Electivity Index (EI) illustrating chimpanzee and baboon preferences and avoidance of habitat types (**W**: Woodland, **R**: Rocky Outcrops, **WG**: Dry Grassland, **WG**: Wet Grassland, **F**: Forest) over the study period in Issa valley.

Table 6.4. Wilcoxon signed ranks test between the number of observations in each habitat and the expected number if each habitat was used in proportion to its availability. **+ve** indicates baboons are using habitats more than expected and **–ve** shows the opposite. Directions with an asterix represent significant differences between observed and predicted. Chimpanzee results remain the same when tests are re-run from subset of data excluding nest observations.

	Chimpanzee			**Baboon**		
Vegetation	W	p	Direction	W	p	Direction
Forest	28	<0.05	+ve*	0	<0.05	-ve*
Grassland	0	<0.05	-ve*	19	>0.05	+ve
Rock	0	<0.05	-ve*	28	<0.05	+ve*
Woodland	0	<0.05	-ve*	6	>0.05	-ve
Swamp	0	<0.05	-ve*	0	<0.05	-ve*

Discussion

In this chapter I have investigated the overlap in the space-use and diet of sympatric chimpanzees and baboons within the Issa valley. Like conspecifics elsewhere across their respective ranges, I find fruit to be an important component in the diets of both chimpanzees (Wrangham 1977; McGrew et al. 1988) and baboons (Barton 1990; Norton et al. 1987) and many of the fruit species were found to be consumed by both species. Chimpanzees were more frugivorous throughout the study period, and the overlap in fruits consumed was not influenced by the availability of fruit. Fruit and foliage consumption by chimpanzees was continuous and appeared to not be influenced by the availability of fruit, or any other factors measured except sample weight. Baboons, however, consumed more foliage when fruit was less available. Despite the overlap in ranges between the two species, important differences were observed in their habitat preferences. The most obvious of which was the preferential use of forest habitat by chimpanzees compared to its avoidance by the baboons. I continue by discussing the potential for this differential habitat use to be a result of niche separation.

Chimpanzees at Issa were found to consume the fruits of 50 plant species during the study period and, similar to other populations, consume fruit throughout the study (Wrangham et al. 1998). This number, however, likely represents only a part of the actual number of species ingested, for example an earlier study by Hernandez-Aguilar (2006) on the same community of chimpanzees, identified 77 plant species in the diet over a 21 month study period. During each month, fruit was present in a high proportion of the samples (especially *Ficus*), but the average number of fruit species per sample did vary monthly. However, I did not find this variation to be significantly explained by any factor. Most surprising, though, is that the number of fruits consumed is not influenced by FAI. In study sites with seasonally predictable scarcities of fruit, chimpanzees typically respond to increased fruit availability, by increasing their consumption of it (Yamigawa et al. 1988; Head et al. 2011; Wrangham et al. 1998). Moreover, I found no relationship between FAI and foliage consumption, which is contrary to other faecal analysis studies, which found the consumption of foliage by chimpanzees to increase during periods of fruit scarcity (Kuroda et al. 1996; Tutin & Fernandez 1993). As a predominantly frugivorous primate (Ghiglieri 1984; McGrew et al. 1988; Wrangham 1977), chimpanzees often respond to seasonal scarcities of fruit by broadening their diet to include fibrous piths and leaves (foliage) (Wrangham et al. 1991). However, I find no evidence that chimpanzees at Issa are doing this. Macroscopic faecal analysis, though, has well known limitations, which necessitate the careful interpretation of these results (Tutin et al. 1991; McGrew et al. 1988). Specifically, it is difficult to reliably estimate the quantity of fruit in the faecal samples, and so presence and absence is used instead, which substantially reduces the resolution of the data and also, therefore, the robustness of any ensuing analyses (Tutin et al. 1991). Moreover, it is possible that the FAI, as calculated from the phenology transects, was not an accurate reflection of the fruits consumed by the chimpanzees. In total, 14/50 chimpanzee foods were represented on the phenology transects. It is possible then that the remaining foods follow a different fruiting pattern and that periods of fruit scarcity were consequently not accurately identified. Despite these unavoidable methodological limitations, this study has succeeded in identifying the fruits consumed by the chimpanzees, which can be subject to phenological monitoring in future studies to better test these relationships.

Similar to other studies, I find the diets of chimpanzees and baboons exhibit a high degree of overlap in the fruits consumed (Matsumoto-Oda & Kasagula 2000). For example, baboons consumed eight out of the ten most frequently consumed chimpanzee fruits and chimpanzees consumed six out of the ten most frequently consumed baboon fruits. Chimpanzees, however, consistently consumed more fruit than the baboons, which is expected given the different feeding strategies of the two primate species. Baboons, having a more generalist diet (Norton et al. 1987) are able to exploit a broader scope of food types compared to the predominantly fruit specialising chimpanzees (McGrew et al. 1988; Wrangham 1977; Ghiglieri 1984; Wrangham et al. 1998). This is further supported by the observation of baboons eating more leaves and fibre when fruit was less available, whilst the consumption of leaves and fibres by chimpanzees remained uninfluenced by fruit availability.

Dietary overlap in the fruits consumed, as calculated via Renkonen's method fluctuated seasonally with some months exhibiting zero overlap between the primates, compared to other months where overlap was very high. However, in contrast to my prediction, overlap in fruit consumption was not correlated with overall fruit availability. This could be a result of a divergence in the diet between the two species, supported by the observed increase in foliage consumption during periods of low fruit availability by the baboons. Alternatively, despite lack of relationship between overlap and fruit availability, overlap was observed to be at its highest during the period of low FAI (late dry/early wet season). During this time, both primate species consumed large amounts of *Garcinia huillensis.* Perhaps because this corresponded with low overall fruit availability, *Garcinia huillensis* was found in the highest proportion of samples over the study period. For these reasons, it is probable that *Garcinia huillensis* is an important fruit species for both primates. It is also worth mentioning that sample size was low in some months, despite a constant search effort, for unknown reasons. With that said, it is the proportion of faecals containing the relevant food item that I was concerned with, rather than the absolute frequency, therefore the affect of a small sample size should be minimal.

During the study period, no encounters were observed between baboons and chimpanzees. This in part is likely due to the relatively low density of the chimpanzees, perhaps combined with the deterrence of observer presence. However, it could be purposeful avoidance between the species in order to avoid feeding competition, or even predation avoidance by the baboons. Chimpanzees have been observed to eat baboons at both Gombe (Wrangham & van Zinnicq Bergmann Riss 1990) and Mahale (Nakamura 1997). This hypothesised avoidance of chimpanzees by the baboons may be supported by the habitat Electivity Index I present in this chapter. As the most abundant habitat type, the woodland was found to contain the most observations of both species. However, when considered in relation to the relative availability of habitat types chimpanzees significantly underused the woodland, and overused the forest habitat in proportion to its availability. In contrast to this, I find the baboons to significantly underuse the forest habitat. Instead baboons use the vast miombo woodland habitat in proportion to its availability whilst demonstrating a preference for rocky outcrops (see Chapter 5). However, my measure of habitat preference of chimpanzees is derived from nests, faecals and sightings. The nests comprise a large fraction of these, and can only be built where there are trees, thus creating a bias against grassland habitats. Additionally, nesting preferences, between tree species, may be influencing choice of trees between woodland and forest habitats. Chimpanzees at Issa have been found to preferentially nest in the forest compared to woodland, relative to availability (Stewart & Pruetz 2013). It is possible then, that observations from nests do not provide an accurate reflection of habitat-use. Nests only provide evidence of the places used at night, but the relationship between places used at night and those used during the day may not be easy to discern since they can walk long distances in a single day. Nests, therefore, provide only partial evidence of habitat-use. Consequently, the degree to which I observed chimpanzees to be avoiding grasslands and rocky habitats could potentially be exaggerated. However, if this was true then we would expect the distribution of chimpanzee sightings and faecals to be the same whatever the habitat type, as RAs were sensitive to these during all types of fieldwork across all habitats. I find, though, that the distribution of sightings and faecals were not significantly different to the distribution of observations that included nests, or even of nests alone.

As discussed in Chapter 5, the avoidance of the forest habitat by Issa baboons could be a mode of niche separation whereby the forest is avoided in order to avoid competition with the chimpanzees (Schreier et al. 2009). The results I present in this chapter, which suggest the forest is utilised heavily by the chimpanzees, provides support for this hypothesis. Differential utilisation of habitats is a prevalent method of niche separation in two potentially competing animals (Schoener 1974) and has been observed across the primate taxa (e.g. Stevenson et al. 2000; Rodman 1973; Terborgh 1984; Ganzhorn 1989), see Schreier (2009) for a synthesis. However, inferring competition from just niche separation is difficult, and other potentially influential factors must be considered when explaining differential habitat use such as perceived predation risk (Willems &

Hill 2009), and relative food availability and distribution (Clutton-Brock & Harvey 1977b).

In summary, I find some evidence to support the potential for competition between chimpanzees and baboons at Issa, but that it is unlikely to be an important constraint on either species. Comparisons of the fruit component of the diet suggest that although there is the potential for competition on account of occasionally high overlap in the fruits consumed, this is unlikely to impact negatively on either species due to dietary differences and habitat separation (Schoener 1974). Baboons exhibited a range of dietary flexibility in response to the variation in food availability and maybe the presence of a potential competitor. It is possible that the greater dietary flexibility of baboons leads to the greater variability in their diet compared to chimpanzees, and therefore reduces interspecific competition, for example between *Gorilla gorilla* and *Pan troglodytes* (Head et al. 2011). Additionally, the disparity in the utilisation of the forest habitat could be evidence of niche separation, which through the same mechanisms as in dietary separation, reduces interspecific competition in primates. However, further investigation into the non-fruit dietary component of chimpanzees and baboons, and the ranging patterns of chimpanzees would better allow us to infer potential competition and better understand how these species live sympatrically at Issa.

Chapter 7 –Discussion

In this thesis I have examined the feeding and movement ecology of two yellow baboon (*Papio cynocephalus*) troops in the Issa valley of western Tanzania. Yellow baboons are a well-researched species, with a rich literature existing derived from multiple long-term study sites (e.g. Mikumi: Norton et al., 1987; Amboseli: Altmann, 1998; TRPNR: Bentley-Condit, 2009). The Issa study site, however, is climatically and ecologically disparate with it being a predominantly woodland habitat that is at a higher altitude and, which receives more annual rainfall. Thus, Issa provides a unique context in which to investigate baboon feeding and movement ecology, and I have examined baboon diet selection (Chapter 3), resource and space use over the course of a day (Chapters 4) and several months (Chapter 5), and I examined the potential for competition between the Issa baboons and the sympatric chimpanzee (*Pan troglodytes*) (Chapter 6). In this final chapter, I will summarise the main findings of this thesis and how they might inform our understanding of baboon ecology. I discuss these under the following sub-headings: baboon diet, determinants of movement, coexistence in sympatric primates, and end with some concluding remarks.

Baboon diet

Baboon diet at Issa, as with other populations, was broad and variable with food types including fibres, leaves, fruits, seeds, vertebrates and invertebrates. Fruits and foliage (leaves and fibres) were found to comprise the majority of the samples throughout the study period and were present in the diet during every study month. The number of fruit species consumed was comparable across seasons and did not vary in accordance to fruit availability but the species of fruits consumed did change. For example, *Garcinia huillensis* was not consumed during overlapping time periods with species like *Leptactina banguelensis*.

Like many other primate populations studied to date, baboons at Issa were not habituated to the degree where their diet could be directly observed (Chapter 2, page 32). Although ideal for study purposes, habituation is not always possible due to limited time frames within which researchers must work, or because it may facilitate poaching and therefore be irresponsible. Due to insufficient time, I was unable to fully habituate baboons at Issa and so I employed macroscopic faecal analysis (McGrew et al. 2009) to answer questions about their diet. As an indirect measure, though, there are limitations (Moreno-Black 1978; Doran et al. 2002). Most common, is the bias towards the hard components of the diet, which remain identifiable post digestion. At Issa, I found this to be predominantly the case for fruit seeds, whilst other important dietary components including fauna (invertebrates, mammals, birds and reptiles) and foliage (leaves, pith, roots, bark and tubers), though easy to categorise broadly, were impossible to identify to a species level. Therefore, the frugivorous component of baboon diet I reported in Chapter 3 is likely exaggerated compared to the non-frugivorous component (Phillips & McGrew 2013; McGrew et al. 1988).

Irrespective of the bias towards the frugivorous component of baboon diet at Issa, fruit is undoubtedly an important dietary item, as it is for many other baboon populations studied to date (Dunbar & Dunbar 1974; Barton 1990; Harding 1976; Depew 1983; Bronikowski & Altmann 1996; Norton, Rhine, et al. 1987; Rasmussen 1978; Sigg & Stolba 1981; Sharman 1981; Davidge 1978; Ransom 1981). In addition, evidence from Issa suggests the baboons maintain stability in their diet through the switching of the fruits they consume, and again, this mirrors the findings of other studies, where baboons switch between fruit species in concert with local fruiting phenologies, thus maintaining dietary requirements from fruit by successively exploiting the environment (Alberts et al. 2005).

In times of food scarcity, baboons are known to switch their diet altogether, relying more on locally abundant but less desirable foods known as fallback foods including corms, fibres and leaves. The consumption of such fall-back foods normally coincides with a shortage of preferred foods (Hoffman & O'Riain 2010; van Doorn et al. 2010) and also, therefore, diversity in their diet (Post 1982; Norton, R. Rhine, et al. 1987). At Issa, I found that when fruit availability was low, baboons consumed more foliage but that the number of food types consumed increased as well. This is probably a product of the woodland context in which baboons at Issa exist, where, despite some seasonal variation in the availability of fruit there are rarely periods of low fruit availability (Figure 2.7; Chapter 2). Thus, unlike their savannah and mountain dwelling conspecifics (see Post 1982; Norton, Ramon J Rhine, et al. 1987; Byrne et al. 1993), who switch to fall-back foods, Issa baboons can simply reduce their reliance on fewer more abundant fruits and instead exploit a wider diversity of less abundant fruits and foliage to satisfy their dietary requirements.

Due to the limitations I described above, however, the number of food types I reported in the samples may be over-simplified, and therefore may not be an accurate reflection of those actually consumed. Consequently, future descriptions of baboon diet at Issa would benefit from their full habituation so that direct intake of food items can be measured. Additionally, fruit phenology transects used in this thesis were designed prior to any knowledge of the diet of the baboons, with the trees later being identified to produce fruits found in baboon diet being used to calculate fruit availability indices. Therefore future studies will benefit from the inclusion of monthly fruit phenologies being conducted on at least ten individuals of each species of woody plants (Tutin et al. 1991; Head et al. 2011), the fruit of which has now been identified as being important in the diet of baboons (Table 6.3; Chapter 6). This would provide a more accurate reflection of the fruiting phenologies of important baboon foods at Issa and provide a more appropriate basis from which to estimate fruit availability.

Determinants of movement

There is a wide literature base demonstrating that ranging behaviour and patterns of space use in primates are a function of a wide array of social and ecological factors (Harvey & Clutton-Brock 1981). In chapter 4, I built upon a model originally developed by Dunbar (1992) that considers what influences the day path length (DPL) in baboons at a continental scale. An updated version of this model does reasonably well in predicting the DPL in baboons at Issa. This model found that the factors important in determining DPLs included plant productivity index (PPI), group size, anthropogenic influence, and primate species richness. I found these factors are interdependent and mostly revolve around satisfying the dietary requirements of the relevant baboon troops. For example; plant productivity relates to primary production and consequently food production (Houerou 1984); group size denotes the dietary demands of the group (Chapman & Chapman 2000); anthropogenic influence relates to easily accessible, high quality human foods (Hoffman & O'Riain 2012); and primate richness as a probable measure of habitat quality not detected by plant productivity i.e. altitude, latitude

(Cowlishaw & Dunbar 2000). The movement of baboon troops across their range, is therefore largely driven by the drive to search their environment for sufficient foods (i.e. foraging) (Altmann 1974). Therefore, the availability and distribution of these foods, and the ecological and climatic factors which affect these, are of critical importance when understanding the ranging behaviour of any particular baboon troop or population (Dunbar 1992; Hill & Dunbar 2002).

At this local scale, using baboons at Issa, I find the day-to-day ranging behaviour to be dependent not just on the availability of important foods, but also temperature (Chapter 4), habitat type (Chapter 5) and sleep site locations (Chapter 5). As already discussed, fruit is an important component of the diet in many baboon populations, including that of baboons at Issa (Chapter 3). During periods of scarcity, baboons range further in search of higher quality food items to sate nutritional demands (Altmann 1974; Wahungu 2001). Baboons at Issa, however, did not seem to fit this trend, since variation in their DPLs was not predicted by the availability of fruit in the environment (Chapter 4). This could be a reflection of the relatively consistent abundance of fruit throughout the study period (Figure 2.7; Chapter 2). However, as it could also be due to the coarse nature of DPL analysis and potentially the small sample size, I also tested the effect of fruit availability on the movement characteristics of the baboons (e.g. speed and turning angle) during these day paths. In doing this, I increased the resolution of the data and sample size. Unfortunately, my finer resolution analysis also revealed a similar lack of correlation between FAI and movement characteristics.

Evidence for primates using the environment in a goal-directed way according to the learned locations of particular resources is becoming more prevalent in the literature (Noser & Byrne 2007; Pochron 2001; Janson 1998). The result of such goal-directed movement is a more linear foraging route between resources, which in keeping with optimal foraging theory (Schoener 1971), facilitates the more efficient movement between patches. This strategy is particularly effective in the case of fruiting patches, for which the purposeful encounter could be an important adaptation in optimising nutritional intake (Pochron 2001). It was consequently surprising that Issa baboons did not demonstrate more direct travel movements when fruit availability increased. Therefore, in order to test if the movement of the baboons was at all influenced by fluctuations in fruit availability, I proceeded to explore whether fruit availability predicted the time spent moving. I reasoned that the time spent moving should decrease with the proportion of high energy fruits consumed (Noser & Byrne 2007), which would result in decreased moving time compared to other budget variables (Lehmann et al. 2008). Although a simple approach, I was able to determine fruit availability to be important in altering the time spent moving (Clutton-Brock & Harvey 1977b; Isbell 1983). Therefore, whilst no obvious relationship was detected between fruit availability and the movement characteristics, movement to some extent was dictated by the availability of fruit in the environment (REF). I would suggest then that it is worth building on this study and improving upon the methodology outlined in Chapter 4, to better test whether Issa baboons move in a goal directed way according to the learned locations of fruit patches. This could be done via the collection of behavioural data simultaneously with location fixtures in order to accurately isolate the inter-patch movement segments of the day path and test for differences in movement characteristics (Noser & Byrne 2007; Pochron 2001).

In accordance with optimal foraging theory, animals are adapted to take the most direct routes between resources (Schoener 1971). The ability of animals to do this often relies on planning their foraging behaviour in order to move in a goal-directed manner, which may ultimately have played a key role in their cognitive evolution. However, empirical evidence for this contention is lacking with many examples appearing to contradict this contention by demonstrating dramatic deviation from least-distance routes (e.g. green turtles, *Chelonia mydas*, Hays 2002). Ostensibly, the ability to plan foraging journeys should be selected for in animals that live in large home ranges within seasonally variable habitats where food sources are scarce and stationary (Milton 1988). Accordingly, there is a growing body of evidence that suggests primates in the wild are capable of spatial representation with increased route linearity over large spatial scales being reported for a number of primate species (Sigg & Stolba 1981; Garber 1989; Janson 1998; Pochron 2001; Noser & Byrne 2007). Therefore, through enhanced habituation of Issa baboons it would be possible to use *Papio cynocephalus* at Issa as an additional model to test this theory.

Temperature also appeared to act as a constraint upon the ranging behaviour of baboons at Issa (Chapter 4), with the troops travelling significantly slower and over shorter distances on warmer days (Tables 4.5, 4.4; Chapter 4). The primate brain, as with all vertebrate brains is extremely sensitive to even slight temperature fluctuations, thus the need for them to maintain a constant internal temperature is essential (Precht & Brück 1973). Baboons, especially, are known to lack common mechanisms of cooling the brain (Brain & Mitchell 1999; Mitchell et al. 1987). High temperatures are, therefore, of great relevance to the thermoregulation of baboons. The Issa valley is situated at low latitude and consequently maintains a high ambient temperature (Figure 2.4; Chapter 2). As such, high radiant heat poses a challenge to the thermoregulation of baboons at Issa. To avoid overheating, it is likely then that baboons at Issa are forced to rest (Korstjens et al. 2010) and consequently reduce the distance and overall speed during the day. The constraint of thermoregulation has been reported to be an important ecological factor in primates. Numerous studies find primates to adjust their activity according to their thermoregulatory needs, with temperature being a negative function of activity in hot environments (Stoltz & Saayman 1970; Hill 2006; Bernstein 1976; Bernstein 1975; Bernstein 1972; Stelzner 1988) and a positive function of activity in cold environments (Baoping et al. 2009). Moreover, in baboons in particular, temperature has been shown to significantly predict differences in the behavioural ecology across populations of baboons (Dunbar 1992; Hill et al. 2000; Hill & Dunbar 2002). But, adapting activity according to thermal stress is perhaps not an option available to all baboon populations, especially those inhabiting marginal and hot environments such as deserts (e.g. Cowlishaw 1997b). In these more marginal habitats, the demands of foraging can often out-weigh the costs of thermal loading and result in a reduced thermoregulatory response (Hill 2006). Therefore, provided the time budget of the baboons is not constrained by foraging demands, the thermal environment is likely to be an important ecological constraint in baboon populations.

The environment at Issa is comprised of several habitat types (Table 2.2, Figure 2.6 B; Chapter 2), the use of which, by the baboons, was not proportional to their availability. Instead, I found habitat-type to influence the ranging behaviour and patterns of space-use in the Issa baboons (Chapter 5). Habitat selectivity is not uncommon in baboons and can largely be explained by the variation in the availability and distribution of foods between them (Altmann & Altmann 1970; Post 1978; Barton et al. 1992). For example, baboons at Issa demonstrate stark avoidance of the wet grassland habitat, which likely contains little food due to the homogenous, low-density vegetation. In contradiction to this, baboons also demonstrate an avoidance of the forest habitat at Issa, which boasts fruit availability throughout the study year (though fluctuates seasonally) (see Chapter 5 and Figure 2.7). It can be argued that the avoidance of forest is a result of *Papio sp.* being an open-country primate (Altmann 1974). However, the preferential use of forest habitats has been observed in other populations elsewhere across their range (e.g. Nagel, 1973; Kunz & Linsenmair, 2008; Bentley-Condit, 2009) suggesting the avoidance of forest is not typical for the genus. Therefore, I must assume that habitat selectivity is occurring for reasons other than food availability at Issa. Two of the most probable factors in this case are (1) niche separation from other primate species (Schoener 1974), and (2) the reduction of predation risk (Cowlishaw 1997b).

The Issa environment is inhabited by seven primate species, three of which were qualitatively known to utilise the forest habitat extensively. These include *Pan troglodtyes* (Hernandez-Aguilar 2006), *Cercopithecus ascanius* (Tapper et al. 2014) and *Procolobus tephrosceles* (*Observation only*). In Chapter 6, I confirm this by showing that relative to the proportional availability of habitats, *P. troglodytes* significantly over-used the forest habitat and underused the woodland habitat. Moreover, *C. ascanius* demonstrated a pattern of habitat-use very similar, if not more pronounced, to *P. troglodytes* (see Appendix 4). Due to the observed overlap in the fruit species consumed by *P. troglodytes* and *P. cynocephalus*, it is possible that the observed habitat segregation is a mode of niche separation that reduces competition and facilitates coexistence (Schreier et al. 2009) (Chapter 6). This will be discussed in further detail later.

In the case of reducing predation risk, baboons are at risk from a number of predators, particularly the leopard (*Panthera pardus*) (Altmann 1974). As an ambush predator (Bertram 1982; Bothma & Riche 1986), leopards rely on dense vegetation to conceal their approach to within a critical striking distance. At Issa, the leopard is the most abundant of the baboons potential predators (Stewart & Pruetz 2013), with sightings, scat and vocalisations being relatively frequent during the study period. It would, therefore, reduce the risk of predation if troops at Issa were to avoid habitats with low visibility and consequently higher perceived risk, like the forest, and adhere to habitats with high visibility and therefore lower perceived risk, like rocky outcrops (Berger 1991; Willems & Hill 2009). Habitats like these rocky outcrops provide multiple escape routes and higher visibility, enhancing predator detection and consequently form refuges for baboons, the presence of which are known to influence patterns of habitat use (Cowlishaw 1997b). It seems likely then that the over-use of rocky outcrops by baboons at Issa is a function of predator avoidance (Chapter 5). However, tall trees also provide refuge for baboons from terrestrial predators (Saayman 1971; Stelzner & Strier 1981) and leopards (Bailey 1993), which in the forest at Issa – there is an abundance. Therefore, whilst perceived predation risk does well in explaining the over-use of rocky outcrop habitats, it does less well for explaining the avoidance of the forest.

Whilst baboons are at risk from predation during daily activities, they are most at risk from nocturnal predation (Rasmussen 1979). Baboons minimise this risk by utilising very specific sleeping sites, which offer valuable protection (Kummer 1968; Altmann & Altmann 1970). As a result, the baboons are constrained by the need to depart from and return to a sleeping site every day, which inevitably influences their ranging patterns and habitat-use (Barton et al. 1992). In Chapter 5, I show baboons at Issa are consistent in this by exhibiting ranging behaviour that was influenced by the location of sleeping sites.

Coexistence in sympatric primates

In Chapter 6, I looked at how *P. troglodytes* and *P. cynocephalus* at Issa overlap in their diet and habitat-use in order to determine the potential for inter-specific competition. Issa is one of the driest, most marginal habitats in which the endangered *P. troglodytes* (IUCN 2014) is found (Kano 1972; Ogawa et al. 2007; Moore 1994), and consequently may be more susceptible to any additional pressure from inter-specific competition that exacerbate these already marginal conditions. My results indicated the overlap in the fruits consumed between primates was periodically high, but that diets diverged during periods of low fruit availability. Similarly, both species overlapped in space (see Figure 6.4; Chapter 6) but habitat-use differed significantly between them (see Figure 6.5 and Table 6.4; Chapter 6).

In terms of what species were eating, I found that both primates were frugivorous and overlapped to a reasonable degree in the consumption of fruiting species. The degree of frugivory in the chimpanzees was, however, overall higher than that observed in the diet of the baboons. Chimpanzees are classed as fruit specialists (McGrew et al. 1988;

Wrangham 1977; Wrangham et al. 1998) and are more reliant on fruits compared to baboons, which exhibit the ability to consume a broader variety of foods (Norton, R. Rhine, et al. 1987). Consistent with this, baboons at Issa were shown to diverge in their diet compared to the chimpanzees, by increasing foliage consumption during the low fruit availability at Issa (Chapters 3 and 6). Chimpanzees on the other hand, maintained a comparable state of frugivory and folivory throughout the study period (Chapter 6). The outcome of these dietary differences, likely contributed to absence of a relationship between fruit availability and overlap of fruits each species consumed, and thus facilitated their coexistence (Schoener 1974).

In addition to dietary dissimilarities, both baboons and chimpanzees at Issa exhibit patterns of habitat-utilisation that differ from one-another. Patterns of habitat utilisation in primates is normally dictated by resource availability and distribution (Milton & May 1976; Clutton-Brock & Harvey 1977b), but other factors including predation risk (Willems & Hill 2009) and inter- and intra-specific competition are also important (Schreier et al. 2009). As described already, in baboons, a primary underlying determinant of habitat-use is the distribution and availability of food (Altmann 1974; Harding 1976; Barton 1992; Pebsworth, MacIntosh, et al. 2012), and the mitigation of predation risk (Cowlishaw 1997b). At Issa, I show that fruit is available in the forest habitat (Figure 2.7; Chapter 2), but that baboons are substantially underusing it compared to its availability. As discussed above, this is a potential result of higher perceived risk in the forest due to lower visibility, but due to the high density of tall trees which provide refuges (Saayman 1971; Stelzner & Strier 1981), it seems likely there remains an additional factor influencing the decision of baboons to avoid the forest. In Chapter 5 I hypothesise this could be a component of niche separation with other primates at Issa and in Chapter 6, I support this by showing that in stark contrast to the baboons, chimpanzees and red tail monkeys (see Appendix 4) both substantially over-use the forest habitat in proportion to its availability. In agreement with theories of resource partitioning (Schoener 1974), sympatric primate species often reduce inter-specific competition by demonstrating differential utilisation of habitats (Stevenson et al. 2000; Rodman 1973; Terborgh 1984; Ganzhorn 1989). I therefore find it possible, that the differential patterns of habitat-use observed between chimpanzees and baboons at Issa are a mode of niche separation between the species to facilitate their coexistence (Schreier et al. 2009).

Conclusions and Future Work

This thesis provides the first description of the dietary ecology and ranging behaviour of a population of woodland baboons in the Issa valley of western Tanzania. Almost all work to date exploring these topics in baboons have been limited to savannah dominated environments. Consequently, woodland/forest populations like those at Issa are underrepresented. This thesis has provided much important information to begin to address this. I have shown that despite the ecology and environment at Issa being very different (compared to other baboon sites) in many respects, Issa baboons are comparable to other populations. Their DPLs are dictated by similar variables (Chapter 4), and like conspecifics elsewhere, their ranging behaviour is constrained temperature (Chapter 4), sleep site availability (Chapter 5), and habitat type, which I interpret to result from perceived predation risk (Chapter 5) and niche separation with sympatric primate species (Chapter 6). Moreover, my results suggest their diet, like baboons elsewhere, is consistent with that of a generalist, but that also but that also selectively exploits their environment according to the availability of preferred foods (Chapter 3). These data then allowed subsequent comparison with sympatric chimpanzees, which showed coexistence between them is facilitated by differential utilisation of niche components (Chapter 6). However, as highlighted in the preceding discussion, there are still a number of areas where future work at Issa might best be directed in order to better answer some of the questions that have arisen in the thesis.

Most notably, now that preliminary descriptions of the diet of baboons at Issa have been provided (Chapter 3), the phenology of fruiting trees known to be important to baboons can be better monitored. This will in turn allow fruit availability indices to be calculated that include all fruits important to the baboons (see Table 6.3; Chapter 6) and consequently to better test the influence of this on the ranging and dietary behaviour of the baboons. This would allow us to answer the question of how baboons in a woodland environment respond to periods of low food availability and what behavioural adaptations they initiate to cope. Similarly, the application of remotely sensed data at Issa could assist in better parameterising plant productivity at Issa (Kerr & Ostrovsky 2003; Turner et al. 2003). The rise of use of more available remotely sensed data in animal ecology has led to great strides being made in identifying causal relationships between environmental conditions and animal characteristics including migration patterns (Boone et al. 2006; Ruegg et al. 2006), and species distributions (Osborne et al. 2001; Mueller et al. 2008). In particular, information on plant productivity and phenology is of great value to terrestrial ecologists. The Normalised Difference Vegetation Index (NDVI) is a well-established measure of photosynthetic activity and vegetation structure (Myneni et al. 1995). As a result, it has been successfully employed in identifying relationships between animal characteristics and vegetation properties (Pettorelli et al. 2005), especially over broad scales. However, more recently Willems et al. (2009) demonstrated NDVI can also be used successfully at small scales to account for the distribution and space-use of *Cercopithecus aethiops*. Monthly NDVI could, therefore, be employed at Issa to provide a comprehensive measure habitat productivity (and therefore food availability: Willems et al. 2009), which might better refine our understanding of Issa baboon space-use. Moreover, NDVI values could elucidate other key characteristics of the ecological environment within the home ranges of baboons at Issa, which could prove important such as leaf cover, which in turn can be an effective proxy for visibility and therefore guild-specific predation risk (Willems et al. 2009).

Also important, is that although diet was recorded over an entire annual cycle (Chapter 3), ranging data was only collected for seven months between January – July (see Chapter 2, page 32), meaning that no ranging data exists for the driest part of the year (August-October). During this dry period, surface water at Issa becomes increasingly confined to water holes (Hernandez-Aguilar 2006). Consequently, I was not able to test the influence of surface water availability on the ranging patterns of the baboons, which as obligate drinkers (Altmann 1974), can be an important determinant of ranging patterns (Sigg & Stolba 1981). A longer study period, which encompasses the driest part of the year at Issa might, therefore, elucidate whether the availability of surface water becomes an ecological constraint for baboons at Issa. If so, then this could be an important factor in defining their ranging behaviour (Altmann & Altmann 1970; Chapman 1988).

As described in the above text, habitat preferences of Issa baboons do not necessarily agree with food availability. Instead, I infer from the data that patterns of habitat use are at least partly explained as a behavioural response to predation risk (Chapter 5). Predation risk is defined as "an animal's own perception of the likelihood of that it will be subject to an attack by a predator" (Hill & Weingrill 2007, p. 340). Accordingly, baboons are observed to modify their behaviour according to which habitat they are in. Habitats with high perceived risk are used exclusively for feeding, whereas behaviours with no specific habitat requirements, such as grooming, resting and moving, are confined to habitats with low perceived risk (Cowlishaw 1997b; Stacey 1986). Characteristics that have been observed to be instrumental in defining perceived risk in baboons, between habitats, include visibility and refuge availability (Cowlishaw 1997b; Hill & Weingrill 2007). Baboons at Issa appear to support these generalised perceptions of risk by overusing habitats with high refuge availability, and underusing those habitats with a high perceived risk (Chapter 5). However, in order to properly ascertain the importance of predation risk in determining habitat use at Issa, locational data would benefit from frequent, associated behavioural scans through the full habituation of troops. This would allow us to better see how the baboons were using each habitat and consequently provide a coarse map of their perceptions of predation risk across habitat types at Issa (Willems & Hill 2009).

Ultimately a map of risk perception could be compared to actual predator occurrence at Issa. Perceived risk by the baboons will be influenced in part by their encounter rate with predators (Hill & Weingrill 2007). However encounter rate is difficult to measure between predators and prey, especially with the presence of an observer (Isbell et al. 1991). Instead predator habitat preferences can be used as a proxy for encounter rates. For baboons, the leopard is the primary predator (Cowlishaw 1994), and leopards are known to prefer dense vegetation and avoidance of more open habitats (Bailey 1993). Whilst I can, therefore, infer that baboons are underusing the forest habitat at Issa because this is comprised of comparatively dense vegetation, and is thus a preferred habitat of leopards, I cannot be certain. Additionally, further convolution arises when considering forest habitats are characterised by a high density of tall trees, which serve as refuges from predators. However, having a refuge nearby is only useful if the predator is seen and can be reacted to in time to utilise it. It could be the case that visibility within the forest is insufficient to permit this. Consequently, it would be useful to map the actual density of leopards at Issa to determine a working estimate of the frequency of interactions (Abrams 1994; van Schaik & Hörstermann 1994). This could be done using camera traps that have been in place at the study site since 2010, which are distributed throughout both the woodland and forest habitats. Observations of leopards from these could be used to confirm the preference of the forest habitat by leopards at Issa, which would lend itself to the underuse of the forest by the baboons being a result of higher perceived risk.

The occasional scarceness of data presented in this thesis is an inevitable outcome of the partially habituated nature of the study subjects. Irrespective of this though, this thesis provides the first look at baboons at Issa, and hopefully provides a foundation on which to build a more complete understanding of their ecology. In conclusion, I hope this thesis goes some way in contributing to the collective understanding of baboon ecology by reducing the paucity of ecological contexts from which our current understanding, of baboon ecology, is based.

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Appendix

Appendix 1

Table 1. All mammals >0.5 kg observed in Ugalla since 2005 (Hernandez-Aguilar 2006; Stewart 2011) .

	Scientific name	Common name
Artiodactyla		
	Alcelaphus lichtensteini	Lichtenstein hartebeest
	Philantomba monticola	Blue duiker
	Damaliscus lunatus topi	Topi
	Hippotragus equinus	Roan antelope
	Hippotragus niger	Sable antelope
	Kobus ellipsiprymnus	Common waterbuck
	Kobrus ellipsiprymnus	Defassa waterbuck
	Oreotragus oreotragus	Klipspringer
	Ourebia ourebi	Oribi
	Phacochoerus africanus	Warthog
	Potamochoerus porcus	Bushpig
	Redunca redunca	Bohor reedbuck
	Madoqua kirki	Kirk's dikdik
	Sylvicapra grimmia	Common bush duiker
	Syncerus caffer	African buffalo
	Taurotragus oryx	Eland
	Tragelaphus scriptus	Bushbuck
Carnivora		
	Aonyx capensis	African clawless otter
	Bdeogale crassicauda	Bushy-tailed mongoose
	Canis mesomeles	Black-backed jackal
	Civettictis civetta	African civet
	Crocuta crocuta	Spotted hyena
	Felis serval	Serval
	Felis sylvestris	African wild cat
	Genetta tigrina	Large spotted genet
	Genetta genetta	Common genet
	Helogale parvula	Dwarf mongoose
	Herpestes ichneumon	Lesser mongoose
	Herpestes naso	Long-snouted mongoose
	Herpestes sanguinea	Slender mongoose
	Lycaon pictus	East African wild dog
	Mellivoria capensis	East African honey badger
	Panthera leo	Lion
	Panthera pardus	Leopard
	Viverridae sp.	Mongoose

Appendix 1 continued

	Scientific name	Common name
Hyracoidea		
	Heterohyrax brucei	Bush hyrax
	Dendrohyrax arboreus	Tree hyrax
	Heterohyrax brucei	Yellow spotted rock hyrax
	Dendrohyrax validus	Rock hyrax
Lagomorpha		
	Lepus capensis	Cape hare
Perissodactyla		
	Eqqus burchelli	Zebra
Pholidota		
	Manis temminckii	Ground pangolin
Primates		
	Chlorocebus pygerythrus	Vervet monkey
	Cercopithecus ascanius	Red-tail monkey
	Cercopithecus mitis	Blue monkey
	Galago senegalensis	Senegal galago
	Otolemur crassicaudatus	Greater galago
	Pan troglodytes schweinfurthii	Chimpanzee
	Papio cynocephalus	Yellow baboon
	Papio anubis	Olive baboon
	Procolobus tephrosceles	Red colobus
Rodentia		
	Hystrix africae-australis	Porcupine
Tubulidentata		
	Orycteropus afer	Ant-bear/Aardvark

Appendix 2

Table 2: Fruit species consumed by Issa baboons (CT & MT) from August 2011 – July 2012. There were an additional 28 unique seeds found in the faecals but which were not identified or known locally.

Local name	Family	Genus/species
Matunguru	Zingiberaceae	*Afromomum mala*
Mswindi	Anisophylleaceae	*Anisophyllea boehmii*
Mtopetope poli	Annonaceae	*Annona senegalensis*
Mnyenye	Fabaceae	*Brachystegia longifolia*
Miombo	Fabaceae	*Brachystegia spiciformis*
Kampandampanda	Rubiaceae	*Canthium burtii*
NA	Sapotaceae	*Chrysophylum banguelensis*
NA	Rubiaceae	*Fadogia triphyalla*
Mlumba	Moreaceae	*Ficus variifolia*
Mbukuswa	Flacourtiaceae	*Flacourtia indica*
Myeye	Clusiaceae	*Garcinia huillensis*
Kankula masigo	Tiliaceae	*Grewia rugosifolia*
Kabamba	Fabaceae	*Julbernadia unijugata*
Keetia gueinzii	Rubiaceae	*Keetia gueinzii*
NA	Anacardiaceae	*Lannea schweinfurthii/schimperi*
Nyanya poli	Rubiaceae	*Leptactina banguelensis*
NA	Annonaceae	*Monanthotaxis poggei*
Ibungu	Apocynaceae	*Saba comorensis*
Lihuagu	Loganiaceae	*strychnos panganiensis*
NA	Rubiaceae	*Trycalysia ruandensis*
Makusu F	Euphorbiaceae	*Uapaca kirkiana*
NA	Annonaceae	*Uvaria angolensis*
Mfulu	Verbenaceae	*Vitex doniana/mobassae*
Msantu	Olacaceae	*Ximenia caffra*
Gugunwa	Unknown	*Unknown*
Missile	Unknown	*Unknown*
Matango Poli	Unknown	Unknown

Appendix 3

To test what factors predicted activity in baboons (i.e. not moving, or moving) we fitted a GAM with a binomial error structure (mgcv package, R: (R Development Core Team 2010)). Our response was defined by speed with <1m/min defined as not moving, and moving defined as >1m/min. Since we observed temporal auto-correlation in our data, we randomly sub-sampled n=30 data points from each observation day to remove this effect. We then fitted FAI, season (wet, dry), rainfall and maximum temperature as fixed effects, whilst controlling for any effect of day (of study period). We then selected the best model according to the lowest AIC value (Akaike 1998), but models within two AIC points were considered to be plausible alternatives and the model that was the most parsimonious (i.e. the model with the fewest fixed effects) was selected preferentially (Burnham & Anderson 2002). The results of our analyses are provided in Table below.

Estimates, standard error, test statistics and P-value for predictors of activity (not moving, or moving; <1m/min versus >1 m/min) in the selected General Additive Model at a local scale. The best fitting model included those terms shown in bold text. Effect of smoothing factor is also shown with estimated degrees of freedom (edf), reference df, chi squared value (Chi.sq) and *p* value.

Model term	**Estimate**	**Standard error**	***z*-value**	***df***	***p***
Fruit Abundance Index	-0.51	0.13	-3.85	1	<0.001
Max. temperature	-0.008	0.02	-0.31	1	0.76
Season (dry, wet)[1]	0.45	0.42	1.11	1	0.29
Rainfall	0.0004	0.007	0.05	1	0.05
Smoothing factor	**edf**	**Ref.df**	**Chi.sq**		***p***
Day	7.69	8.58	56.53		<0.0001

[1] Reference category was wet season.

Appendix 4

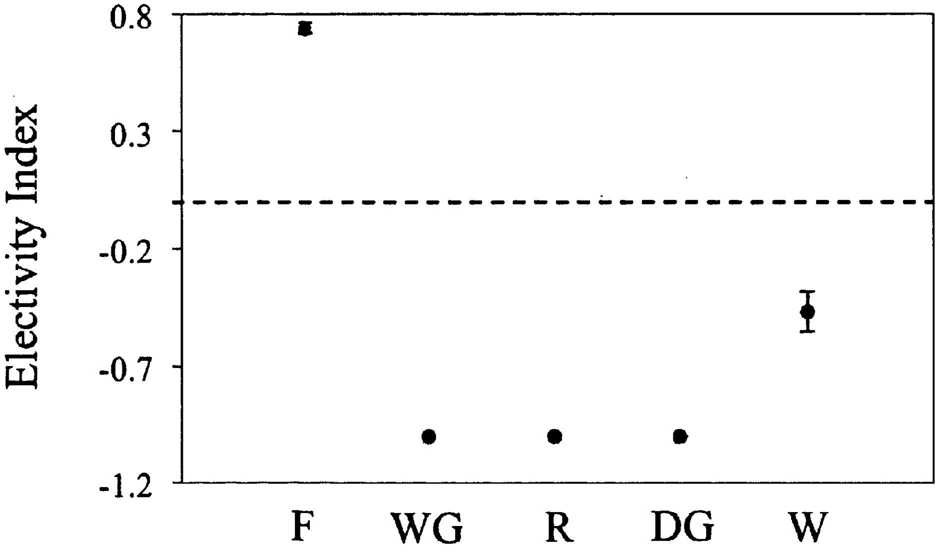

Figure 2. Average monthly Kreb's habitat Electivity Index (*EI*) for redtail monkeys (*Cercopithecus ascanius*) at Issa, illustrating baboon habitat preferences (**W**: woodland, **F**: Forest, **DG**: Grassland, **R**: Rocky Outcrops, **WG**: Wet Grassland) during the study period for **A**: Both troops separately and **B**: Both troops combined.

Appendix 5

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MOVEMENT ECOLOGY

RESEARCH **Open Access**

The ecological determinants of baboon troop movements at local and continental scales

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Abstract

Background: How an animal moves through its environment directly impacts its survival, reproduction, and thus biological fitness. A basic measure describing how an individual (or group) travels through its environment is Day Path Length (DPL), i.e., the distance travelled in a 24-hour period. Here, we investigate the ecological determinants of baboon (*Papio* spp.) troop DPL and movements at local and continental scales.

Results: At the continental scale we explore the ecological determinants of annual mean DPL for 47 baboon troops across 23 different populations, updating a classic study by Dunbar (Behav Ecol Sociobiol 31: 35-49, 1992). We find that variation in baboon DPLs is predicted by ecological dissimilarity across the genus range. Troops that experience higher average monthly rainfall and anthropogenic influences have significantly shorter DPL, whilst troops that live in areas with higher average annual temperatures have significantly longer DPL. We then explore DPLs and movement characteristics (the speed and distribution of turning angles) for yellow baboons (*Papio cynocephalus*) at a local scale, in the Issa Valley of western Tanzania. We show that our continental-scale model is a good predictor of DPL in Issa baboons, and that troops move significantly slower, and over shorter distances, on warmer days. We do not find any effect of season or the abundance of fruit resources on the movement characteristics or DPL of Issa baboons, but find that baboons moved less during periods of high fruit availability.

Conclusion: Overall, this study emphasises the ability of baboons to adapt their ranging behaviour to a range of ecological conditions and highlights how investigations of movement patterns at different spatial scales can provide a more thorough understanding of the ecological determinants of movement.

Keywords: Day path length, Baboon, *Papio cynocephalus*, Season, Space-use, Ranging, Modelling, Speed, Turning angle, Human-modified habitat, Movement characteristics, Comparative analysis

Background

A simple, but revealing measure of an animal's space use is the distance it moves within a 24-hour period. This distance is described as the Day Path Length (DPL). The simple parameters required to quantify DPL make it easily transferable and applicable to terrestrial and/or arboreal animals [1,2], thus affording comparative investigations of DPL across species. For example, DPLs provide the basis of analyses of mammalian day range [3], and some of the most comprehensive studies of what determines how far animals travel have been undertaken on primates [4]. Like most mammals, primate ranging behaviours are primarily influenced by the distribution and abundance of essential resources [4-6], specifically food [7], but a suite of other factors are also important.

In general, primates tend towards an energy maximising strategy [8] whereby, in response to low food availability, they increase their DPLs in search of higher quality food items [9-13]. Since plant biomass and net plant productivity can be reliably inferred from rainfall data [14,15], especially in seasonal habitats [16], rainfall can be used as an indirect measure of food resources and predicts primate DPLs [7,17]. Similarly, recent studies have demonstrated that remotely sensed data, particularly the normalized difference vegetation index (NDVI), provides an adequate measure of photosynthetic activity and, therefore, vegetation structure [18], which can hence be used to further understand primate movement ecology [19]. Increasing primate group sizes also results in longer DPLs [20] since

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larger groups experience greater intragroup feeding competition [21] and exhaust food patches quicker, forcing more frequent travel between patches [21-23]. Note, however, that primates with a more leaf-based and herbaceous diet lessens the effect of group-size on DPLs because the spatial-temporal distribution of leaves is more homogenous (e.g. *Brachyteles arachnoides hypoxanthus*, [24]; *Colobus badius tephrosceles*, [5]; *Gorilla* spp., [25,26]).

Baboons (*Papio* spp.) range throughout sub-Saharan Africa, across a multitude of habitat types making them the most widespread African primate genus [27] and perhaps coincidentally, are one of the best studied primates, particularly with respect to DPL. Numerous studies have shown that baboon DPLs respond to extrinsic changes in biotic and abiotic factors, attributed to the highly seasonal environments in which they live [9-13], and also to intrinsic social factors [11,28]. Accordingly, baboon troop DPLs across their range can be reliably predicted by group size and rainfall, as shown by a classic study by Dunbar in 1992 [29].

Since Dunbar's original study [29] there have been further studies of the climatic determinants of foraging and ranging behaviour in baboons (e.g. [30-32]), and new data on baboon DPL and ecology now exist. We therefore revisit the question of what determines baboon troop DPLs at a continental scale with the addition of 29 data points (DPLs) taken from recent literature, whilst considering additional ecological variables. We adopt a mixed modelling/model selection approach instead of the stepwise linear regression approach used originally [29], and also consider the potential impact of anthropogenic influence, primate species number, and NDVI. We consider anthropogenic influence because where baboons rely on predictable and high-quality food sources (e.g. crops or food/waste) that occur in human modified habitats (e.g. [20-22]), DPLs are found to be reduced and not predicted well by models that include rainfall and group size as predictors [33]. We consider primate species number on the basis that a high number of primate species may result in increased levels of inter-specific competition, which is known to drive longer DPLs, especially in frugivorous primates (e.g. [20,21,30,34]). Additionally, as a more recent technological development, not available to Dunbar in his 1992 study, we also consider NDVI data as it provides a good proxy for photosynthetic activity and vegetation structure for study sites [19,35].

Our understanding of the ecological determinants of baboon day path lengths at a finer (local) scale comes primarily from arid savannah habitats [9,36-40], even when considering more recent studies on the topic [13,22,33,41-46]. To provide a fuller analysis of the ecological determinants of movement at a local scale, and to complement our continental scale analyse (see above), we investigated the daily movements of two troops of yellow baboons, *Papio cynocephalus*, inhabiting the primate-rich, seasonal, and predominantly woodland habitat of the Issa Valley in Ugalla, western Tanzania. This represents the first study of baboons in this region. We begin by exploring how well our inter-population model predicts DPLs for the Issa baboons, and then go on to consider what local ecological factors predict variation in DPLs and movement characteristics.

Variation in food resources are predicted to have a large effect on baboon space use. The proportion of fruit-based versus leaf-based forage in the diet, in particular, can have a large effect upon day ranges, with DPL increasing with the quantity of fruit in the diet [4]. Since fruit tends to grow ephemerally in small, finite patches, which are distributed heterogeneously, it is quickly exhaustible [23,47] and necessitates longer DPLs. Reliance on high-quality fruit can also drastically alter movement characteristics to maximise efficiency [21] and primates foraging on fruit show faster [48], straighter, and more goal-directed movement characteristics [49-51]. In contrast, leaf-based and herbaceous foods have a more homogeneous distribution in space and time [26] affording shorter DPLs and slower, more tortuous movement [52,53]. Regardless of food type, food abundance is dependent upon local, temporal variation in climate [16,54], and when food is scarce, individuals typically increase their DPLs in search of these food items (e.g. *Papio hamadryas*, [43]; *Papio anubis*, [12]; *Eulemur rubriventer* and *Eulemur fulvus rufus*, [55]; *Gorilla gorilla*, [56]; *Rhinopithecus* sp., [57]; *Colobus satanas*, [58]; *Cercocebus galeritus*, [59]). We therefore expected the baboons at Issa to demonstrate slower, less direct travel, and an increased DPL in times of reduced fruit availability [9-13].

Other climatic variables can also directly influence primate, and specifically baboon, ranging behaviour. If temperatures are too low, or too high, for example, primates reduce time spent travelling in order to conserve energy (e.g. *Rhinopithecus bieti*, [60]; *Papio ursinus*, [61]). Thus, ambient temperature can be an important climatic constraint on primate ranging behaviour, and we therefore tested the prediction that the baboons DPLs will be constrained by maximum daily temperatures in the warm Tanzanian climate, resulting in slower movement [32] and reduced DPL [61]. Finally, given that Issa's baboons experience distinct wet and dry seasons, we also tested for any effect of season that might have additional and independent effects upon DPLs and movement characteristics because, for example, the availability of water sources change [9].

Methods

Continental scale

Data collection

For our continental scale analysis we used data provided in Dunbar's (1992) study [29] and updated this with DPLs of 29 more recent studies from the literature (see Additional file 1). If data were available for more than one group at a study site, we use each troop's DPL, and we collected information on the rate at which troop locations were taken throughout the day, i.e. sampling frequency, and whether annual mean DPL was calculated from >12 months study, <12 months, or if this was unknown, i.e. sample size. This enabled us to test for/control for any potential effect of differences in how annual mean DPL were estimated across studies in our analyses. We also collected information on troop size, anthropogenic influence (whether or not the diet of the troop was supplemented by human derived foods [yes/no]) and the number of primate species occurring at each study site. Nocturnal primates were included in the primate species count so as to account for any indirect competition that may result from their spatial overlap with the baboons. These ecological data for each study site are summarised in Table 1, and troop specific data on group sizes and DPLs are summarised in Additional file 1.

In keeping with previous comparative studies (e.g. [29-32,62]), we investigated the effect of the following climate variables on mean annual DPL: mean annual temperature (Tann), mean annual rainfall (Pann), variation (standard deviation) in monthly temperature (TmoSD), variation (standard deviation) in monthly rainfall (PmoSD), the number of months per year with less than 100 mm of rainfall ($P < 100$), and the primary productivity index (PPI: the number of months in the year where rainfall was more than twice the average annual temperature). PPI is a useful measure of productivity during the growing season in tropical habitats and is therefore a useful index of seasonality

Table 1 Ecological data for the 23 baboon populations used in the DPL continental comparison model

Species & study site	Latitude	Longitude	Altitude	#Study troops	#Primate Spp.	Anthropogenic influence?[1]	References[2]
Papio anubis							
Bole, Ethiopia	9.42	38.00	1700	1	4	No	[80]
Budongo, Uganda	1.93	31.67	700	1	7	No	[113]
Chololo, Kenya	0.40	36.95	1660	1	2	No	[79]
Gashaka Gumti, Nigeria	7.51	11.61	320	2	9	Yes (1/2)	[114]
Gilgil, Kenya	−0.49	36.32	1770	1	1	No	[12]
Ishasha, Uganda	−0.62	29.66	950	1	4	No	[115]
Metahara, Ethiopia	8.91	39.93	950	1	2	No	[116]
Mulu, Ethiopia	9.30	40.83	1275	1	2	No	(Dunbar, *unpublished*)
Papio cynocephalus							
Amboseli, Kenya	−2.64	37.25	1130	6	3	Yes (1/6)	[17,33,117]
Mikumi, Tanzania	−7.09	37.42	550	1	5	No	[77]
Tana, Kenya	−1.93	40.14	30	1	6	No	[118]
Issa, Tanzania*	−5.51	30.56	1600	2	6	No	This study
Papio hamadryas							
Awash, Ethiopia	8.84	40.01	950	5	2	No	[43,45,119]
Erer-Gota, Ethiopia	9.56	41.38	1200	1	1	No	[120]
Papio papio							
Mt. Assirik, Senegal	12.87	−12.80	150	2	6	No	[38]
Papio ursinus							
Blouberg, SA	−23.03	29.06	900	1	3	No	(Noser, *unpublished*)
Cape Point, SA	−34.27	18.43	50	10	1	Yes (7/10)	[13,39,121]
Drakensberg, SA	−29.47	29.26	2250	2	1	No	[41,122]
Honnet, SA	−22.63	30.18	310	2	2	Yes (1/2)	[61]
Mkuzi, SA	−27.60	32.05	125	1	2	No	[42] from [123]
Suikersbosrand, SA	−26.50	28.22	1600	1	2	No	[124]
Tsaobis, Namibia	−22.55	15.73	1000	1	1	No	[44]
DeHoop, SA	−34.43	20.57	10	2	1	No	(Hill, *unpublished*)
Mt. Zebra, SA	−32.20	25.39	1500	1	1	No	[125] from [123]

[1] Indicates whether baboons studied experience anthropogenic influences, and if so, how many troops. [2] Unpublished data are acquired from authors listed.

[62,63]. These climate data were taken from the original studies and/or Dunbar's (1992) study [29]; where this information was not available, we followed the methods provided in Bettridge et al. [31] and used data from the Willmott & Matsuura [64] meteorological database. This database provides a global dataset of annual and monthly temperatures and rainfall in grids of 0.5° latitude by longitude, which are derived from a combination of Legate and Willmott's [65,66] weather station records and the Global Historical Climatology Network (version 2). We calculated average values across all data points in the Willmott & Matsuura dataset that fell within 0.5° latitude and longitude to the relevant site. All temperatures are provided in °C, and rainfall in mm. We also collected remotely sensed information on NDVI, since it is a well-established measure of photosynthetic activity and vegetation structure [18] with proven applications in understanding species' ecology [19,35]. NDVI data was retrieved for an area of 10.25 km^2 for each study site from the Oak Ridge National Laboratory Distributed Active Archive Centre (http://daac.ornl.gov/MODIS/) and a 14-year average for each site was calculated from the available MOD 13Q1 data set (2000–2014). All climate data for each specific baboon study site are summarised in Table 2.

Table 2 Climate and environmental data for 23 baboon study populations

Species & study site	Pann	PmoSD	Tann	TmoSD	PPI	P < 100	NDVI
Papio anubis							
Bole, Ethiopia	1105	85.75	19.50	1.30	8.0	8.0	0.47
Budongo, Uganda	1679	68.18	22.10	0.75	10.0	4.5	0.84
Chololo, Kenya	549	40.31	22.90	1.03	5.0	9.5	0.29
Gashaka Gumti, Nigeria	1800	109.90	26.60	1.00	8.0	5.0	0.38
Gilgil, Kenya	595	20.95	18.10	0.69	5.0	11.0	0.46
Ishasha, Uganda	1292	37.87	22.00	0.93	10.0	6.0	0.68
Metahara, Ethiopia	639	58.99	24.50	1.56	6.0	9.0	0.26
Mulu, Ethiopia	1105	64.00	15.90	1.61	8.0	7.0	0.42
Papio cynocephalus							
Amboseli, Kenya	336	23.44	22.86	1.43	3.0	11.0	0.26
Mikumi, Tanzania	832	63.27	25.21	2.72	6.0	6.0	0.6
Tana, Kenya	803	49.57	28.00	1.12	5.0	9.0	0.72
Issa, Tanzania*	1200	79.69	20.00	0.32	7.0	5.0	0.6
Papio hamadryas							
Awash, Ethiopia	639	49.28	24.62	1.68	6.0	8.8	0.28
Erer-Gota, Ethiopia	665	59.12	24.20	1.61	5.0	9.0	0.32
Papio papio							
Mt. Assirik, Senegal	953.9	97.90	30.50	2.45	5.0	7.7	0.47
Papio ursinus							
Blouberg, SA	343	35.42	20.75	3.67	7.0	12.0	0.50
Cape Point, SA	743	36.86	17.90	3.47	6.9	10.0	0.42
Drakensberg, SA	1197	82.57	14.60	4.18	8.3	6.0	0.45
Honnet, SA	307	45.01	21.33	3.58	3.0	10.3	0.29
Mkuzi, SA	630	37.77	22.40	2.92	6.0	9.8	0.68
Suikersbosrand, SA	700	44.42	15.95	4.50	7.0	9.0	0.56
Tsaobis, Namibia	122	16.45	13.80	2.33	3.0	12.0	0.12
DeHoop, SA	428	9.23	16.50	3.07	7.0	12.0	0.58
Mt. Zebra, SA	343	16.11	15.00	4.57	6.0	12.0	0.32

Pann average annual rainfall, *PmoSD* standard deviation for average monthly rainfall (mm), *Tann* average annual temperature (°C), *TmoSD* standard deviation for average monthly temperature (°C), *PPI* primary productivity index (number of months in the year in which rainfall was twice the average annual temperature), *P < 100* number of months with less than 100 mm rainfall, *NDVI* normalised difference vegetation index retrieved from remote sensing data. *Current study; not included in continental analysis.

Statistical analyses

We fitted annual mean DPL as the response variable in a linear mixed model (LMM) in R (lme4 package [67], R version 3.1.0) to determine which of the aforementioned ecological and climatic variables best explained variation in mean baboon troop DPLs. We fitted 'population' as a random effect to control for the potential non-independence of data from multiple troops within the same population. Co-linearity between all effects was checked using Spearman's rank correlation tests, with a cut-off criterion of $r_s = 0.60$ [68] for including effects in the same model. We then fitted a series of models entering combinations of ecological and climate variables as continuous fixed and/or categorical fixed effects. Additional file 2 provides the top ten candidate models used to predict variation in annual mean DPL at a continental scale. To choose among models, we adopted a minimum adequate model selection procedure that considered all biologically meaningful combinations of the fixed effects described. Candidate models with the lowest Akaike information criterion (AIC) value [69] were consequently selected. Where models had AIC scores within two points of each other, both models were considered to be plausible alternatives and the model that was the most parsimonious (i.e. the model with the fewest fixed effects) was selected preferentially [70]. The significance of individual terms were then calculated from the selected model and terms not included in the selected model were put back into the model to obtain level of non-significance (lmerTest package, R: [71]).

Local scale

Study site

Local scale data was collected in the Issa valley of western Tanzania (05° 23 S 30° 35 E), 81 km East of Lake Tanganyika. The Ugalla region extends over 3352 km^2 and is comprised of steep, broad valleys and flat hilltop plateaus that range in altitude from 900 -1800 m. The habitat of the study area is described as being a diverse mixture of vegetation types including swamp, dry grassland, wooded grassland, woodland, gallery forest, thicket forest, and hill forest [72].

Movement data

Movement data were collected by CJ and field assistants from January to August 2012 in accordance with the regulations of the Tanzanian Wildlife Research Institute. In total 81 days were spent tracking two troops of yellow baboons over the study period. These were Matawi Troop (MT, N = 31 group members) and Camp Troop (CT, N = 22 group members). The baboons were successfully located on 61 of these tracking days. Once found, the troop was followed until they reached a sleeping site, typically around 19:00. Observers would then return the following morning to the same place at 07:00 (before baboons left the sleeping site). This was repeated until they were lost, or a full three days of follows were completed. In total this yielded a total observation time of 546 hrs (CT: 349 hrs, MT: 197 hrs). On all occasions the troops were followed, troop movement was recorded at 5-minute intervals, at a distance of 20-50 m behind the troop, using hand-held Garmin 520Hcx Global Positioning Systems (GPS). These GPS data were used to record the distance troops travelled from sunrise (07:00 ± 15 mins) to sunset (19:00 ± 30 mins).

To calculate DPLs, distances between consecutive GPS points were calculated using the Great-Circle Equation [73]. DPL's were only calculated from full-day follows, or where the baboon locations were unknown for a period of less than 60 minutes representing a mean of 4.8 full day follows per month (CT: 3.1 days per month, MT: 1.7 days per month). Movement characteristics, as described by speed and turning angle distributions can provide information on orientation and searching behaviour [74]. Speed (m/min) and turning angle (θ) were calculated for successive GPS locations using the adehabitatLT package, R [75].

Temperature and season

An Onset H8 Pro series Hobo temperature logger was deployed in woodland plateau vegetation. This device recorded ambient temperature every 30 mins and provided minimum, maximum, and mean temperature readings daily (range: 12.5 – 38.7°C; mean ± Standard Deviation: 20.5°C ± SD 3.8°C: Figure 1). Rainfall was recorded using an Onset HOBO data logging rain gauge RG3-M deployed in the woodland plateau near camp. From January to July 2012, rainfall averaged 111 ± SD 93 mm/month, range: 0–248 mm (Figure 1). There were two distinct seasons at Issa, a rainy season (November-April) and a dry season (May-September), with dry months being defined as having <100 m of rainfall [72].

Food availability

Whilst baboons rely on a variety of food sources [40], fruit comprises a large portion of their diet [12,33,37-40,76-80] and is selected for when available [9]. We therefore utilised a pre-established phenology transect, that intersected the miombo woodland habitat, that was 1.7 km in length and 10 m in width and was fully contained within the home range of CT. Only woody plants known to produce fruits or seed pods that were consumed by the baboons and that were ≥ 2 m in height with a diameter at breast height ≥ 5 cm were monitored. This resulted in a total of 288 shrubs, lianas and trees from 17 species. The transect was walked every month for the duration of the study period, and the presence/absence of fruit or seed pods for each plant was noted [81]. Fruit abundance (we use this as

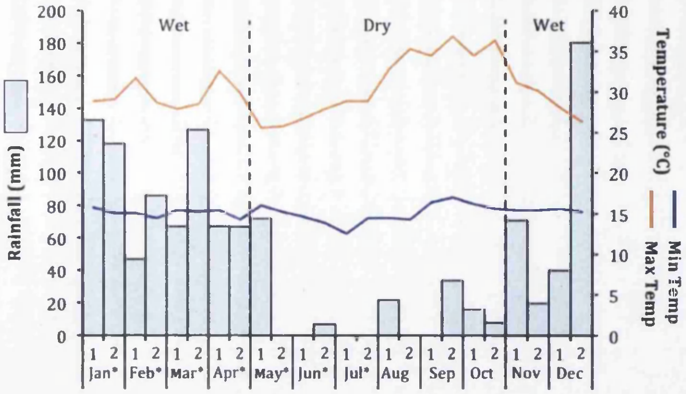

Figure 1 Issa climate. Minimum and maximum average bi-monthly temperatures and rainfall at Issa during 2012. The study period is depicted by months with an *. Months belonging to the dry season are those with <100 mm of rainfall and are highlighted with dashed lines.

a proxy for fruits and seed pods combined) was then estimated with a commonly used measure, the monthly fruit abundance index (FAI_m) [82-85]:

$$FAI_m = \sum_{k=1}^{n} D_k B_k P_{km}$$

where D_k is the density of species k per km^2, B_k is the mean DBH of species k, and P_{km} is the percentage of trees of species k in a fruiting condition in a month m (Figure 2).

Statistical analyses

To test for differences in DPLs of the two Issa troops, a Mann Whitney *U*-test was used. To investigate what factors predicted variation DPL we used a linear model (LM) (lme4 package, R: [67]), with normal error structure. We fitted a series of fixed effects in accordance with our predictions. Our two continuous effects were maximum temperature (°C) and FAI, and we fitted season (wet, dry), and troop ID as categorical effects. We used maximum temperature as a reflection of the hottest part of the day, which is most likely to constrain baboon DPL.

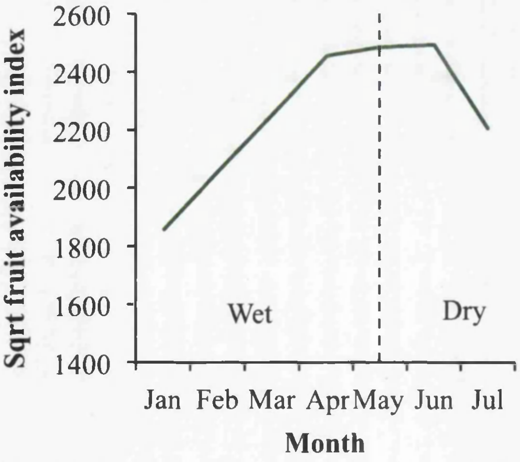

Figure 2 Fruit abundance. Fruit abundance at Issa for duration of study period. The dashed line represents the division between seasons.

To test what factors predicted variation in speed and/or distribution of turning angles we implemented generalised additive models (GAM) (mgcv package, R: [67]). We only analysed speed and turning angle data where baboons were not stationary (i.e. speed > 1 m/min), and randomly sub-sampled n = 10 data points from each observation day to remove any temporal auto-correlation in our data. We then fitted maximum temperature, FAI and season (wet, dry) as fixed effects, whilst controlling for any effect of day (of study period) and troop (CT, MT). We used a GAM here rather than a standard linear model because GAMs are more capable of recognising nonlinear temporal variation [86]. The smoothed effect of time (day of study period) was based on penalized regression splines, to take into consideration the cyclic pattern of patterns of space-use.

For both our LMM (DPL analyses) and GAMs (speed, turning angle analyses) minimum adequate model selection was based on a procedure that considered all biologically meaningful combinations of fixed effects. The best model was subsequently selected by the lowest AIC value [69], but models within two AIC points were considered to be plausible alternatives and the model that was the most parsimonious (i.e. the model with the fewest fixed effects) was selected preferentially [70]. The significance of the individual terms was then calculated from the selected model and all dropped terms were put back into the model to obtain the level of non-significance (lmerTest package, R [71]).

Results and Discussion

Continental scale

Our analysis of the effects of ecological and biological variables on DPLs at a continental scale indicates that mean DPLs for 47 baboon troops across 23 different populations were best explained by a model that considered the independent effects of mean monthly rainfall, mean annual temperature, and anthropogenic influence (Table 3; Figure 3 and see Additional file 2 for best candidate models). All other fixed effects tested did not significantly predict variation in annual mean DPL (Table 3). We discuss each of the main effects in turn.

With higher mean monthly rainfall we found shorter baboon DPLs. As higher levels of precipitation typically result in more productive habitats and therefore more food [15,16], troops should encounter food more frequently and thus travel shorter distances at sites that experience high rainfall [9]. A more direct measure of vegetation (NDVI) did not, however, predict annual mean DPL. One possible reason for this might be because of baboons reliance on surface water, that they require on a daily basis [17], and whilst NDVI may represent "better" quality habitat, it does not necessarily reflect water availability, which might act as a constraint on baboon movement. We also found that baboons in hotter habitats travel further than those in cooler habitats. If the relationship between temperature and DPL in this case were causal, we would expect baboons to travel less far in hotter habitats, due to enforced rest as a result of thermal loading [87]. Instead, it is likely that higher ambient temperatures reflect more arid and therefore less productive environments with less surface water [88]. We therefore interpret the positive effect of hotter environments on annual mean DPL to be a consequence of variance in productivity and surface water across sites. Given the significance of annual temperature and monthly rainfall at this scale, it would be instructive to gather information on the availability of drinking sites/surface water in future work to quantify directly the importance of this resource in determining baboon DPL. We also found that DPLs were shorter where troops experienced anthropogenic influence. Anthropogenic influence was not considered by Dunbar [29] in his original model, but has since been highlighted as an important factor mediating DPLs [22,33]. This is because baboons in human-modified habitats typically have access to high quality and predictable food resources meaning baboons are able to sate their nutritional requirements within a smaller daily ranging distance, e.g. by crop-raiding and/or scavenging human foods [22,89-94].

Contrary to Dunbar [29] and our own expectations, we did not find that group size predicts variation in annual mean DPL. The negative effect of increasing group size on ranging behaviour has been well documented across the primate order [4,95] and within the baboon genus [11,28,29]. The lack of any group size effect here might be explained by the importance of the key ecological variables retained in our final model; these appear to be far more important, perhaps reflecting the changing environments and associated increase in exposure to human-modified habitats that baboons are experiencing. The effect of human-modified habitat use has also been reported to negate the effect of group size at a local scale. In the Cape Peninsula, South Africa, Hoffman & O'Riain [22] found that the largest group in the population (N = 115) had a DPL that did not differ significantly from the two smallest troops (both troops N = 16), which was explained by their near 100% use of human-modified habitat.

Table 3 Estimate, standard error, test statistic and P-value for compatible predictors of annual mean DPL for baboon troops at a continental scale

Model term	Estimate	Standard error	*t*-value	*df*	*p*
Temperature (mean annual)	**0.24**	**0.07**	**3.61**	**1**	**0.002**
Rainfall (mean annual)	**−0.003**	**0.0007**	**−4.14**	**1**	**0.0005**
Anthropogenic influence[1]	**−2.04**	**0.46**	**−4.39**	**1**	**0.0001**
Sample size (months)[2]	0.34	0.79	0.44	2	0.08
Temperature (monthly SD)[3]	0.41	0.27	1.51	1	0.14
Troop size	0.005	0.005	0.92	1	0.36
Altitude	−0.0006	0.0005	−1.25	1	0.22
Sample frequency (GPS)[4]	−0.03	0.02	−1.65	1	0.14
NDVI	−0.84	1.89	−0.44	1	0.66

The best fitting model included those terms shown in bold text; for AIC values of the best candidate models tested see Additional file 2.

[1] Categorical effect (yes, no); reference category was no anthropogenic influence. [2] Categorical effect representing whether the mean DPL was calculated from >12 months study, <12 months, unknown. [3] Standard deviation in rainfall across months. [4] The frequency of GPS fixes taken per hour to calculate DPL.

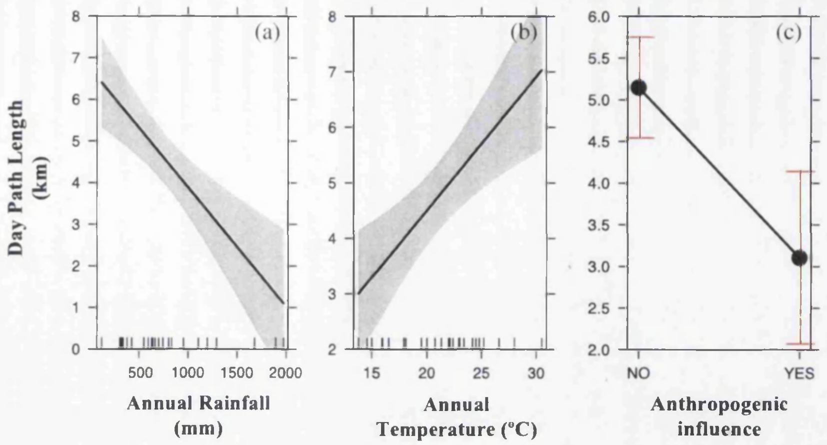

Figure 3 Predictors of DPL for N = 47 baboon troops across Africa. Significant effects of **(a)** average monthly rainfall (effect[SE] = 0.04[0.01]; df = 1; p = <0.0003); **(b)** average annual temperature (effect[SE] = –0.23[0.06]; df = 1; p = 0.001); **(c)** Anthropogenic influence (effect[SE] = –2.01[0.42]; df = 1; p = 0.0001). Effects shown are predictions from our LMM (see Table 3) and upper and lower 95% confidence limits are indicated by shaded areas for **(a)** and **(b)** and whiskers for **(c)**.

Local scale

At a local scale, we found that the median DPL for CT and MT were 4.7 km (range: 3.1–8.5) and 4.3 km (range: 1.5–6.0) respectively (Figure 4), and there was not a statistical difference between the DPLs of the two troops (Mann Whitney *U*-test: $n_{CT} = 22$, $n_{MT} = 12$, $P = 0.725$). Comparison of these observed DPLs and those DPLs predicted by the best continental-level model (see above) that considers monthly rainfall, annual temperature, and anthropogenic influence, whilst accounting for population, revealed that the actual DPL of Issa baboons was similar to the predicted DPL (Figure 5). Therefore, it appears that yellow baboons at Issa are not atypical and the same ecological factors that impact on baboon troop DPLs throughout their range are also good predictors of Issa troops DPLs.

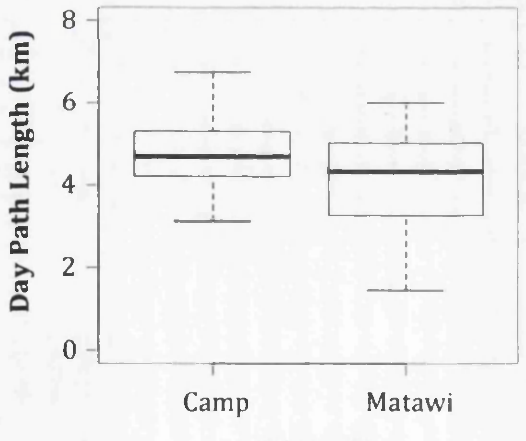

Figure 4 DPL of Issa baboon troops. Median DPLs of CT and MT troops during the study period. The upper and lower quartiles are shown by the range of the 'box', median value by the horizontal line within the box, and the full extent of the data given by the 'whiskers'.

Consideration of local ecological factors revealed that Issa baboon troops travelled significantly further (Table 4; Figure 6 and see Additional file 3 for best candidate models) and faster (Table 5) on cooler days. Due to the sensitivity of the vertebrate brain to even slight changes in temperature, the need for primates to regulate their internal temperature is vital [96]. In order to cool the brain, baboons dissipate heat through panting [97], however, they lack more typical mechanisms for the effective cooling of the brain (i.e. carotid rete) that are present in other similar sized, sympatric mammals [98]. This likely makes high radiant temperatures a greater challenge to their thermoregulation [98]. To avoid overheating, baboons have been observed to adjust their activity according to their thermoregulatory needs, with temperature being a negative function of activity in hot environments [33,61,87,99]. During periods of intense thermal loading, baboons are found to respond by seeking shade and engaging in more sedentary behaviours such as resting and grooming [32,87,100]. Similarly, Stelzner [99] found that travel rate in Amboseli baboons was dependent on ambient temperature at a microhabitat type level, and on hot days the baboons would slow down when traversing more shaded areas. It is plausible then, that as heat stress increases, baboons at Issa are forced into more sedentary activities, which could result in the reduced DPLs and

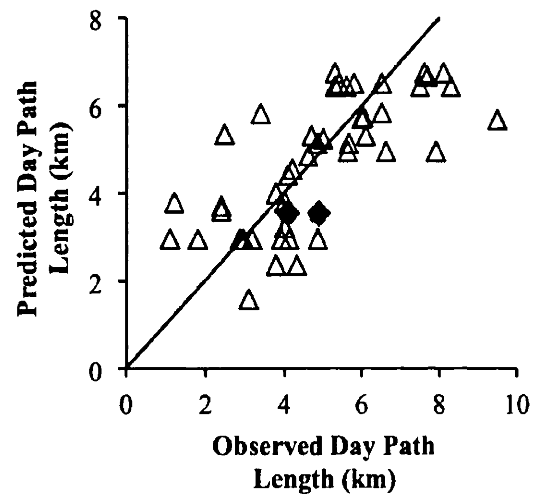

Figure 5 Predicted DPL against observed DPL for baboons on a continental scale. Predicted DPL calculated from a best fitting model model considering the effects of average monthly rainfall, average annual temperature, and anthropogenic influence, for troops listed in Additional file 1. The straight line passing through (0,0) is a hypothetical perfect 1:1 fit between the model and data. Predictions from the model are for N = 47 troops with data for the Issa troops (Ugalla, current study) omitted; observed DPLs for the Issa troops are shown by filled diamonds.

speeds we observed. Concurrent direct observations of individual and troop level behaviours would be required to confirm that Issa baboons move less on hotter days due to enforced resting.

Contrary to our expectations, we did not find FAI to significantly affect either DPL (Table 4 see Additional file 3 for best candidate models) or the movement characteristics of baboons at Issa (Table 5; Table 6). A critical influence on ranging patterns of *P. cynocephalus* is the distribution of foods [9]. In contrast with other studies [9,10] local fruit abundance (here, FAI) did not significantly predict DPL (Table 4). Our finer resolution analysis of the baboon's movement characteristic similarly found no effect of FAI on speed or turning angles. This is surprising, as primates have been consistently shown to use the space in their habitats according to the learned locations of particular resources and consequently move efficiently between them [48-51]. This is especially true of fruiting trees, a core food group for baboons [12,33,37-40,76-80]. In support of this, Noser & Byrne [101] found baboons demonstrated increased route linearity and speed when travelling to sparse, out of site, fruit patches indicating the tendency for baboons to use their space in an efficient, goal-directed way. For this reason, we expected Issa baboons to demonstrate more direct travel movements when fruit availability increases. The difference between the two studies is instructive, and highlights the need for combining behavioural (or at least basic activity data) with movement information, so that it is possible to analyse segments of travel between known resources [101]. We therefore proceeded to explore whether FAI and/or season predicted the time troops spent moving (i.e. speeds of <1 m/min versus >1 m/min). We reasoned that time spent feeding should decrease with proportion of carbohydrate-rich fruits [101,102] in the diet [30] resulting in decreased moving time as compared to other time budget variables [102]. Therefore, we expected to see less time spent moving during periods of high FAI, and our model (Additional file 4) confirmed this to be the case. Thus, whilst fine-scale movement of Issa baboons was not predicted by the availability of fruit resources, fruit availability did fundamentally alter the time they spent moving [4,5,17].

We found no significant effect of season (wet, dry) on baboon DPLs or movement characteristics (Tables 4, 5 and 6), although the effect of season on the distribution of turning angles was P = 0.055 (Table 6), indicating a trend for troops' movements to become more direct during the dry season in line with our original predictions. It may be possible that the lack of any strong seasonal patterns on movement characteristics may be due to the availability of water. Baboons are obligate drinkers [9] relying heavily on surface water, the availability of which is subject to large variation in sub-Saharan Africa. Surface water is therefore an important determinant of baboon ranging patterns [37], and its availability is ultimately determined by seasonal rainfall [40] (also see above continental model). During our study period, surface water was readily available to the baboons, and so

Table 4 Estimate, standard error, test statistic and P-value for predictors of baboon troop DPL at a local scale

Model term	Estimate	Standard error	*t*-value	*df*	*p*
Max. temperature	**−261.8**	**75.2**	**−3.48**	**1**	**0.0017**
Fruit Abundance Index	27.6	204.7	0.14	1	0.89
Season (dry, wet)[1]	−512.61	408.24	−1.26	1	0.22
Troop ID (CT, MT)[2]	−276.18	405.24	−0.68	1	0.50

The best fitting model included those terms shown in bold text; for AIC values of the best candidate models tested see Additional file 3.
[1]Reference category was wet season. [2]CT = Camp Troop. MT = Matawi Troop; reference category was Camp Troop.

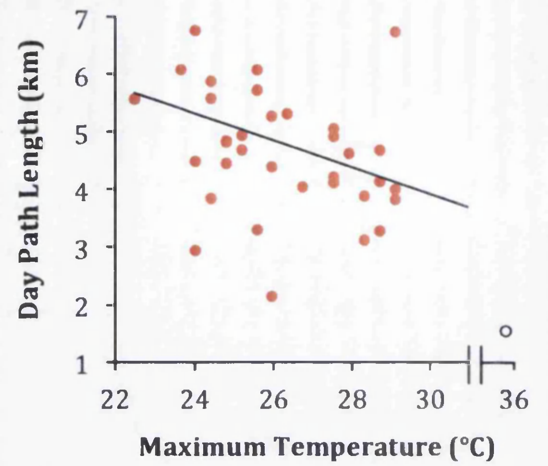

Figure 6 Relationship between maximum daily temperature and DPL in Issa baboons. The fitted line represents DPL as predicted by temperature (LMM: effect[SE] = −235.8[104.8]; df = 1; p = 0.025; see Table 4 for full model results). The empty circle to the right hand side represents the highest daily temperature and lowest DPL reading recorded; removing this data point does not quantitatively change the model results.

was unlikely to constrain movement paths. However, our study period did not extend through the driest months at the end of the dry season when running water at Issa becomes stagnant and gradually more confined to water holes [103]. Thus, the influence of surface water availability on ranging patterns cannot be fully determined without further study.

Table 5 Estimate, standard error, test statistic and P-value for predictors of baboon troop travel speed at a local scale

Model term	Estimate	Standard error	*t*-value	*df*	*p*
Max. temperature	**−0.04**	**0.01**	**−2.79**	**1**	**0.005**
Fruit Abundance Index	−0.003	0.03	−0.09	1	0.93
Season (dry, wet)[1]	0.004	0.14	0.027	1	0.98
Rainfall	0.007	0.005	1.43	1	0.16
Smoothing factor		***F***	**edf**	**rdf**	***p***
Day		0.16	1	1	0.69

The best fitting model included those terms shown in bold text. Effect of smoothing factor is also shown with estimated degrees of freedom (edf), reference degrees of freedom (rdf), test statistic (*F*) and *p* value.
[1]Reference category was wet season.

Table 6 Estimate, standard error, test statistic and P-value for predictors of baboon troop turning angle at a local scale

Model term	Estimate	Standard error	*t*-value	*df*	*p*
Max. temperature	−0.008	0.009	−0.98	1	0.33
Fruit Abundance Index	−0.0006	0.03	−0.19	1	0.98
Season (dry, wet)[1]	−0.14	0.072	−1.93	1	0.055
Rainfall	−0.00009	0.003	−0.04	1	0.97
Smoothing factor		***F***	**edf**	**rdf**	***p***
Day		1.98	1	1	0.16

Effect of smoothing factor is also shown with estimated degrees of freedom (edf), reference degrees of freedom (rdf), test statistic (*F*) and *p* value.
[1]Reference category was dry season.

There may well be other key ecological factors that are important drivers of Issa baboon movements that we did not measure. For example, baboons mitigate the serious threat of nocturnal predation by utilising sleeping sites (i.e. specific sleeping trees or cliffs) [17,104], and it is possible that the lower limit of DPL is set by the troops having to reach or travel between these sleeping sites [13,105,106]. Also relevant is the capacity of predation, especially by ambush predators, to influence ranging behaviour of primates [107]. Areas perceived to be 'high-risk' (vegetation allowing predators to conceal their approach) are commonly avoided by baboons [108], and leopards (*Panthera pardus*), the primary predator of baboons [109], were encountered frequently at Issa [110]. Their impact on the movement ecology of Issa baboons may be significant [107], and this offers yet another interesting area for future research.

Conclusions

Overall, this study emphasises the ability of baboons to adapt their ranging behaviour to extrinsic variables [111], and provides much needed data on baboon space-use from a woodland context. This adaptability is reflected, at least in part, by the ubiquity of baboons across a multitude of ecological and climatological contexts throughout sub-Saharan Africa (e.g. from the forests of Gombe in Tanzania, to the deserts of Tsaobis in Namibia). At a continental scale, we demonstrate the importance of including the role of human derived food sources in predicting the ranging patterns of baboons [22]. Human-derived foods are becoming increasingly available to baboons as the distinction between "wild" and "human" landscapes becomes blurred [112], and this factor, it seems, has a stronger effect upon variance in DPLs than group size, for example [29]. Moreover, this study highlights how investigations of movement patterns at different spatial and temporal scales can provide a fuller analysis of the ecological determinants of movement. Site-specific considerations in particular are important, for example, temperature. At a continental scale, baboons in hotter places travel further, whilst baboons on a local scale travel less far on hotter days. In this instance, we find the role of temperature changes depending on the spatial scale at which it is investigated.

Additional files

Additional file 1: Ecological data for DPL continental comparison model.

Additional file 2: Akaike Information Criteria (AIC values for the top ten candidate models that predict variation in annual mean DPL (continental scale).

Additional file 3: Akaike Information Criteria (AIC) values for the top ten candidate models that predict variation in DPL (local scale).

Additional file 4: Model testing variables predicting travel speed of baboon troops (local scale).

Abbreviations

CT: Camp Troop; MT: Matawi Troop; DPL: Day path length; GAM: Generalized additive model; LMM: Linear mixed model; AIC: Akaike's information criterion; PPI: Primary productivity index; GPS: Geographical positioning system; Pann: Average annual rainfall; Tann: Average annual temperature; PmoSD: Standard deviation across average monthly values for 12 months; TmoSD: Standard deviation across average monthly values for 12 months; P < 100: Number of months with less than 100 mm of rainfall.

Competing interests

The authors declare that they have no competing interest.

Authors' contributions

CJ collected all Issa baboon ranging data with supervision from DF, AP and FS. AP and FS provided data on phenology, temperature and rainfall for Issa. CJ and AJK analysed the data and wrote the manuscript with input from all other authors. All authors read and approved the final manuscript.

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