Fission fusion dynamics of olive baboons (Papio anubis) in Gashaka Gumti National Park

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Fission-fusion dynamics of olive baboons (*Papio anubis*) in Gashaka-Gumti National Park

by

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Voor pappa

Abstract

Primate societies have been classified into discrete categories based on the flexibility of their social organisation. However, due to growing evidence of intra-specific and temporal variation in grouping patterns, it has been suggested that instead, primate societies should be characterised by their relative degree of fission-fusion dynamics, which indicates the extent to which groups vary in spatial cohesion and the temporal variation in the size and composition of parties. While perceived predation risk and food availability are known to be key factors shaping primate societies, it is not clear if fission-fusion dynamics reflect short-term behavioural adaptations to these factors, and if social preferences also influence fission-fusion dynamics. Furthermore, little is known about the impact of fission-fusion dynamics on social relationships. These issues are addressed in this thesis by investigating the grouping patterns and social relationships of two troops (Gamgam and Kwano) of free-ranging olive baboons (*Papio hamadryas anubis*) in Gashaka-Gumti National Park, Nigeria. Grouping patterns were measured through association networks and the temporal variation in party size, party composition, and spatial cohesion, and were related to variations in food availability, predation risk, and habitat use. Variations in patterns of associations and fission-fusion dynamics were found both between troops, and between seasons within troops. As these variations could largely be accounted for by differences in ecology and demography, it seems that fission-fusion dynamics reflect a short-term optimisation of the trade-off between the cost and benefits of group living. The network of associations of the fluid Kwano troop, but not of the cohesive Gamgam troop, was found to be substructured in a way that indicates infanticide avoidance may play an important role in association patterns. Both the frequencies of social behaviours, and the structures of networks based on five types of social interactions, were related to differences in fission-fusion dynamics. The degree of fission-fusion dynamics appears to influence social relationships, as a quantitative difference in social behaviour was linked to variation in fission-fusion dynamics.

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Chapter 1

Introduction

Understanding the evolution of group living is a key aim in evolutionary biology. Primates are amongst the most social of animals (Dunbar 1988), and individual fitness is largely dependent on this sociality (Silk 2007). Consequently, the study of primate social systems and their ecological determinants have long been the basis of primatological research (Crook and Gartlan 1966; Denham 1971; van Schaik and van Hooff 1983; Sterck *et al.* 1997). Traditionally, primate societies have been classified according to the flexibility of their social organisation (Kappeler and van Schaik 2002), with species being classified as cohesive, or fluid, flexible social groups. As more field studies are conducted, it has become increasingly clear that many primate groups do not readily fall into these discrete categories; primates can show a degree of flexibility in their grouping patterns both between populations and within populations over time (Anderson 1981; Strier 2003b; Schulke and Ostner 2005; Izar 2008). Recently, a new framework on 'fission-fusion dynamics' has been introduced to account for this flexibility, which challenges the traditional categorical notions of primate societies. While this framework has gained acceptance over the past few years, it has not yet been *applied* to primate societies. Currently therefore, it is not clear how fission-fusion dynamics should be estimated and how much primate groups vary in their fission-fusion dynamics. Quantifying fission-fusion dynamics is particularly important for investigating whether traditional socioecological explanations can account for variation in the degree of fission-fusion dynamics and how such variations may affect social relationships, and ultimately, social structure. In this thesis, the fission-fusion dynamics of two troops of free-ranging olive baboons (*Papio hamadryas anubis*) are analysed and compared, and variations in fission-fusion dynamics are related to social and ecological factors, and to variations in social structure.

In this introductory chapter, an overview of primate social systems is given along with a review of socioecological theory, before outlining areas for which our current understanding is limited, and which this study aims to address. Finally, an overview is given of the social network approach, one of the main analytical techniques used in this thesis.

1.1 Primate social systems

A great diversity is found in primate social systems, ranging from solitary individuals seen in dwarf lemurs (Kappeler *et al.* 2002), to the association between a single male and female seen in gibbons (Palombit 1994), to a single adult male associating with several adult females and their offspring as is often seen in gorillas (Stewart and Harcourt 1987), and to the multi-male multi-female groups of chimpanzees (Lehmann and Boesch 2004). This diversity of social systems does not only include variations in grouping patterns, but also in patterns of spacing and mating, and the types of social relationships individuals have (Kappeler and van Schaik 2002). For these reasons the study of primate social systems has long been the bedrock of primatological research.

Here, a primate social group or 'society' is defined as a set of conspecific animals that regularly interact, and on average do so more with each other than with individuals who are not in their social group (Struhsaker 1969; Sailer and Gaulin 1984; Kappeler and van Schaik 2002). Primate societies have traditionally been classified according to their social organisation, particularly the association between adult males and females. Three primary forms of primate societies are recognised (Kappeler and van Schaik 2002). In solitary species, individuals are not synchronized in their activity, but their home ranges may overlap (*i.e.* neighbourhood systems). Pair-living describes a social system in which there is a permanent association of one adult female with an adult male. Group-living primates are those that live in bisexual groups of three or more adults. Group-living primates are further distinguished by sex ratio, differentiating between polyandrous, polygynous and multi-male, multi-female groups (Kappeler and van Schaik 2002). The latter category can be further subdivided based on social cohesion (Kappeler and van Schaik 2002), with species being either cohesive or flexible. Furthermore, there are two types of flexible groups; in multi-levels societies groups regularly split into *subtroops*, which are subgroups that are consistent in membership (Emory 1979 cited in

Anderson 1981), whereas in fission-fusion societies groups split into *parties*, which are subgroups that vary in size and composition (Kappeler and van Schaik 2002). Although this classification is based on social organisation, primate societies have two additional distinct elements, namely the social structure and mating system (Kappeler and van Schaik 2002). Since these three aspects do not always coincide, it is important to define each separately. The social organisation 'describes the size, sexual composition, and spatiotemporal cohesion of a society' (Kappeler and van Schaik 2002: 709). The mating system has two dimensions; the social aspect, the mating couples, and the genetic aspect, the genetic outcome of matings (Kappeler and van Schaik 2002). The social structure refers to the patterns of interactions between individuals in a society, and the social relationships that are a result of these interactions (Hinde 1976; Kappeler and van Schaik 2002).

Thus, social systems are the result of individual behavioural strategies that are largely driven by ecology, such as the distribution of resources and risks in the environment. Socioecology is the study of how the interaction of an individual with its environment shapes the society it lives in. Primate socioecology has seen several paradigm shifts over the years. Because unresolved issues tend to reoccur in time, the history of these paradigm shifts can help the understanding of current issues (Crook 1989). Below, the main ideas and changes in primate socioecology are reviewed, leading to an examination of current socioecological theory in primatology.

1.2 Trends in primate socioecological theory

1.2.1 Early beginnings

Primate socioecology has its beginnings in the 1930s with the work of Carpenter who carried out a number of field studies in Central America and Asia. Carpenter was one of the first to describe the relationship between primate environments and social systems (Carpenter 1934). Over the next decades there was a sharp increase in the number of primatological field studies (e.g. DeVore and Washburn 1963; Kummer 1968), and some links were made between ecology and primate social systems. For example, DeVore hypothesised on the relationship between group size and degree of terrestriality, and related levels of sexual dimorphism to levels of predation risk (1963). However it was not until the second half of the 1960s that an attempt was made to formulate a general theory on the relationship between environmental variables and primate social systems. In 1966, Crook and Gartlan (1966) published a short paper on the evolution of primate societies that has been enormously influential in subsequent primatological research. Inspired by the work of ornithologists at the time, Crook and Gartlan saw primate social systems as a set of behavioural features that co-evolved as adaptations to particular environments, and they consequently outlined a generalized framework for the relationship between environmental variables and primate social organisation. Primate groups were categorised into ‘grades’ according to their habitat type and diet. Differences in food availability and dispersion, and levels of predation risk present different selective pressures on group size and structure. Species in forested environments with insectivorous or frugivorous diets were considered to have small groups because food sources are very locally distributed and predation risk is low. Species in savannah environments were thought to form larger and more cohesive groups, due to higher predation pressures and more uniformly distributed food sources. Groups in grassland and desert environments were thought to have multi-level societies due to less abundant food that has an unpredictable distribution, and high levels of predation risk that was thought to be characteristic of these open habitats (Crook and Gartlan 1966).

These earliest socioecological models were flawed in several ways (Janson 2000). First, the majority of primate field studies available to formulate the model dealt with savannah or desert species in Africa. As rain forest species vastly outnumber the non-forest species in Africa, Struhsaker (1969) pointed out that data on these species should be considered in the formulation of socioecological theory. Struhsaker (1969) showed that the social systems of several forest *Cercopithecus* species and drills did not match with their expected ecological grade. Similarly, some of the primate groups Crook and Gartlan grouped in a single grade had quite different social systems, and this variation within categories could not be explained by their model (Clutton-Brock and Harvey 1977; Janson 2000). The second major problem of this framework was that there were no systematic environmental variables that were measured, making it unclear what selection pressures were driving the social systems of each grade (Denham 1971; Janson 2000). Thirdly, despite having very different environments, several *Cercopithecinae* species have very similar social systems (Struhsaker 1969). This suggests that primate social systems may be less flexible than was outlined in the socioecological model, and that social systems have at least some genetic underpinnings. The model proposed by Crook & Gartlan (1966) failed to take the effects of phylogenetic inertia into account (Struhsaker 1969; Clutton-Brock and Harvey 1977; Janson 2000).

1.2.2 Seventies: energetics and sociobiology

In response to these flaws, in the seventies, the socioecological model was expanded and several hypotheses on the causal effect of ecology on primate social systems were put forward. In these hypotheses environmental variables were more clearly defined, and the focus in these years was on energetics, and how it constrains primates both at an individual and a group level (Janson 2000).

Denham expanded on Crook & Gartlan's model (Denham 1971), but rather than just looking at habitat and the types of food primates eat, Denham tried to quantify these environmental variables by looking at the size and density of food patches, and at anti-predator strategies. He classified primate societies according to dispersal of food patches in the environment (uniform or clumped), the density of food within those patches (high or low), and anti-predator strategies (active or passive). He hypothesised how these would affect primate social organisation in terms of sex ratio, group structure and mating strategies. According to this model the distribution and density of food mainly determines the sex ratio and structure of a population. Anti-predator strategies were suggested to determine whether primates are solitary (passive strategies of concealment) or whether males and females associate permanently (active strategies where males protect females, leading to sexual dimorphism).

At this time Hladik (1975) proposed a mechanism by which the availability and distribution of food affects competitive regimes. When food occurs in large clumps, primates should feed in groups rather than individually finding alternative patches in order to keep their costs of travel low. Klein & Klein found a relationship between group size and the size and density of food patches in spider monkeys, red howlers, tufted capuchins and squirrel monkeys (Klein and Klein 1975), supporting Hladik's hypothesis.

These hypotheses on the relationship between ecology and social systems found further support in an analysis by Clutton-Brock and Harvey (1977) who compared features of the social systems of 100 primate species. They found that home range size was closely related to the density and distribution of food sources, and that group size was shaped by several factors including the distribution and abundance of food, and predation risk (Clutton-Brock and Harvey 1977).

At this time there were also significant developments in evolutionary theory led by evolutionary biologists such as Hamilton, Williams and Maynard Smith who criticised the pervasive group selection arguments (e.g. Wynne-Edwards 1962). These gene-centric ideas were applied to animal behaviour in the 1970s by Wilson, Trivers, and Hamilton, generating the new field of sociobiology. Of particular importance to socioecological theory was the realisation that genetic inheritance not only involves parents and offspring, but that actions towards related individuals could also increase the probability of shared genes being represented in the next generation, and consequently shape individual behaviour (Hamilton 1964). These ideas of 'inclusive fitness' and 'kin selection' had a great influence on the study of social relationships, because individuals might behave differentially towards their kin. Secondly, Trivers' (1972) work on parental investment had a big influence on socioecological theory. He theorised that because males and females invest differentially in their gametes, males and females may have different strategies for maximising their reproductive success. Female reproductive success is largely limited by the ability to produce eggs, therefore female behaviours and strategies should be mainly concerned with access to resources. Male reproductive success on the other hand is limited by their ability to fertilise eggs, and consequently male behaviours and strategies should concern access to females (Trivers 1972). Thirdly, the game theoretical approach put forward by Maynard Smith (1972) became widely used. This approach considers all the alternative behavioural strategies an animal has, and their fitness consequences, and then determines which strategy cannot be invaded by new strategies over evolutionary time (the evolutionary stable strategy or ESS). For example, the type of mating system was predicted by looking at how effective various male and female parental care strategies are (Crook 1989).

These sociobiological ideas began to be influential within primatology. In 1972 Goss-Custard, Dunbar and Aldrich-Blake published the first paper in which the effect of variation in primate social systems was examined in terms of individual reproductive success (*i.e.* natural and sexual selection), criticising previous models for only considering the adaptive functions of social systems in terms of survival. They argued that primate social organisation is largely driven by the abundance and distribution of food, and the type and rate of predation, whereas mating systems are largely driven by sexual selection (Goss-Custard *et* *al.* 1972). Sociobiological ideas were further expanded and researched in the following decade.

1.2.3 Eighties: costs and benefits

During the 1980s primate social systems were generally analysed using a cost-benefit approach, where social systems were seen as the result of an optimisation process in which primates balanced the cost and benefits of sociality. Based on Maynard Smith's game-theoretic approach (1972), several adaptive behaviours would be considered, and according to the trade-offs of costs and benefits, the optimality of strategies could be ranked. It was generally accepted that competition with group members for access to food was the main cost of living in groups and consequently, within-group competition was proposed as a constraint on group size (Terborgh 1983). Thus, the size, density and distribution of food patches were suggested to determine individual behavioural strategies, and consequently social systems (van Schaik and van Hooff 1983). When food patches are large, or food is densely distributed within a patch, intra-group competition may be lower, which may allow more individuals to feed in one patch at a particular time. It was also suggested that larger groups may be formed when food patches are close together, because members of a group can feed in neighbouring areas, keeping travel costs low. If food patches are small, food is sparse within each patch, and patches are relatively spread out, within-group competition and travel costs were argued to be higher, therefore limiting group size (Chapman *et al.* 1995).

There was less agreement over the benefits of group living, and several hypotheses were proposed. It was suggested that group living might increase individuals' foraging efficiency or that females may associate with a male to reduce harassment by other males (Wrangham 1979). However, increases in group size were found to reduce individuals' foraging efficiency (Janson and Goldsmith 1995) and the hypothesis could not explain why females associate with other females.

Two other hypotheses explaining group living proved to be more robust. Firstly, it was suggested that there are two types of primate groups, female-bonded and non-female-bonded groups, and that female-bonded groups evolved in response to competition for high quality food patches (Wrangham 1980). Primates, and particularly females, may thus associate to defend patches of food communally (Wrangham 1980) as primates are better able to defend a food source in groups than as individuals, and larger groups are better at defence than smaller groups. Secondly, it was proposed that primates might associate to reduce the risk of predation (Hamilton 1971; Terborgh 1983; van Schaik and van Hooff 1983; van Schaik *et al.* 1983; Dunbar 1988). By living in groups animals may reduce individual probability of attack (Hamilton 1971) and primates in larger groups are also more likely to detect an approaching predator (van Schaik and van Hooff 1983; van Schaik *et al.* 1983; Dunbar 1988), and detect predators earlier (van Schaik *et al.* 1983), which could be crucial in escaping. Larger groups also deter predators from attacking because it is more difficult for a predator to single out a victim for attack in larger groups (Dunbar 1988) and predators are at greater risk of counterattack (van Schaik *et al.* 1983; Dunbar 1988). The benefits of predator avoidance were thought to be traded-off against the costs of within-group resource competition (van Schaik 1983; Dunbar 1988). In an influential paper van Schaik (1983) tested between these two hypotheses by generating contrasting predictions on the relationship between group size and birth rate per adult female, and between population density and group size, using data from 23 monkey populations. In the majority of populations (81%) female reproductive rate declined with group size, suggesting that resource defence does not account for the formation of primate groups (van Schaik 1983). Secondly, group size did not increase steadily with population density, as predicted by the resource defence hypothesis. Rather, the relationship between group size and population density followed an inverted U-shape, suggesting that initially group size increases with population density, to the point where within-group competition outweighs the benefits of grouping, at which points groups should split, resulting in the decline of group sizes with high population density (van Schaik 1983). Primate grouping patterns were thus thought to be the result of an optimisation process in which individuals minimize the cost of feeding competition whilst maintaining a large enough group to reduce predation pressure to acceptable levels (e.g. van Schaik and van Hooff 1983).

However, by the late eighties the focus had shifted to the relative importance of various types of food competition on primate sociality (Janson and van Schaik 1988). Following a symposium held at XIth Congress of the International Primatological Society, it was recognised that there were two types of resource competition (Janson and van Schaik 1988), contest and scramble, which occur both within and between groups. Within-group contest competition occurs when individuals can aggressively monopolise access to food sources, leading to differential food intake rates among members of a group. Within-group scramble competition occurs when individuals cannot monopolise access and food items get eaten before others can locate them. In between-group contest competition, groups in an area compete over access to food patches. Lastly, between-group indirect scramble competition reflects the demands on food of all the groups in an area (Janson and van Schaik 1988).

Another important understanding at this time was that the trade-offs between the costs and benefits of group living might affect members of a group differently (Dunbar 1988; Janson and van Schaik 1988). For example, rates of food intake may be influenced by an individual's status in its group (*e.g.* dominance rank) and the different types of food competition influence the individual gain rate in different ways. Janson and van Schaik (1988) outlined the various patterns of individual gain rates under different competitive regimes. When competition is mainly within-groups, differential gain rates are seen within a group, and dominance rank was thought to be important for individual intake rates. When between-group competition is more important, differences in gain rates are seen between groups, and factors such as group size may be important for the intake rates of individuals in a group.

These ideas sparked off an interest in more fine-grained analyses of social systems. Rather than examining the ecological influences on the formation of groups as a whole, primatologists started looking at how they influenced types of social relationships (Janson 2000). In a landmark chapter van Schaik (1989) outlined a framework that explained within-species variation in the patterns of female social relationships in diurnal primates. Building on the ideas set out above, and combining various types and strengths of feeding competition, van Schaik expanded the number of categories of social systems to four, by presenting four types of competitive regimes with their respective ecological conditions, and linked these to aspects of female social structure (*e.g.* dispersal and residence patterns, type and stability of hierarchy). When competition is mainly within group and scramble, females were suggested to develop an individualistic and egalitarian system, in which female bonding may take several forms. If, on the other hand, within-group competition is contest, females were suggested to develop nepotistic and despotic ranking, with female residence. When competition is mainly between groups, it was thought that females form egalitarian social systems, either individualistic or nepotistic, with female residence. At the end of the 1980s it seemed much of the selective pressures shaping primate social systems had been worked out. Nevertheless, since some primates did not fit the model, some doubts about its generality started to form.

1.2.4 Nineties: questioning socioecological theory

In the 1990s, the field of primate socioecology underwent a major transition (Janson 2000) in which the validity of the socioecological model was questioned because a growing number of primate populations studied did not fit in the categories outlined by the model (e.g. Boesch 1991; Isbell 1994; Chapman *et al.* 1995; Henzi *et al.* 1997a). This questioning led to three developments in socioecological theory. First, the methodology to measure the ecological variables was refined. For example, it had been difficult to get an accurate indication of the pressures primates are under. Predation rates are not accurate, as they do not measure *a priori* risk (Cowlishaw 1994; Hill and Dunbar 1998), whereas behavioural measures of predation risk are problematic as they are usually not specific to anti-predator behaviour (Cowlishaw 1997a). Cowlishaw (1997b; 1997c; 1998) developed a methodology to measure perceived predation risk by measuring aspects of habitat physiognomy, reasoning that animals react to the conditions that facilitate predator attack, rather than the presence of predators itself (Hill and Cowlishaw 2002). Likewise, Janson & Goldsmith (1995) proposed a novel way to measure levels of within-group food competition by measuring increases in foraging effort. When primates face reduced foraging efficiency, individuals may increase their foraging effort in order to take in enough nutrients. This effort is estimated by the group's daily path length. Consequently, the relationship between daily path length and group size reflects the level of indirect food competition. To normalise the data, this measurement was scaled by the foraging effort of a solitary animal to give the relative ranging costs, making it possible to make inter-specific comparisons (Janson and Goldsmith 1995). This study found that two-thirds of variation in group size of frugivorous primates was explained by relative ranging costs (Janson and Goldsmith 1995), indicating that food competition indeed limits group size in these species and thus reaffirming the socioecological model. Nevertheless, this study also found that feeding competition was not related to group size in folivores, and that residual variation in group size was explained by taxonomy, indicating that phylogenetic history constrains species in the responses they have to particular environments (Janson and Goldsmith 1995), and thus also questions the universality of the socioecological model.

Secondly, there was a fine-tuning of the mechanism by which ecology and types of food competition were thought to impact on individual reproductive success. Chapman, Wrangham and Chapman (1995) proposed that reduced foraging efficiency is the major cost of living in groups and that travel costs impose a limit on group size. In environments where food patches are depletable, the density and the distribution of those patches determine travel costs. For example, if patches occur at high density, groups do not have to spend long to travel to the next patch and can therefore form larger groups regardless of the size of food patches. When food patches are distributed at low densities, groups have to travel further to their next patch, increasing their travel costs. Chapman *et al.* (1995) found that travel costs limit subgroup size in spider monkeys and chimpanzees, supporting their hypothesis.

Thirdly, some additions were made to the existing socioecological model to account for the fact that female interactions with males may also affect social relationships between females. Sterck, Watts and van Schaik (1997) expanded on van Schaik's ecological model (van Schaik 1983) by adding a demographic factor, habitat saturation, and a social factor, male reproductive strategies. In the case of habitat saturation, the cost of dispersal is high for females, and due to the large group size there is strong within-group contest competition. In this situation, females may target other females aggressively in order to evict them (Sterck *et al.* 1997). Additionally, infanticide by males was now also thought to influence social systems. Hrdy first described male infanticide among primates as an evolved reproductive strategy (Hrdy 1977; Hrdy 1979). Due to the critical effect this has on female reproductive success, females are expected to have evolved counterstrategies. One of the strategies open to females is to get a male to protect her infant, either the father or the male most likely to be the father. Thus, the avoidance of infanticide could be another external force bringing females together through association with a protector male. In a new socioecological model proposed by Sterck *et al.* (1997), infanticide avoidance, along with predator avoidance, select for the formation of groups. Female sociability is therefore determined by conflicting responses to infanticide and predation risk on one hand, and food competition on the other. The association of males depends on the distribution of females and female choice of protector males (Sterck *et al.* 1997). The distribution of food sources and female sociability together determine the type of competitive regime, which in turn determines female social relationships.

During the nineties the potential impact of social factors and individual association preferences on social systems was also beginning to become apparent. Several studies found that chimpanzee males associated preferentially with fertile females (Sakura 1994; Matsumoto-Oda *et al.* 1998), and chimpanzee parties were found to be larger when there were more oestrous females (Boesch 1996). Individual-level decisions can thus impact on group-level structure.

Despite these refinements to both the model and the methodology, some theoretical questions remained. For example, the importance of phylogeny on primate social organisations was once again stressed. Di Fiore and Rendall

(1994) found that cercopithecoid primates showed notable uniformity in their social systems, yet they are, ecologically speaking, the most diverse primate taxa with the largest geographical range and the biggest range of habitat types. This suggests that phylogenetic inertia plays an important role in primate social organisation and questions the extent of the role of the environment. Furthermore, questions relating to the interaction between social and ecological pressures were now being asked. Chapman (1990) found that although spider monkeys' subgroups varied with the distribution and availability of food, this could not explain all the observed variation in their size. Males preferred to band together and had larger home ranges than females, which allowed them to monitor the reproductive state of a large number of females and to defend their territory communally. Females were more solitary and had smaller home ranges than males. Females with dependant infants were found in smaller subgroups, were more solitary, and avoided boundaries more. Chapman argued that these females protected their offspring by avoiding conspecifics in their own and in neighbouring groups (Chapman 1990). These results indicate that, in spider monkeys at least, social organisation is the result of individuals meeting their own social needs, and being limited by ecology.

These unresolved theoretical questions about phylogenetic inertia and the interaction between social and ecological pressures are important themes in current socioecological theory.

1.2.5 Current socioecological trends

Since the foundation of primatology, researchers have attempted to classify primate societies into distinct categories (Izar 2008) and to explain how ecological factors have shaped these categories (Crook and Gartlan 1966; Denham 1971; van Schaik and van Hooff 1983; Sterck *et al.* 1997). However, the review above highlights that since the foundation of primatology, as field studies on more species were conducted, variation in the social systems between and within species has been found, and this has led to the successive refinements of the original socioecological model presented by Crook and Gartlan (1966). Equally, a recurring theme in the study of primate social systems is the importance of phylogenetic constraints (Struhsaker 1969; Clutton-Brock and Harvey 1977; Di Fiore and Rendall 1994; Strier 1994; Janson and Goldsmith 1995). Several current areas of interest, such as intersexual and male-male relationships, time budget models, and biological market theory, are further refinements to the socioecological model, while new analytical techniques make large-scale comparisons across the primate order possible.

First, there has been continued interest in the importance of social factors in shaping primate social systems, especially in terms of intersexual and male-male relationships. Infanticide avoidance has become more generally accepted as a constraint on primate social systems (Crockett and Janson 2000; Janson 2000; Steenbeek and van Schaik 2001; Henzi and Barrett 2003; Thierry 2008; Chapman and Rothman 2009). It became apparent that not only the rates of infanticide are variable among primate species, but also the role infanticide plays in shaping social systems (Chapman and Rothman 2009), with infanticide avoidance constraining group size in some species, but selecting for larger groups in others. It was shown that females maximize their fitness by preferring particular social bonds (Van Horn *et al.* 2007; Korstjens 2008) such as 'friendships' with unrelated males (Smuts 1985) who help protect their infants from infanticidal attacks (Palombit *et al.* 1997; Lemasson *et al.* 2008; Nguyen *et al.* 2009). It has further been suggested that males may intervene in female-female food competition in order to secure mating opportunities, and consequently males can influence competitive regimes (*e.g.* bonnet macaques (Cooper *et al.* 2004), guerezas (Fashing 2001)). Furthermore, male-male relationships may also influence aspects of the social system. Chapman & Pavelka (2005) have suggested that the group sizes of black and white colobus and black howler monkeys are limited by the nature of male-male relationships. In these groups, levels of aggression increase sharply with the number of males in a group, making group living increasingly costly for females (Chapman and Pavelka 2005).

Second, a new area of focus within primate socioecology is that of time budgets. In 1992, Dunbar described how time could be a limiting factor on the size of primate social groups (Dunbar 1992). Time is a finite resource, and time that has been allocated to one activity cannot be used for another. As primates use grooming to maintain social relationships (Dunbar 1988; Aureli *et al.* 1999; Sueur *et al.* 2011b), the amount of time available for grooming may limit the number of social relationships an individual can maintain (Dunbar 1992; Dunbar 1993). When animals live in very marginal habitats and are forced to choose between activities, grooming time might be compromised. This would make social relationships unstable and could lead to permanent group fission

(Dunbar 1988; Dunbar 1992; Lehmann *et al.* 2007b; Pollard and Blumstein 2008). Consequently, time budgets have been proposed to limit the size of primate societies. For instance, Pollard and Blumstein (2008) collated data from 50 primate species to test hypotheses on the relationship between time allocation and group size. Controlling for phylogeny, diet, and body mass, they found a strong negative correlation between group size and resting time (Pollard and Blumstein 2008), suggesting that the time a species needs to rest (*e.g.* for thermoregulation or bodily repair) sets an upper limit on group size. When group size increases, time that was initially allocated to resting will now be needed to meet other demands, such as foraging or travelling. There is a point at which resting time cannot be further decreased, after which animals will have to compromise on their grooming time. Similarly, Lehmann *et al.* (2007b) suggest that cognitive abilities, via the number of social relationships an individual can monitor, and time budgets, via the number of social relationships an individual can maintain through grooming, constrain primate group size. They found that time available for grooming is limited by the environment. Primates in larger groups may need to spend more time feeding or travelling, possibly compromising their grooming time, leading to less cohesive groups, or group fission (Lehmann *et al.* 2007b). Thus, cognitive abilities set an upper limit to social groups via time constraints, and in marginal habitats time may also constrain group size. With predation setting the lower limit, the distribution and availability of food determines the number of individuals in a social group. This time-budget model has subsequently been used to examine the trade-off that primates face between minimising predation risk and maximising reproductive success by modelling the interaction of the various ecological constraints in baboons (Bettridge *et al.* 2010), apes (Lehmann *et al.* 2008a), gorillas (Lehmann *et al.* 2008b), spider monkeys (Korstjens *et al.* 2006), and red and black-and-white colobus (Korstjens and Dunbar 2008).

Third, primate socioecological theory has further been refined by the increasingly accepted view that social groups are market places, in which animals exchange behaviours as commodities (*e.g.* grooming, infant handling, tolerance) following laws of supply and demand (Henzi and Barrett 2002; Barrett and Henzi 2006), an idea first proposed by Noë and Hammerstein (1994). This approach is more dynamic and individualistic than the established optimality model of behaviour, as an individual has the option of several alternative trading partners, and should choose the partner that maximises profit at that particular time (Barrett and Henzi 2006). Laws of supply and demand determine the value of the exchanged commodities. For example, Henzi & Barrett (2002) looked at the impact grooming has on access to infants in chacma baboons. They found that the length of grooming bouts varied with the number of infants present in the group. Thus, when the supply of infants increased, the value of access to them in terms of grooming time decreased (Henzi and Barrett 2002). This is a further refinement of the socioecological model in that particular market forces are generated by ecological conditions and corresponding competitive regimes (Barrett and Henzi 2006).

Fourth, the development of new analytical techniques and modelling approaches have led to a renewed interest in the socioecological model, as it is now possible to do large-scale comparative analyses (Lehmann *et al.* 2007b;

Majolo *et al.* 2008; Pollard and Blumstein 2008; Bettridge *et al.* 2010). Majolo *et al*. (2008) used meta-analysis of 122 primate studies to estimate the balance between the costs and benefits of living in groups. These types of analyses make it possible to determine an effect across taxa, whilst overcoming problems such as small sample sizes and error in measuring environmental variables. They found larger groups spend more time feeding and travel further per day because they deplete patches faster, suggesting that primates in larger groups face higher foraging and reproductive costs than those in smaller groups (Majolo *et al.* 2008). This study thus re-affirms the validity of the socioecological model and its applicability to folivores, which had previously been questioned (i.e. 'the folivore paradox' - Snaith and Chapman 2005; Snaith and Chapman 2007).

In addition to these refinements, more recent studies also continue to stress the importance of a species' evolutionary history. An important shift in thinking about phylogenetic inertia followed from the realisation that traits are not necessarily linked, and that therefore some traits may more readily adapt to current social or ecological conditions, whilst others might show more inertia (Chapman and Rothman 2009). In other words, it is possible that primate social structure remained relatively unchanged, whilst other traits, for example morphological traits, evolved more rapidly. Among the baboon subspecies it has for example been shown that populations with similar mitochondrial haplotypes can be morphologically and behaviourally very different, while populations with different mitochondrial haplotypes can be similar in morphological and behavioural terms (Zinner *et al.* 2009). This indicates that the rates of evolution of different traits are not necessarily linked, and can thus differ. The way variation in primate social organisation is phylogenetically constrained was highlighted recently in a study that used Bayesian comparative methods to investigate primate social evolution (Shultz *et al.* 2011). Such methods indicate that there is a phylogenetic signal in the distribution of social systems across the primate order, and thus that the flexibility of a species' social system is likely to be constrained. This has been suggested to be important for the social systems of savannah baboons, for example (Henzi and Barrett 2005). It was proposed that differences in social systems of populations are in a large part due to a species 'reaction norm', which evolved in particular ecologies, and presently limits flexibility in social systems.

While the socioecological model has been refined over the past decades, as yet very little is known about intra-specific behavioural variation in primates. Now that the number of field studies of primates has grown, intra-specific behavioural variation has been highlighted as one of the key areas that need to be addressed within primatology (Strier 2003b). Certain aspects of social systems, such as spatiotemporal associations, vary within species or within a population over time (Aureli *et al.* 2008a). For example, platyrrhine primates show great variability of their social organisations within species, and all species show a greater or lesser extent of fragmentation of their social groups (Kinzey and Cunningham 1994). Chimpanzees, for instance, are known to have very fluid grouping patterns, yet populations may vary in the extent to which they fragment; in East-African populations, parties often consist of males, and females are described as being solitary (Pusey *et al.* 1997; Itoh and Nishida 2007) whereas in West-African populations females are more often part of parties (Lehmann and Boesch 2009). Similarly, some degree of fluidity of grouping patterns is seen in all observed populations of grey mouse lemurs, but some populations form all-female groups while males are solitary; in other populations males join these female groups at sleeping sites (Schulke and Ostner 2005). By simply labelling these populations ‘flexible’, nuances in their social organisation may be lost.

In addition to intra-specific variation, there are also a growing number of field studies that show temporal variation in social organisation within a population (Aureli *et al.* 2008a). In a study of muriqui ranging patterns, for example, it was not only found that a troop changed over a 15-year period from being spatially cohesive to having relatively fluid grouping patterns, it was also found that the size of subgroups varied seasonally (Dias and Strier 2003). In fact, this type of flexibility of grouping patterns has now been observed in so many primate taxa that it has been suggested that ‘this type of social flexibility is common among a range of primate species and not simply restricted to those taxa exhibiting a fission–fusion system’ (Sussman and Garber 2007: 644).

In all, it is becoming increasingly clear that primate social organisation is more variable than previously thought, with variation occurring both within populations and within groups over time. This had led researchers to suggest that the traditional binary ‘flexible’ and ‘cohesive’ categories of primate social systems should be abandoned altogether, and that instead, primate societies should be characterised by their relative degree of fission-fusion dynamics (Aureli *et al.* 2008a).

1.3 Fission-fusion sociality and fission-fusion dynamics

The term fission-fusion was first used in a social context by anthropologists Neel & Salzano (1967) to describe the social structure of the Xavante Indians in Brazil. Xavante villages periodically split as a result of heightened social tensions. These fissions generally occur along kinship lines, and the fissioned groups will either join another village, start a new village, or re-join their original village after the tensions have cooled down, leading Neel & Salzano to describe this social system as 'fission-fusion'. Kummer was the first to use the term within primatology, describing the multi-level societies of Ethiopian Hamadryas baboons (Kummer 1968). These baboons live in troops of up to 750 individuals, yet over the course of a day various types of smaller subgroups were seen, and the splits and fusing of these groups ran along certain lines within the troop. These types of flexible social systems, with a relatively stable composition of subgroups, are called 'multilevel societies' (Kummer 1968) with 'molecular' (Rodseth *et al.* 1991) or 'group-based' (van Schaik 1999) fission-fusion. Fission-fusion *sociality* describes a social system of, for example, chimpanzees or spider monkeys, in which communities regularly split into smaller parties that later join together in larger groups, so that the size and composition of parties varies over time (Kummer 1971; Symington 1990; Lehmann and Boesch 2004; Aureli *et al.* 2008a). Such social systems are also referred to as 'atomistic' (Rodseth *et al.* 1991) or 'individual-based' fission-fusion societies (van Schaik 1999).

However, in the past four years, the traditional classification of primate social groups as either cohesive or flexible (Kappeler and van Schaik 2002) has come under scrutiny, as an increasing number of studies found that primate social systems did not readily fall into these categories, and that the flexibility of social systems varied not only between but also within species and within populations over time (Chapman and Chapman 1999; Struhsaker 2000; Strier 2003a; Aureli *et al.* 2008a; Struhsaker 2008; Chapman and Rothman 2009), suggesting that primate sociality varies along a continuum, rather than falling into distinct categories (Aureli *et al.* 2008a). Moreover, research on fission-fusion sociality has largely focused on fluctuations in group or party size, yet primates also show variation in the composition and spatial cohesion of their social groups. The concept of fission-fusion *dynamics* has been introduced (Aureli *et al.* 2008a) to account for these issues.

1.3.1 Fission-fusion dynamics

In a landmark paper (Aureli *et al.* 2008a) a framework was proposed to capture this complexity of primate social systems more adequately; the degree of fission-fusion dynamics describes "*the extent of variation in spatial cohesion and individual membership in a group over time*" (Aureli *et al.* 2008a: 628), and varies along three dimensions, namely the temporal variation in spatial cohesion, in party size and in party composition. This multidimensional framework is outlined Figure 1.1. Thus, any social system can be described according to its relative degree of fission-fusion dynamics by measuring variation in party size, party composition and spatial cohesion (Aureli *et al.* 2008a).

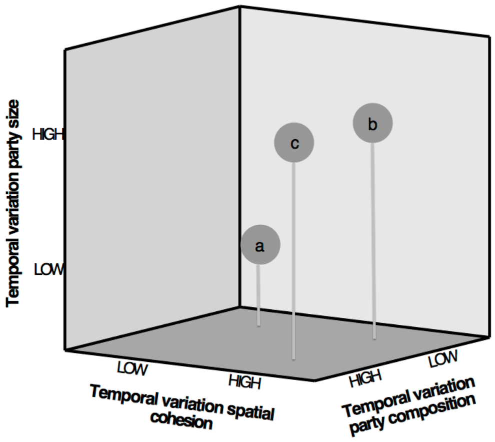


Figure 1.1: Graph representing the three-dimensional framework for the degree of fission-fusion dynamics. The degree of fission-fusion dynamics is measured by the temporal variation in spatial cohesion (x-axis), party composition (y-axis) and party size (z-axis). Examples are given for a) groups with low variation in all three dimensions (*i.e.* traditional 'cohesive' groups); b) groups with high variation in spatial cohesion and party size, but low variation in party composition (*i.e.* multi-level societies); c) groups with high variation in all three dimensions (*i.e.* traditional 'fission-fusion' societies). Graph was adapted from Aureli *et al.* (2008a).

Up to now, research into the flexibility of primate grouping patterns has focused on species traditionally classified as having fission-fusion sociality, such as chimpanzees and spider monkeys (Symington 1990; Lehmann and Boesch 2004; Coles *et al.* 2012). With the proposal of the fission-fusion framework, there is now a clear need for research into the flexibility of grouping patterns (Kerth 2008), particularly in groups that are likely to have a lower degree of fission-fusion dynamics (Coles *et al.* 2012). Research in this area would greatly improve our understanding of the continuum of fission–fusion dynamics, of how species and populations fit into this 3-dimensional fission-fusion space, as well as the evolutionary routes and behavioural consequences of the various degrees of fission-fusion dynamics (Coles *et al.* 2012). Moreover, to date no study has *quantified* the degree of fission-fusion dynamics by measuring the extent of variation along the three fission-fusion dynamics axes. Therefore, it is essential that standardised methods for the quantification of fission-fusion dynamics are developed, and it would be particularly interesting to look at the flexibility of grouping patterns in a species other than spider monkeys or chimpanzees (Coles *et al.* 2012).

In summary, while the concept of fission-fusion dynamics has been introduced to reflect the flexibility of primate grouping patterns, research is now needed to investigate if these flexible patterns can be accounted for by the socioecological model, in other words, if fission-fusion dynamics reflect a short-term optimisation of the cost-benefit ratio of group living. Furthermore, research is needed to examine if other factors, such as social strategies, play a role in the flexibility of primate grouping patterns, and how fission-fusion dynamics may affect social relationships.

1.4 Fission-fusion dynamics and social relationships

The vast majority of primates form long-lasting social relationships with members of their social group, through repeated social interactions (Hinde 1976). Primates interact through visual, gestural, tactile, vocal, and olfactory communication (Rowell 1972; Charles-Dominique 1977) and communicate a wide array of states, including fear, threats, submission and dominance, reconciliation, and reassurance (Rowell 1972). The degree of fission-fusion dynamics is likely to affect both the form of communication and the type of social interactions used in a primate group (Maestripieri 1999; Milton 2000; Aureli *et al.* 2008a); the spatiotemporal distance between individuals is likely to influence the form of social interactions, whereas the cohesion of the group is likely to influence the function.

1.4.1 Fission-fusion dynamics and the form of social interactions

For certain interactions, primates need to be in close proximity to another individual. Primates for example use their gaze, body posture and gestures to communicate a wide array of states, including fear, threats, submission, dominance, and reconciliation (Rowell 1972), and for these individuals need to be in visual contact. In tactile communication, proximity is even more important, as individuals touch each other for example to reassure, in greetings or grooming, or aggressively, for example by biting or grabbing of fur (Rowell 1972). Certain quiet vocalisations, such as the grunts in baboons, also require relatively close proximity of two individuals, and these interaction often function to facilitate further interactions between individuals (Rowell 1972). However, primates do not necessarily need to maintain close proximity in order to interact as communication is possible over long-distances, through long-distance vocalisations, and over long time periods, through scent (Aureli *et al.* 2008a).

Relatively little is known about olfactory communication in primates (Heymann 2006a), however, the use of smell has been noted in several field studies (e.g. Rowell 1972; Charles-Dominique 1977), particularly in New World primates (Heymann 2006b). Primates' inter-group calls have been suggested to allow scattered communities to remain in contact and share information about food, predators, and conspecifics; such systems have been found among spider monkeys, chimpanzees and bonobos, (Milton 2000), Guinea baboons (Byrne 1982), mangabeys (Waser 1977), mandrills (Kudo 1987), Diana monkeys (Shultz *et al.* 2003), and drills (Kudo 1987). Long-distance calls might help individuals keep in contact with their preferred associates (Cheney *et al.* 1996), inform others of the composition of a subgroup (Ramos-Fernández 2005), and help individuals decide to join or avoid a subgroup (Waser 1977). Loud calls may also help subgroups to locate others for a reunion and evidence for this has been found in spider monkeys, chimpanzees and bonobos, (Milton 2000), Guinea baboons and mangabeys (Byrne 1982), and mandrills (Kudo 1987). Guinea baboons maintain contact through loud barks, and use these to locate other small, scattered parties for regrouping before crossing an open area, or for aggregating at a sleeping site (Byrne 1981). Individuals also use these barks to regain contact when they have become separated from their group (Byrne 1981). These loud calls may even allow subgroups to manipulate the size of their party according to local conditions. Spider monkey subgroups use loud calls more often when food is dense and abundant, suggesting they try to keep party sizes small when resources are limited (Chapman and Lefebvre 1990).

Across the primate order, increases in group size and the strength of social bonds are associated with an increase in the size of the vocal repertoire (McComb and Semple 2005). Similarly, the degree of cohesion may have influenced the evolution of social behaviours. For example, it has been suggested that the short-distance contact calls that are widely used by baboons, have largely disappeared from the vocal repertoire of the closely related mandrill, partly due to lower spatial cohesion (Kudo 1987). These grunts have been replaced by two types of long-distance calls that help to maintain group cohesion (Kudo 1987).

However, the types of social behaviours may also vary within a species or group, depending on the degree of cohesion. For example, in the golden brown mouse lemur (*Microcebus ravelobensis*), the type of signals used differed with group cohesion; individuals exclusively used scent marking when the group was dispersed to regulate the distribution of different groups in space, whereas vocalisations were used to coordinate group movements when the group was cohesive (Braune *et al.* 2005).

1.4.2 Fission-fusion dynamics and the function of social interactions

The *types* of social interactions, in terms of which function they serve (*e.g.* reconciliatory behaviours or bond-testing behaviours), that are common in a group are thought to be related to a combination of the spatial cohesion of that group, and the complexity of social relationships individuals have. In groups that are relatively cohesive, conflicts may arise over, for example, food or mating. However, in cohesive groups, fragmentation is avoided and consequently there is likely to be a focus on social behaviours that function to resolve conflicts (Aureli *et al.* 2008a). Grunts in baboons and rhesus macaques are an example of such a behaviour that facilitates friendly interactions and is used to restore and maintain social relationships, which help to preserve group cohesion (Silk *et al.* 1996; Cheney and Seyfarth 1997; Rendall *et al.* 1999; Silk 2002a).

Conflict resolution might be less important in groups with a high degree of fission-fusion dynamics as the group can simply split when conflicts arise. Instead, social signals that help to asses and re-establish relationships (*e.g.* third party, dominance or coalitionary relationships) are more important in these groups. Here, individuals are separated more frequently and for longer periods and as a result changes in hierarchy or coalitions may take place whilst part of the group is out of sight (Barrett *et al.* 2003; Aureli *et al.* 2008a). In order to monitor their social marketplace effectively, individuals need to update their social information after a period without contact (Barrett *et al.* 2003). An experiment with captive chimpanzees suggests that some primates do this by increasing affiliative behaviours, such as grooming, towards joining subgroup members (Okamoto *et al.* 2001). Male baboons are known to engage in ritualised greetings, which involve risky intimate contact such as embracing, pectoral sniffs and kisses, posterior presenting, grasping of the posterior, mounting, and touching of the penis and/or scrotum (Whitham and Maestripieri 2003). Spider monkeys frequently embrace members of joining subgroups when subgroups merge. These potentially costly behaviours give reliable information about a partner's willingness to cooperate and invest in their relationship (Smuts and Watanabe 1990; Whitham and Maestripieri 2003). Therefore, after subgroups merge, individuals may test the quality and strength of their social bonds with members of the joining subgroup through intimate and risky contact.

The degree of cohesiveness, for example, influences the type of social behaviours used in chimpanzees; captive chimpanzees have very complex reconciliation gestures that are not seen in wild populations, potentially because wild chimpanzees have the option to fission when there is conflict (Aureli *et al.* 2008a). Apart from intra-specific variation in social behaviours, group cohesion may have also influenced inter-specific variation. Several species that are thought to have a high degree of fission-fusion dynamics, such as spider monkeys, bonobos, and spotted hyenas, have relatively simple reunion displays, in comparison to, for example, the complex and long displays of capuchin monkeys, who have lower degrees of fission-fusion dynamics (Aureli and Schaffner 2007). This suggests that in groups where members are more frequently separated and reunited, bond-testing behaviours are ritualised to make the signal more efficient (Rowell 1972).

Overall, the type of social behaviours, in terms of the function that they serve, may vary with the degree of group cohesion, social complexity and the encounter rate of group members. It is therefore very likely that the degree of fission-fusion impacts on the nature of social relationships, as relationships may have, for example, a larger agonistic or affiliative element. Naturally, this is also influenced by a species' evolutionary history (Aureli *et al.* 2008a). By comparing two troops of a single species, this issue of phylogeny is avoided and it is therefore possible to explore the effect of fission-fusion dynamics on the nature of social relationships.

1.4.3 Quantifying primate social organisation and social relationships

Due to their great diversity, primate social systems have been difficult to classify (Kasper and Voelkl 2009), and as was outlined above (section 1.2), various classification schemes have been criticized for being too simplistic. In the study of fission-fusion dynamics, it is therefore particularly important to adopt a continuous, rather than a categorical approach. However, to date it has been challenging to characterise primate groups in a comparative way (Kasper and Voelkl 2009).

Furthermore, while Hinde's (1976) framework of social interactions, relationships and structure is generally accepted, it has been difficult to implement (Kasper and Voelkl 2009; Brent *et al.* 2011), because there has not been an appropriate method to study social relationships in such a way (Kasper and Voelkl 2009). Analyses of social relationships have usually focused on dyadic interactions or associations (Kasper and Voelkl 2009); however, it is not clear how these types of analyses translate to group-level structures (Brent *et al.* 2011; Sueur *et al.* 2011a).

Social network analysis seems to be a promising approach for the study of fission-fusion dynamics and social relationships, as it allows for continuous measures of network structure, and because it enables multilevel analyses. The social network approach consists of a set of analytical tools that are based on graph theory. In the next section, a short overview of the history of social network analysis and of the method itself are given, before discussing the application of social network analysis in the study of non-human primates and its use for the study of fission-fusion dynamics and the effect on social relationships.

1.5 Social network analysis

The application of social network analysis to the study of animal behaviour has become increasingly popular over the last decade. The approach however is far from a recent development, and has its foundations in 1930's psychology where it was developed to measure interpersonal relationships in small groups (Wasserman and Faust 1994). With the development of the sociogram, Moreno (1934) laid the foundations for the field of sociometry, the precursor of social network analysis. Combined with analytical techniques (*e.g.* matrices that represent networks) and mathematical models (*i.e.* graph theory, statistics and probability theory, algebraic models), researchers, especially in the field of anthropology, started to use these methods to study more complex human groups, such as complete societies.

Recent developments in computer processing power have made it possible to analyse larger databases (Wey *et al.* 2008), and subsequent developments of specialised network analysis software such as UCINET (Borgatti *et al.* 2002) have led to a surge in the use of the network approach in the study of animal societies (e.g. Lusseau 2003; Croft *et al.* 2004; Cross *et al.* 2005; Ramos-Fernández *et al.* 2006; Sundaresan *et al.* 2007; Sueur and Petit 2008; Wolf and Trillmich 2008; Lehmann and Boesch 2009; Lehmann and Dunbar 2009; Henkel *et al.* 2010). Below the social network approach is outlined, after which its application to the study of non-human primates and the study of fission-fusion dynamics is discussed.

1.5.1 The social network approach

In the network approach a society is seen as a network of interrelated individuals (Figure 1.2). Individuals, also called *actors* or *nodes*, are linked through *ties* or *edges*, which can be based on any kind of relationship, such as a biological relationship, social interactions or associations (Wasserman and Faust 1994). These ties can be binary, and merely record the occurrence of a relationship, or weighted, in which they also measure the strength of that relationship (Croft *et al.* 2008). Furthermore, ties can be undirected, for example when they are based on associations, or directed, involving an actor and a receiver. Examples of these types of networks are given in Figure 1.3. Apart from these relational data, networks can also contain attribute data, which describe the characteristics of the individuals in the network, such as their age or sex.

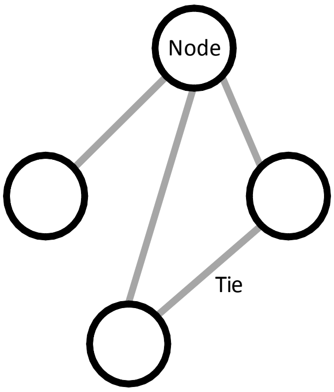


Figure 1.2: Example of a social network. Individuals, or nodes, are linked through ties.

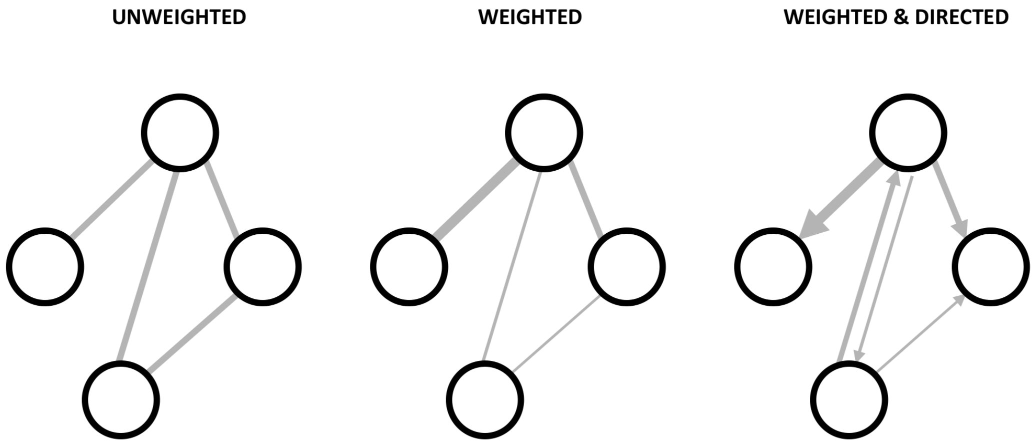


Figure 1.3: Examples of an unweighted, a weighted, and a weighted, directed network.

The social network approach provides three types of analytical tools. First, social networks can be drawn as graphs to help visualise the data. This can, for example, help to identify key individuals and subgroups or to show how cohesive a network is (Croft *et al.* 2008).

Second, the network approach has a range of descriptive statistics to quantify the structure of a network, such as the distribution of ties or the connectedness of a network (Krause *et al.* 2007; Croft *et al.* 2008; Borgatti *et al.* 2009). These metrics can be used to describe the network at various levels. On an individual, node-level analysis, *centrality* measures are the most widely used (Borgatti *et al.* 2009). These measures help to identify the importance of individuals and the roles they play in their social network (Wey *et al.* 2008; Borgatti *et al.* 2009). Apart from describing the role of individuals in a network, when averaged over the network these measurements also characterise the network as a whole (Croft *et al.* 2008). Network metrics can also be used to characterise intermediate levels of social organisation by looking for groups of individuals that have stronger connections to each other than to the rest of their network. The network metrics used in this study are discussed in detail in section 2.5.2.

Third, the network approach has a range of inferential statistical methods. Traditional inferential statistics can often not be used because network data are relational and consequently values are not independent, violating the assumptions of standard tests (Croft *et al.* 2008). Instead, these statistics rely on comparisons of observed networks to networks that have been randomised, for example through Monte Carlo simulations (Croft *et al.* 2008; James *et al.* 2009).

1.5.2 Social network analysis in the study of non-human primates

Social network analysis has been applied to study a wide range of topics in primatology, including social learning (Voelkl and Noë 2008), the role of individuals in societies (Mitani 1986; Flack *et al.* 2006; Sueur and Petit 2008; Ramos-Fernández *et al.* 2009; Henkel *et al.* 2010), the evolution of cooperation (Voelkl and Kasper 2009), vocalisations (Mitani 1986), social complexity (Lehmann and Dunbar 2009), the characterisation of social systems (Kasper and Voelkl 2009), sociality (Henzi *et al.* 2009; Lehmann and Boesch 2009) and fission-fusion dynamics (Ramos-Fernández *et al.* 2006). These studies include individual level analysis, the analysis of the structure of a society as a whole, intermediate levels analysis of substructures, and often focus on how these levels interact.

At the level of the individual, social network analysis has been used to investigate how the characteristics of individuals may affect their behaviour, and thus their networks. For example, male Barbary macaques that carried infants were found to have relationships with more other males than those who did not carry infants (Henkel *et al.* 2010).

Additionally, social network analysis has been used to investigate the role individuals have within their networks. Black-handed spider monkey networks are largely segregated by sex (Ramos-Fernández *et al.* 2009). Analysis of the ties of individuals showed however that maturing males have bonds with adult males as they try to integrate into the male network, but also with adult females, such as their mother; this suggests that maturing males have an important role as a ‘broker’ between groups of adult males and females (Ramos-Fernández *et al.* 2009). Female matriarchs also serve as brokers in macaque societies (Mitani 1986). Vocalisation networks based on ‘coos’, a vocalisation often used in the context of group movement, showed that female macaques give coos mostly within their own kin group. The exceptions to this were the matriarchs of kin groups, who gave these vocalisations most frequently to each other, suggesting that macaque societies consists of small subunits of kin that remain cohesive through the interactions of a few females (Mitani 1986). In the hierarchical and nepotistic societies of rhesus macaques, dominant individuals have the highest centrality, indicating their importance in group movement and the formation of subgroups; this is not seen in Tonkean macaques, who have a much more tolerant social system (Sueur and Petit 2008).

The networks approach has proven particularly useful in investigating the role of individuals in their networks because it allows for experimental simulated removal of individuals from the network. For example, Lehmann and Dunbar

(2009) explored the relationships between grooming network cohesion, brain size and group size in eleven species of Old World monkeys. By experimentally removing the most central female in each network, it was possible to assess the role of these females. As groups got larger, the removal of broker females caused more change in the connectivity of the network, suggesting that in larger Old World monkey groups, females play a key role in maintaining the overall cohesion of the group (Lehmann and Dunbar 2009). Similarly, Flack *et al.* (2006) showed the importance of a few individuals who intervened in conflicts ('policers') on the structure of networks of captive pig-tailed macaques. Social networks were built for three conditions: an observed control in which all individuals were present; an experimental condition in which policers were physically removed from the group; and a topological experimental condition of simulated removal, in which the data on policers were removed. By comparing the two experimental networks, it was possible to see how behaviour changed due to the removal of policers. They found that when policers were removed networks were smaller, less diverse and much less integrated, suggesting that policing prevents conflict and consequently maintains the stability of the society (Flack *et al.* 2006).

At an intermediate level, the network approach has been used to characterise the structure of subgroups. Ramos-Fernández *et al*. (2006) characterised spider monkey substructures under varying distributions of food sources in networks generated through agent-based modelling. These were compared to characteristics of observed subgroups, leading the authors to conclude that the complexity of the environment alone can influence patterns of fission-fusion, as a result of aggregation of individuals at food patches. Similarly, the substructures seen in chacma baboons may simply be the result of food availability. Female chacma baboons do not seem to have enduring companions, as affiliations between females largely disappear when food is abundant; consequently associations between them seem to be the result of aggregation at food patches (Henzi *et al.* 2009).

With the social network approach it is also possible to characterise networks at a global level (Jacobs and Petit 2011) and make comparisons between networks. This for example has been useful in investigations into the effect of food availability on social relationships. Lehmann & Boesch (2009) investigated how the association and grooming networks of female chimpanzees differed with levels of food competition. They found evidence that the competitive regime had an important effect on female social networks, with smaller groups (less intragroup competition) being less clustered and better connected (Lehmann and Boesch 2009). Similarly, networks of captive primates before and after a relocation have been compared to investigate the impact relocation has on social relationships (Dufour *et al.* 2011). In both squirrel monkeys and capuchins, proximity networks were more cohesive after the move as a way to deal with the stress of a relocation (Dufour *et al.* 2011). Furthermore, it is possible to compare networks based on different behaviours. For female chimpanzees, there was little correspondence between the grooming and the association network, suggesting grooming and association serve two different social purposes. Association is used to increase tolerance and facilitate the formation of coalitions, whereas grooming may serve shorter-term goals (Lehmann and Boesch 2009). Comparison of social networks based on several different behaviours can reveal the social complexity of a primate group (Lehmann and Ross 2011; Tiddi *et al.* 2011).

The characterisation of networks as a whole has been particularly important in investigations into the spread of information or disease in primate groups, and the emergence of cooperation. Voelkl & Noë (2008) found that the structure of a network greatly influences the spread of information. For example, information spreads much faster in decentralised networks than in networks with a few central individuals (Voelkl and Noë 2008). Similarly, primate group size affects the spread of infectious disease, because larger groups have more subdivision in the network, which slows the spread of disease (Nunn 2012). Voelkl & Kasper (2009) compared simulations on cooperation in networks based on sociopositive behaviours from 70 primate groups, as compared to random networks and well-mixed networks of the same size. They found that the global group structure found in primate societies facilitates the emergence of cooperation more than the model networks. This again seems to be due to the levels of sub-structuring in the overall network (Voelkl and Kasper 2009).

Finally, global social network metrics could be used on a much wider scale. Kasper & Voelkl (2009) analysed 70 primate networks based on sociopositive interactions (*e.g.* grooming or play). They found a high degree of variability in global metrics, suggesting a high variability in primate social groups. They proposed the use of global network metrics as an alternative to the traditional classification of primate social systems (Wrangham 1980; van Schaik 1983; Sterck *et al.* 1997), as it allows for a much finer picture of social structure, than the traditional socioecological classification.

1.5.3 Social network analysis in the study of fission-fusion dynamics and social relationships

The social network approach is particularly valuable for the study of fission-fusion dynamics (Cross *et al.* 2005; Ramos-Fernández *et al.* 2006; Sundaresan *et al.* 2007; Wolf *et al.* 2007; Wolf and Trillmich 2008; Lehmann and Boesch 2009; Ramos-Fernández *et al.* 2009), because it provides tools to provide a detailed characterisation of the social system in complex societies. In societies with flexible grouping patterns, it has proven difficult to determine association patterns, assortative forces and social relationships (Whitehead 1997; Lusseau *et al.* 2006; Ramos-Fernández *et al.* 2006; Sundaresan *et al.* 2007; Wolf *et al.* 2007; Wolf and Trillmich 2008; Ramos-Fernández *et al.* 2009) because individuals may not all be associated simultaneously. Especially in populations with high levels of fission-fusion dynamics, it might be difficult to record recurrent interactions between dyads in order to understand structural features of a population (Ramos-Fernández *et al.* 2006; Sundaresan *et al.* 2007; Wolf and Trillmich 2008; Ramos-Fernández *et al.* 2009). The social network approach can provide quantitative measures of social structure in complex societies, where this structure is not readily apparent (Lusseau *et al.* 2006; Wolf and Trillmich 2008).

Social network analysis further helps to identify 'layers' within the social structure and analyse how such layers interact. Animal societies are made up of several layers (Ramos-Fernández *et al.* 2006; Wolf *et al.* 2007), from individual-level behaviours, to group and population-level phenomena (Krause *et al.* 2007; James *et al.* 2009). It has been generally accepted that these layers influence each other, for example the notion that the social structure affects individual level fitness or that individual association preferences influence grouping patterns. However, it has thus far not been possible to quantify this in detail (Krause *et al.* 2007; Sih *et al.* 2009). Social network methods can identify layers in the social structure, even ones hitherto unknown, and examine the driving factors shaping each of these layers (Lusseau *et al.* 2006). For example, in a study of Galápagos sea lion social structure, Wolf *et al.* (2007) used association networks and examined assortment patterns, community structure, and substructures. In previous studies, it had been identified that sea lions segregated by sex and age class at a population and group level, probably due to the different reproductive strategies of males and females. However, Wolf *et al.* (2007) identified a further two tiers, at a community and clique level. These additional layers were shaped by different factors; communities were based on the use of space, with members of the same community having almost exactly the same home range. Although age and sex class segregation was ruled out, the factor affecting the formation of cliques remained unclear. Nevertheless, based on these findings Wolf *et al.* (2007) refuted the old notion that sea lion social structure is entirely based on the distribution of male territories.

Furthermore, social network metrics can capture a much finer social structure than do traditional measures (Krause *et al.* 2007; James *et al.* 2009; Kasper and Voelkl 2009). Using a social network approach, researchers have been able to define more precisely the social structure of several species with highly fluid social organisations. For example, bottlenose dolphin social systems are often described simply as 'fission-fusion'. However, by using social network analysis, Lusseau *et al.* (2006) found that the finer structure of bottlenose dolphin social systems may differ dramatically between populations, the fission-fusion structure being driven by longstanding preferential associations in some populations, or many short-term acquaintances with a few longer-lasting bonds in other populations (Lusseau *et al.* 2006). Similarly, Grevy's zebras and onager have been described as having a similar 'fission-fusion' social organisation, in which males defend access to an area in order to retain access to a group of females. However, the two species showed very different levels of predation risk, food competition and vegetation (Sundaresan *et al.* 2007). Using association networks, Sundaresan *et al.* (2007) found differences in social organisation that were in line with these environmental differences. Zebras were found to former larger groups, with tightly knit cliques, and were more selective about their associates, potentially in response to higher levels of predation risk. Conversely, the onager population had smaller subgroups of a more frequently changing composition that was associated with lower levels of predation and higher visibility (Sundaresan *et al.* 2007).

The higher precision in quantification of social structure using social network metrics is in part due to the use of continuous rather than categorical measures (Kasper and Voelkl 2009). Continuous measurements of social structure are particularly important given the current challenges to the socioecological classification of primate social systems (Janson 2000; Thierry 2008), and are in line with the framework for fission-fusion dynamics that proposes continuous measurements of primate grouping patterns to capture the complexity of primate social systems more adequately (Aureli *et al.* 2008a).

Finally, the social network approach is valuable in the study of fission-fusion dynamics because it allows the identification of individuals that have an important role in the overall structure of the network, and the analysis of the characteristics of these individuals to determine why they have these roles (Krause *et al.* 2007; Sih *et al.* 2009; Sueur *et al.* 2011b). This might be especially important in the study of fission-fusion dynamics, as it helps the understanding of how various subunits of a network maintain cohesion and coordinate group movement (Ramos-Fernández *et al.* 2009; Sueur *et al.* 2011b).

In sum, social network analysis is a particularly promising approach for the study of fission-fusion dynamics and its effects on social relationships, as it provides a quantitative measure of the structure in complex societies, and allows for the identification of patterns, layers and important individuals. Social network analysis gives a finer and more complete picture of social systems, which may be especially important when making comparisons between troops within a population, where differences are likely to be fine-grained. Furthermore, it can give insights into how individual-level strategies may influence troop-level structures.

1.6 Aims of this study

As was described above, the traditional modal classification of primate groups does not take account of intra-specific and temporal variation in grouping patterns, and this has led to a proposal to characterise primate groups by their relative degree of fission-fusion dynamics. It was highlighted that it is not clear if the socioecological model can account for this flexibility in grouping patterns. In other words, it is unclear to what extent fission-fusion dynamics reflect an optimisation to environmental conditions, to what extent individual social preferences affect the structure of primate groups, and if the degree of fission-fusion dynamics impact on the social relationships.

In this thesis these questions are addressed by investigating the grouping patterns and social relationships of olive baboons (*Papio hamadryas anubis*), using a social network approach alongside established statistical methods. Social network analysis allows for the characterisation of a social system as a whole, and for the identification of substructures within that system, while traditional measures allow for analyses over a shorter period, and thus for the investigation of the extent of primate flexibility. This study is the first to quantify the degree of fission-fusion dynamics, and to relate these dynamics to variations in ecology and social relationships.

The study has three major aims:

1) To test if fission-fusion dynamics reflect short-term responses to local ecological conditions

In chapter 3, variation in food availability and predation risk over habitats, seasons, and between troops, is identified, and analysed to determine how these affect the way individuals range in, and use their environment. In chapter 6, the flexibility of olive baboon grouping patterns is investigated; variations in the environment are related to differences in measures of three grouping patterns: party size, party composition change, and spatial cohesion, across habitats, seasons, and between troops. In this chapter, a method for the estimation of fission-fusion dynamics is suggested and applied to olive baboons.

2) To investigate the extent of flexibility in the choice of associates

In chapter 4, association patterns are analysed to investigate if these show a non-random pattern. Following this, a social network approach is used to compare the structure of associations between troops, and across four seasons, to investigate how flexible olive baboon association patterns are. Networks are investigated for substructures of individuals that associated more frequently with each other than with the rest of their troop. These results are related to variation in ecological factors found in chapter 3. The influence of social factors on the structure of association networks is tested.

3) To investigate the effect of fission-fusion dynamics on the nature and maintenance of social relationships

In chapter 5, the complexity of olive baboons social relationships is investigated with a social network approach, by comparing the structure of social networks, and individuals’ positions within networks, that are based on affiliative, agonistic, grooming, and grunting interactions, and the exchanges of grunts. Comparisons are made between-troops, and differences are related to variation in food availability and predation risk found in chapter 3. The influence of social factors on the structure of behavioural networks is also investigated. In addition to the effect of fission-fusion dynamics on the broader structure of social relationships, in chapter 6 the extent of the flexibility in social behaviour is investigated, by relating rates of social behaviours to party size, party composition change, and spatial cohesion.

Olive baboons are an ideal model to address these questions. Olive baboons are generally said to have a cohesive social system; however, they have been observed to form smaller foraging subgroups (Anderson 1981; Henzi and Barrett 2003; Henzi and Barrett 2005; Swedell 2011). To date, the majority of research into the flexibility of primate social groups has focused on the traditional 'fission-fusion societies', that are thought to have a high degree of fission-fusion dynamics. However, to investigate the continuum of primate sociality, there is a clear need for the investigation into grouping patterns of species that are likely to have a relatively low degree of fission-fusion dynamics (Aureli *et al.* 2008a; Coles *et al.* 2012). Furthermore, in the development of standardised estimates that can be used across species, it is important that measurements can pick up the subtle variations in grouping patterns of species with a lower degree of fission-fusion dynamics.

In this study, comparisons will be made not only across seasons, but also between two troops within the same population, allowing testing of the extent of flexibility of grouping patterns. Such a comparative analysis is crucial to the understanding of the relationships between the degree of fission-fusion dynamics, ecology, and social relationships (Aureli *et al.* 2008a). This study population is particularly well-suited to address these questions as some troops, but not others, have been observed to fragment into smaller subgroups in previous studies (Walravens 2005; Ey 2008).

Overall, this study aims to evaluate the degree of flexibility in grouping patterns as a response to variations in environmental conditions, to examine the extent individuals have choice in their associates, and the effect of variations in the degree of fission-fusion dynamics on social relationships. Therefore, this study contributes to the understanding of primate social systems and their relation to the environment.

Chapter 2

Methods

Data were collected on two troops of olive baboons in Gashaka-Gumti National Park, Nigeria, between March 2009 – June 2009 and August 2009 – March 2010. In this chapter, the study species, sites, and troops are described along with information on data collection. A general outline of the social network approach is given, and the statistical analyses used in this study are discussed. More detailed descriptions of specific data collection protocols and analyses are given in the Methods section of each chapter.

2.1 Study species

Baboons are divided into five species: olive baboons (*Papio anubis*), chacma baboons (*Papio ursinus*), yellow baboons (*Papio cynocephalus*), Guinea baboons (*Papio papio*), and Hamadryas baboons (*Papio hamadryas*) (Jolly 2012; Zinner *et al.* 2012). They are found throughout sub-Saharan Africa, occupying a variety of habitats ranging from woodland savannahs, to rain and gallery forests and semi-deserts (Altmann and Alberts 2003; Henzi and Barrett 2003). Olive, chacma, and yellow baboons are often grouped together as 'savannah baboons' (Jolly 1993) because the majority of the populations of these subspecies range in savannah habitats, although they are also found in tropical dry forests, rain forests, and high-altitude bamboo forests (Swedell 2011).

This variation in ecology is thought to underlie the wide range of social structures and mating systems observed among the baboon subspecies (Henzi and Barrett 2003; Maestripieri *et al.* 2007). Hamadryas baboons have a rigid multi-level social structure (Kummer 1968; Colmenares 1992; Henzi and Barrett 2005; Swedell 2011). In this system, the smallest unit is a stable group of a single male with several females and their offspring, the harem or one-male unit (OMU) (Kummer 1968; Colmenares 1992; Henzi and Barrett 2005; Swedell 2011), and it is in this social group in which the majority of mating and social behaviour occurs (Schino *et al.* 1988). Philopatric males form and maintain OMUs through herding of females, and the OMUs of several closely related males join to form a clan (Kummer 1968; Colmenares 1992; Henzi and Barrett 2005; Swedell *et al.* 2011). Several clans may fuse into a band, and several bands make up a troop (Kummer 1968; Colmenares 1992; Henzi and Barrett 2005). Units split and fuse throughout the day; troops often occur at sleeping sites, bands may fission into clans or OMUs during foraging (Kummer 1968).

Savannah baboons live in multi-male, multi-female social groups (Napier and Napier 1967; Smuts 1985; Dunbar 1988; Henzi and Barrett 2005) of about 8 to 200 individuals (Napier and Napier 1967), although under certain conditions, *e.g.* when population density and predation pressure are low, females may form small groups with a single male (Whiten *et al.* 1991; Swedell 2011). As female savannah baboons remain in their natal troop (Strum and Western 1982; Smuts 1985), savannah baboon troops are female-bonded, and females have stable linear dominance hierarchies both within and between matrilines (Napier and Napier 1967; Barton and Whiten 1993; Barton *et al.* 1996). Individual food intake rates are in part determined by these dominance relationships (Barton and Whiten 1993), and these affect individual females' fertility (Barton 1993). Male savannah baboons emigrate to a new troop after maturation, usually when they are around 10 years old (Smuts 1985). Male dominance rank is often determined by time resident in the troop, and is less stable than female rank (Smuts 1985). Savannah baboons have multi-male, multi-female mating systems, and breed throughout the year (Smuts 1985; Higham *et al.* 2008). Females typically mate with more than one male per oestrus cycle (Domb and Pagel 2001) and show sexual swellings around the fertile period. Males and females form consortships during the latter's receptive period, lasting from several hours to several days (Hall and DeVore 1965), during which much of their behaviour is synchronised (Seyfarth 1978). It has been suggested that sexual swellings prompt males to form a consortship with a female (Higham *et al.* 2008). In addition to consortships, females may also form long-lasting social relationships ('friendships') with one or two males in their troop. These involve mutual grooming, joint foraging and travelling, and defence against aggression from other troop members (Smuts 1983; Smuts 1985; Lemasson *et al.* 2008; Swedell 2011). It has been suggested that these friendships are a strategy against infanticide (Collins *et al.* 1984). Savannah baboon troops are generally cohesive, but may break into smaller foraging parties of variable composition during the day (Anderson 1981; Henzi and Barrett 2003; Henzi and Barrett 2005; Swedell 2011) particularly when feeding in marginal habitats (Barton *et al.* 1996). Subtroops, in which membership is consistent, and which may last for up to several days, have been observed in chacma baboons, and are thought to be a strategy to cope with food scarcity (Anderson 1981).

Although relatively little is known about the social and mating system of the West-African Guinea baboon (Henzi and Barrett 2003; Patzelt *et al.* 2011), it has been suggested that it falls somewhere between the cohesion of savannah baboons troops, and the stable subtrooping of Hamadryas baboons. Several studies suggest that Guinea baboon groups are not stable, and that they break into smaller subgroups throughout the day, but these subgroups vary in composition and thus do not show the same rigid modularity as in Hamadryas baboons (Swedell 2011). It has been noted that Guinea baboons form large troops at sleeping sites, but break into smaller units whilst foraging or resting (Anderson and McGrew 1984; Henzi and Barrett 2003). A recent study has shown that these smaller units are unlike the Hamadryas OMUs in which membership is consistent, and instead that the composition of these smaller units is variable (Patzelt *et al.* 2011). It was suggested that the social organisation of the Guinea baboon is distinct from other baboon subspecies (Patzelt *et al.* 2011), although it is not clear to what extent the subgroups of Guinea baboons differ from the foraging subgroups of savannah baboons.

Baboons are opportunistic, selective omnivores that eat a wide range of foods including grasses, fruits, roots, leaves, flowers, sap, insects and vertebrates

(Altmann and Altmann 1970; Whiten *et al.* 1991). Although there is little direct competition for these foods, subtle competition does occur, for example through supplants at feeding sites (Altmann and Altmann 1970). Additionally, baboons have cheek pouches which are used to temporarily store food away from conspecifics (Hayes *et al.* 1992), suggesting that there is at least some within-group feeding competition.

The size of baboon home ranges can vary widely; ranges from 4.7–43.75 km^2 have been observed (Milton and May 1976; Mitani and Rodman 1979; Harvey and Clutton-Brock 1981; Isbell 1991; Barton *et al.* 1992; Henzi *et al.* 1992; Swedell 2002). Differences in habitat and food quality are important factors underlying this variation in range sizes (Dunbar 1988; Strier 2003a); baboons in forested habitat for example generally have smaller ranges than baboons in savannah or desert habitats (Dunbar 1988). However, troop size and the spatiotemporal distribution of food are also important (Dunbar 1988), and access to water and safe sleeping sites may further limit baboons ranges (Altmann and Altmann 1970; Rowell 1972).

Olive baboons have the most extensive distribution of all the subspecies, ranging from Sierra Leone to Sudan, inhabiting a variety of habitats, including woodland savannahs, evergreen forests, deserts (Jolly 1993) and areas close to human habitation (Naughton-Treves *et al.* 1998). This wide range is in part due to the olive baboon's ability to obtain food from nearly all strata of the environment and their flexible foraging strategies which have enabled them to adapt to a wide range of habitats (Whiten *et al.* 1991). The location of the study troops falls in the southern edge of the olive baboon distribution (see section

2.2). Compared to other savannah baboons, olive baboon troops are generally small, with troops usually ranging between 20-100 individuals (Ransom 1981). Although infanticide is rare in olive baboons, friendships between males and females have been observed (Altmann 1980; Smuts 1985). It has been suggested that friendships in this subspecies may be a strategy against forms of *non-lethal* harassment from conspecifics (Altmann 1980; Smuts 1985; Lemasson *et al.* 2008).

The study population makes for an excellent model to study fission-fusion dynamics, as foraging subgroups have been observed here in previous studies (Walravens 2005; Ey 2008).

2.2 Study sites

Gashaka-Gumti National Park (GGNP) is located in the mountainous regions of north-eastern Nigeria (Figure 2.1) bordered to the west by Cameroon. The park covers an area of 6731 km^2 and is the largest national park in Nigeria (Dunn 1994; Sommer *et al.* 2004; Sommer and Ross 2011). The northern sector of the park (Gumti) extends into Adamawa state and is characterised by northern Guinea savannah, with grasslands and a few, short trees. Savannah animals, such as hyena, wild dog, antelope and eland are found in this sector of the park (Dunn 1999). The southern sector (Gashaka) falls within Taraba state, and includes a diverse range of altitudes, and hence is characterised by a mosaic of woodland savannah, lowland and gallery forest, montane forest, and grassland (Dunn 1999; Sommer and Ross 2011). The Gashaka sector harbours a wide variety of wildlife, including ungulates, such as bushbuck, waterbuck, duikers, buffalo, warthog, red river hog, and giant forest hog; carnivores such as civets, golden cat, and spotted leopard; and several species of primates: tantalus monkey, mona monkey, putty-nose monkey, patas monkey, black-and-white colobus, olive baboon, and the Nigerian chimpanzee (Dunn 1999; Sommer and Ross 2011). Numerous rivers are found in the park throughout the year, and the forests in GGNP are important catchment areas for the river Benue (Dunn 1994; Sommer and Ross 2011).

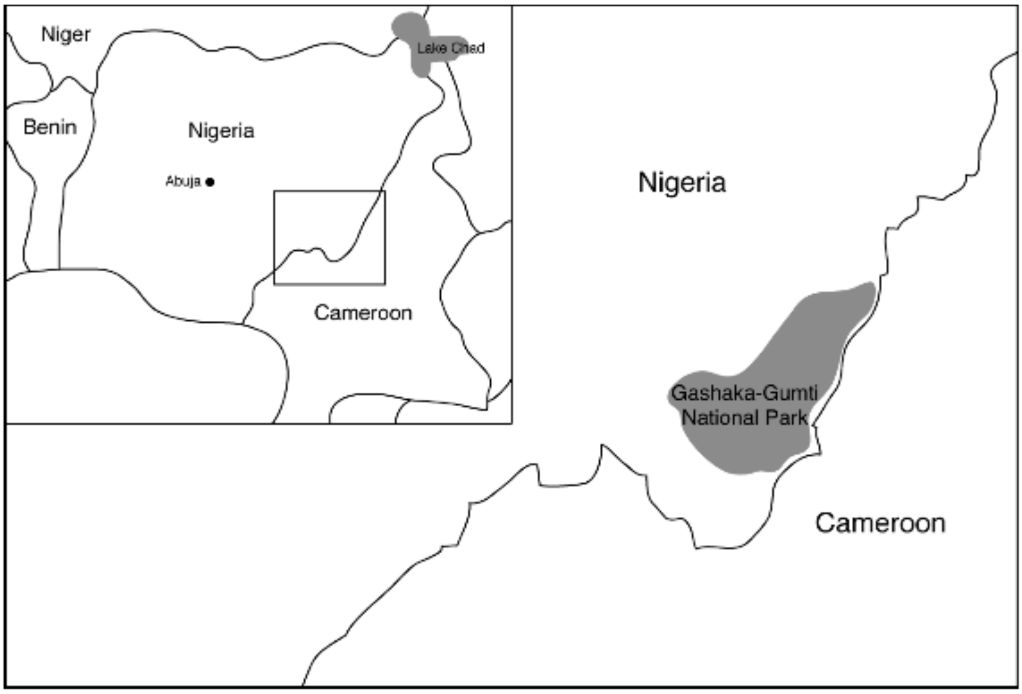


Figure 2.1: Location of Gashaka-Gumti National Park (adapted from Rogge 2009).

Predators of baboons include leopards, lions, hyenas, eagles, and jackals (Altmann and Altmann 1970; Cowlishaw 1994). However, compared to the better-studied East African olive baboon populations, the density of predators in West Africa is generally much lower (Kunz and Linsenmair 2008). This is thought to play an important role in the small troop sizes for olive baboons found in the GGNP population (Warren 2003; Kunz and Linsenmair 2008; Higham *et al.* 2009). Consequently, within-troop competition may be relatively low in the study population.

Baboon troops were studied at two sites approximately 11 km apart. Locations of the study sites are shown in Figure 2.2. The Gamgam troop ranged just outside the National Park, near Gashaka village, along the river Gamgam (7°21’ 25.9”N 11°29’ 50.6”E). The Kwano troop ranged within the southern sector of GGNP around the abandoned settlement Kwano (7°19’ 49.3”N 11°35’ 00.0”E).

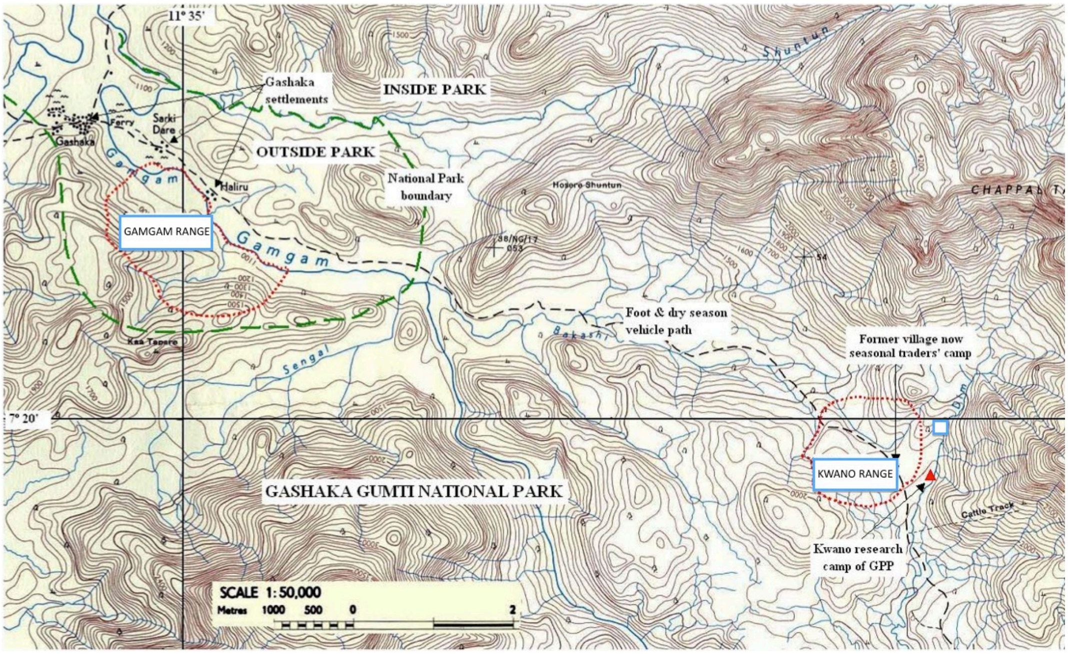


Figure 2.2: Location of the two study sites (adapted from Warren 2003).

2.2.1 Climate

Although GGNP falls within the Guinea zone, the average annual rainfall of 1935 mm is higher than normally found within this zone (Sommer and Ross 2011), and the study sites are amongst the wettest baboon study sites (Higham *et al.* 2009). The weather fluctuates between a wet season (15 April – 14 October) and a dry season (15 October – 14 April) (Schöning *et al.* 2007), in which very little rain falls and the dry and dusty Harmattan wind blows from the Sahara. With an average mean temperature of 26.4°C, the study site is also relatively warm compared to other baboon field sites (Higham *et al.* 2009).

Throughout this study the wet and the dry season were further divided into three-month periods to allow a more fine-grained analysis, as ecological factors such as vegetation cover or fruit availability are likely to differ between the beginning and the end of these seasons. The definition of the wet and dry season are taken from a previous study at this site (Schöning *et al.* 2007), and the 'beginning' of a season was defined as the first three months; the 'end' of a season the last three months. The seasonal periods are as follows:

- Beginning of the wet season (BEG WET): 15 April 2009 – 14 July 2009
- End of the wet season (END WET): 15 July 2009 – 14 October 2009
- Beginning of the dry season (BEG DRY): 15 October 2009 – 14 January 2010
- End of the dry season (END DRY): 15 January 2010 – 3 March 2010

Weather data for the Gamgam troop were collected at the Gashaka field station (7°22' 09.0"N 11°29 40.0"E), which is approximately 1 km from the home range of the Gamgam troop. For the Kwano troop, weather data were recorded at the Kwano field station (7°19’ 49.3”N 11°35’ 00.0”E), which is within the home range of the Kwano troop. At both sites, researchers and staff recorded data at 19:00 each day. In Table 2.1 annual weather data for both troops are shown, and it should be noted that these data were collected during 2009, whereas the study period ran from March 2009 - March 2010. Annual data are given here for ease of interpretation. The minimum, maximum, and mean monthly temperatures are given in Figure 2.3, along with the average monthly humidity and total monthly rainfall. None of these weather variables differed significantly between the two study sites (paired samples t-test: Gamgam mean temp - Kwano mean temp: t = 1.617, df=11, p=0.134; Gamgam humidity – Kwano humidity: t = 0.68, df = 11, p = 0.947; Gamgam rainfall – Kwano rainfall: t = -0.381, df = 11, p = 0.711).

Table 2.1: Annual mean weather data for the Gamgam and Kwano sites in 2009. The mean temperature was calculated from the average daily minimum and maximum temperature over the entire year.

	Absolute min temperature (°C)	Absolute max temperature (°C)	Mean temp (°C)	Total annual rainfall (mm)	Mean humidity (%)
Gamgam	17.9	39.3	26.9 ± 1.66	1953	73
Kwano	17.0	36.5	26.5 ± 1.24	2025	73

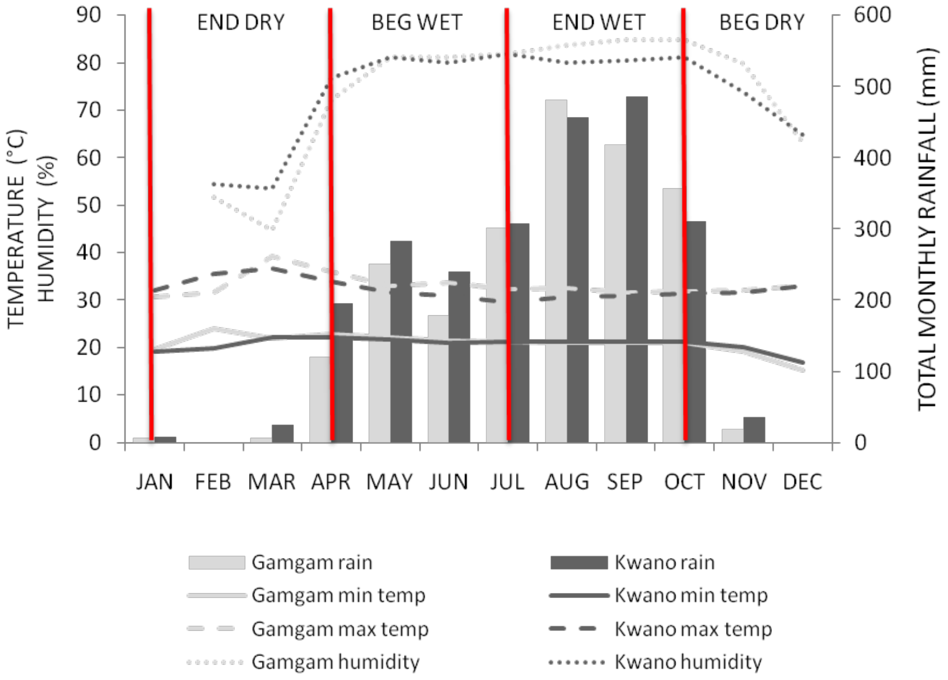


Figure 2.3: Weather at the Gamgam and Kwano field sites in 2009. Vertical lines indicate the delineation of the seasons as used in this study.

2.2.2 Habitat types

Both study sites contain a mosaic of habitat types, including southern Guinea savannah, lowland forest and gallery forest. Southern Guinea savannah (hereafter referred to as Guinea savannah or GS) areas are characterised by coarse grasses that can grow up to 3m tall, woody climbers, and small trees (Dunn 1999). Much of this Guinea savannah habitat is thought to be the result of anthropogenic influences, such as annual burning of grasses and the grazing of cattle, both within and outside the National Park (Sommer and Ross 2011). Trees are often small in this habitat because of the burning of grasses. Due to the abundant rainfall at GGNP, areas of Guinea savannah are interspersed with patches of lowland forest. In the lowland forest, the canopy is formed by trees between 15-35m tall, with trees over 40m rising above this canopy (Dunn 1999). Trees between 2-8m tall make up the understory. Gallery forest is found along the numerous seasonal streams and permanent rivers (Dunn 1999). For further definitions of habitat types see Table 2.2.

Table 2.2: Definitions of habitat types used in this study. Adapted from Warren 2003.

Habitat type	**Definition**
Guinea savannah (GS)	< 50% tree cover Dominant tree species Bakurehi (fulfulde) / kafaffago (Hausa) *Uapaca togoensis* Area subject to seasonal burning
Burned Guinea savannah (BGS)	< 50% tree cover Dominant tree species Bakurehi (fulfulde) / kafaffago (Hausa) *Uapaca togoensis* No plants present due to seasonal burning
Lowland forest (LF)	75-100% tree cover with continuous canopy Dominant species from Fabaceae, Sterculiaceae, Apocynaceae & Moraceae families
Gallery forest (GF)	75-100% tree cover Strip of forest 10-200 m wide, along permanent or seasonal watercourses in an area where the climax vegetation was GS
Agricultural land (AL)	> 90% crop cover Maize, cassava, banana, mango, oil palm, yam, rice, sweet potatoes and groundnuts
Elephant grass (EG)	100% cover of elephant grass *Panicum maximum*
Palm forest (PF)	>75% of tree cover consists of oil palms *Elaus guineensis*
Mango forest (MF)	>75% of tree cover consists of mango trees *Mangifera indica*

The home range of the Gamgam troop largely consists of Guinea savannah, with smaller patches of lowland forest and strips of gallery forest along streams that drain into the river Gamgam (Warren 2003). Two additional habitat types are found in the Gamgam site along the river Gamgam. Firstly, elephant grass (*Panicum maximum*) occurs naturally in the river plains, and can grow up to several meters high. Areas with this type of vegetation are defined as 'elephant grass'. Secondly, large areas along the river are cleared of elephant grass by local people and are used as farms. Crops that are grown on these farms include maize, cassava, banana, mango, oil palm, yam, rice, sweet potatoes and groundnuts. A previous study at this site found that the troop raided crops on 57% of days when crops were growing in the fields, and that animals may get up to 50% of their daily nutritional requirements from crops (Warren 2003). Frequently, farmers remained at their fields to protect their crops against pests, and farmers reacted to about half of the raids of the Gamgam troop by shouting, throwing stones, or chasing the troop (Warren 2003). The Gamgam troop therefore frequently has contact with humans. These areas are labelled as 'agricultural land'.

The Kwano home range contains a greater proportion of forested habitat but is devoid of agricultural land (Warren 2003). The Kwano troop is thus entirely wild feeding and has much less contact with humans, although due to the presence of an ancient footpath through the Kwano home range, contact with humans is not completely absent. At the Kwano site there are two small areas that contain a high density of introduced species, mango (*Mangifera indaca*) and oil palm (*Elaus guineansis*) that were cultivated here before the national park was established. These areas are referred to as the mango forest and the palm forest, and are treated as separate habitat types (see Table 2.2).

In all, compared to other baboon study sites, GGNP is unusual because of the relatively low density of predators, the relatively hot and wet climate, and the mosaic of habitats, which includes dense forests. The mosaic particularly makes this an excellent site for the study of fission-fusion dynamics, as it is possible to test if troops adjust grouping patterns to the habitat types. Furthermore, the inclusion of dense forest is of interest as chimpanzees, a species thought to have a high degree of fission-fusion dynamics, range in this habitat (Sommer *et al.* 2004).

2.3 Study troops and subjects

Study troops were established in 2000 by Y. Warren (Warren 2003), and have been studied by researchers and field staff from the Gashaka Primate Project (GPP) continuously since then. For the current study, baboons were fully habituated to human observers and could be followed at a 2-6m distance.

Kinship and age were estimated from troop demography records that have been kept since 2000, and consequently the exact age or kinship relations are not known for individuals that were born before this time. Adult and subadult males and females were the focal subjects of this study.

The composition of troops changed over the study period. The mean counts per age/sex class are presented in Table 2.3. The definitions of these age/sex classes are given in Table 2.4. The Gamgam troop was smaller than the Kwano troop, with a mean group count of 19 (range 18-20) and was more stable in composition over the study period; one infant was born, and one became a juvenile. A total of 9 animals were focal subjects in the Gamgam troop. The Kwano troop was larger with a mean group count of 34 individuals (31-37), but troop composition was more variable: here, six infants were born, nine baboons, including four focal subjects, disappeared during the study period. A total of 20 animals were focal subjects in the Kwano troop. One recently immigrated adult male (DMN) was excluded from focal follows, as initially he was not fully habituated to observers and he disappeared later in the study period. In Table 2.5 the kinship relations for individuals in both troops are given (if known) along with the age/sex class for each individual, and additionally for males how long they have been resident in the troop.

Table 2.3: Mean number of animals per age/sex class for the Gamgam and Kwano troop during the study period. The range is given in brackets, when no range is given, the number of animals did not change throughout the study period.

	Adult female	Adult male	Subadult female	Subadult male	Juvenile	Infant	Black infant	TOTAL
Gamgam	5	1 (1-2)	0 (0-1)	2	9 (9-10)	2 (1-3)	2 (1-2)	19 (18-20)
Kwano	10 (9-10)	6 (5-8)	2 (1-2)	1 (0-1)	12 (11-12)	2 (1-3)	2 (0-3)	34 (31-37)

Table 2.4: Age/sex classification of olive baboons (adapted from Warren 2003).

Class	**Age**	**Definition**
Black infant	0 – 7 months	Black coat, pink skin from birth. Skin changes to grey around five months. Ventral on mother from birth, dorsal around four months.
Infant	7 months to 2 years	Coat is the adult colour. Nurses occasionally.
Juvenile female	2 – 4 years	Not in association with mother for majority of time. Fully weaned.
Subadult female	4 -6 years	Gradually gains height of adult female, onset of menarche. Tight red genital swellings.
Adult female	6-8 + years	Usually have offspring, have longer nipples, which turn from pink to grey after nursing. Soft pale swellings. Nulliparous females considered adults if show regular sexual cycle or engage in consortships.
Juvenile male	2 – 6 years	Not in association with mother for majority of time. Fully weaned. Scrotum changes from pink to grey at 2-3 years. After 5 years of age, gain height of adult female, scrotum enlarges, canines extend beyond tooth row.
Subadult male	6-10 years	Larger than adult female, growth spurt continues mantle and shoulder hair grows. May migrate in and out of group.
Adult male	10 + years	Long sharp canines, main of hair around neck and shoulders. About twice size of adult female. Unbroken ischial callosities with a slightly raised centre line below tail.

Table 2.5: Focal subjects in the Gamgam & Kwano troops. Age classes were estimated from demographic records kept since 2000. For males the time they immigrated into the troop is also given. AF = adult female; AM = adult male; SF = subadult female; SM = subadult male.

	ID	Age / sex class	Males resident since
Gamgam	BUW	AF	
	MMK	AF	
	KAN	AF	
	GLO	SF ‡	
	MMW	AF	
	AGU	SM	Birth
	STR	AF	
	SAB	SM	Birth
	DWN	AM	February 2009
Kwano	BRA	AF	
	DRK	AF	
	FDI	AF	
	KYE	AF	
	LDI	AF	
	KRM †	SF	
	LMI	AF	
	MOM	AF	
	SAD	AF	
	TJL †	AF	
	RAB	SF	
	YMK	AF	
	DGO †	AM	Before December 2006
	DOR †	AM	Before December 2006
	SND	AM	Before December 2006
	KSA	AM	December 2006
	SMA	AM	December 2006
	BON	AM ‡	Birth
	DRN	AM	January 2009
	DLI	AM	January 2009

†) disappeared during the study period

‡) changed to this age class during the study period

2.4 Data collection

A pilot study was conducted in February 2009, in which the identity of the individuals in the study troops was learned, the data collection protocol and equipment were tested, and the sites for ecological sampling were set up. Behavioural and ecological data were collected from March 2009 – June 2009 and August 2009 – March 2010. During July 2009 no behavioural data were collected, although a research assistant did collect ecological data during this period. Data collection alternated weekly between the two troops.

Throughout the study period behavioural data were collected daily by the research assistant and researcher, with the same data being collected simultaneously on two focal animals. Research assistants received training and data were only included once inter-observer reliability tests indicated that observations were 85% consistent between observers. These reliability tests were conducted monthly throughout the study period using the Observer software (Noldus Information Technology 2008). One day a week I monitored the phenology of plant and tree species, while the research assistant continued behavioural data collection. Predation risk and plot measurements were taken for two weeks every three months, and again, during this time the research assistant continued with the collection of behavioural data. A break down of the data collection schedule is given in Table 2.6. Further details of data collection are given below and in the relevant chapters.

Table 2.6: Break down of the types of data collected, the frequency of data collection, and who collected the data. Shaded areas indicate data that were collected both by the research assistant and the researcher. Unshaded areas indicate data collected by the researcher alone.

Data type	Data			Chapter
Behavioural data	Focal follows (daily)	Behavioural observations (4 hours)	Activity states	3
			Social interactions	5 & 6
		Aggression & displacements non-focal animals (*ad libitum*)		4 & 5
		Scans (hourly)	ID & activity of baboons	4
			Party spread measurements	6
			Habitat type	6
		GPS location focal (15 minutes)		6
		GPS location drinking sites (*ad libitum*)		3
		GPS location sleeping sites (*ad libitum*)		3
Reproductive data	Female reproductive state (daily)			4
Ecological data	Phenology (weekly)			3
	Predation risk (quarterly)	Habitat visibility		3
		Distance to nearest refuge		3
	Plots (quarterly)	Size of food plants & trees		3
		Density of food plants & trees		3

2.4.1 Behavioural sampling

Behavioural data were collected each day over an eight-hour period. The start of data collection was alternated between days; on early days data were collected between 06:00 – 14:00, on late days this was between 10:00 – 18:00. Behavioural data were collected through focal-animal sampling (Altmann 1974) using a Psion handheld computer in combination with The Observer XT software version 8.0 (Noldus Information Noldus Information Technology 2008). Four-hour focal samples were conducted on all adults and subadults in the troops. To determine the focal subjects for a given day, firstly the required combination of the age/sex class of subjects was determined. This was to ensure an even sample was taken across the combinations of age/sex classes (*e.g.* adult female – subadult female, adult female – adult male) for the GPS locations simultaneously recorded for both focals (see below). Focal subjects from a particular age/sex class were then chosen using a random number generator for Windows (Itneccas 2008). Individuals were not re-sampled until all individuals within their age/sex class had been sampled. During focal observations the activity state of the focal animal (see Table 2.7 for definitions of activity states) was recorded continuously. Additionally, all the social interactions (*i.e.* affiliative, agonistic, submissive behaviours and vocalisations) of the focal animal were recorded as events, along with the identity of the social partner and the direction of the behaviour. Definitions of each social interaction that was recorded are given in Table 2.8. Thus, these social interactions were recorded both as state and as point events. A total of 375 hours of behavioural data were collected for the Gamgam troop, and 548 hours for the Kwano troop. These data were used to generate behavioural networks (chapter 5) and to calculate the rates of behaviours (chapter 6). In addition, some behavioural data were recorded *ad libitum;* these were displacements and aggression not involving the focal animal, which were used to determine the dominance hierarchy.

A scan sample (Altmann 1974) was taken every hour, in which the identity of each baboon, their activity, the spread of the troop and the habitat the majority of the troop was in, were recorded. For five minutes before each scan, researchers walked around the area to locate baboons. A total of 319 scans were collected for the Gamgam troop, and 467 for the Kwano troop. Individuals that were seen together in a scan were considered to be associated. The definition of an association used here broader than an association based on individuals being in visual contact. The method used here may be a more appropriate estimation of parties and associations at these sites; the terrain at GGNP is very uneven and large parts are forested, and therefore using a purely visual definition of associations may underestimate the number of individuals in a party. These scan data were used to calculate the Twice Weight Index (see below) that was used to generate association networks (chapter 4) and to calculate estimates of fission-fusion dynamics (chapter 6).

The locations of the two focal animals were recorded every 15 minutes using a handheld GPS (Garmin GPSmap 60CSx). These GPS locations were used to estimate home ranges and day journey lengths (chapter 3), and to calculate the distances between focal animals as an estimate of spatial cohesion (chapter 6). GPS readings were also taken at sleeping and drinking sites.

Further details on behavioural data collection methods are given in the relevant chapters.

Table 2.7: Ethogram showing the activity states along with behaviours included and their definitions. Definitions were adapted from Warren (2003) and Higham (2006).

Activity state	**Behaviour**	**Description**
Feed & forage	Drink	Drinking.
	Feed & forage	Movements of more than 1 1/2 body lengths into or within forage plants and picking, processing and handling foodstuffs. Includes sweeping through leaf litter & turning over rocks in search of invertebrates.
Rest	Cheek pouch	Chewing or manipulation of food items removed from the cheek pouches.
	Nursing	Nursing a dependent offspring.
	Rest	Inactivity with eyes open, or individual maintenance, *i.e.* self-grooming, urination, or defecation.
	Sleep	Inactivity with eyes closed and/or lying down.
Social	Aggression	Interacting aggressively with other individuals (i.e. agonistic behaviours Table 2.8).
	Grooming	Engaged in searching through the fur of another individual using the hands or mouth and picking out items.
	Play	Engaged in play with another individual.
	Sex	Copulation.
	Social	Engaged in social activity that is not agonistic, grooming, play, submissive or sexual behaviour (i.e. affiliative behaviours Table 2.8).
	Submissive	Displaying submissive behaviours (i.e. submissive behaviours Table 2.8).
Travel	Travel	Movements of more than 1 1/2 body lengths, walking, running, climbing & leaping.
Other	Other	Any activities not included in other categories.
Out of sight	Out of sight	Focal animal is outside of the observer's field of view.

Table 2.8: Ethogram showing the behavioural interactions that were recorded as events along with their definitions. Definitions were adapted from Kummer (Kummer 1968 (1968), Rowell (1972), Ransom (1981), Byrne (1981; Byrne 2000), Cheney, Seyfarth & Palombit (1996), and Cheney, Seyfarth & Silk (Cheney *et al.* 1995).

Behaviour	**Description**
Submissive interactions	
Avoid	When moving an individual alters their path to move around another individual.
Avoid eye contact	Gaze fixed on ground, head turned sideways.
Crouch	Flexing and adducting of limbs / lies motionless on ground.
Displace	Individual is approached by another individual and leaves.
Flee	Walk or run away from another individual.
Glance	Repeated sideway glances at an approaching animal.
Grin	Retracted corners of mouth and teeth clenched.
Shoulder shrug	Bending the spine sideways, often when seated.
Tail up	Tail held stiffly upright.
Affiliative interactions	
Present rear	Presenting of hindquarters to another individual.
Inspect after present	Visual and / or tactile inspection of the anal or genital region after the other individual presented.
Approach	An individual moves to within one meter and remains for two seconds or more.
Grasp rear	Touching of hindquarters following presenting.
Groom	Engaged in searching through the fur of another individual using the hands or mouth and picking out items.
Mount	One individual approaches another individual from behind and rubs genitals near the ano-genital region of the other.
Grunt	Short, quiet, low- pitched, and harmonically rich call.
Touch	Makes physical contact with another animal.
Touch genitals	Makes physical contact with the genitals of another animal.
Friendly face	Narrowed eyes and ears flattened.
Offering hand	Offering or holding of hands between two individuals.
Smell hands	Smelling of hands after the individual touched another individual.
Lip smack	Lips are protruded, then smacked together repeatedly.
Tongue protrusion	Tongue sticking out from between lips.
Nuzzle	Two individuals rubbing muzzles against each other.
Embrace	Wrap one or both arms around the trunk of another individual.
Present for grooming	Presenting of a body part for grooming.

Ethogram (continued)

Agonistic interactions

Contact aggression	Aggressive interactions with physical contact.
Bite	Biting another individual.
Hit	Brief and forceful physical contact using the hand or arm.
Non-contact aggression	Aggressive interactions without physical contact.
Tooth grind	Chewing and grinding movement of the jaws, with strong side movements. Noises produced by tongue and teeth.
Open-mouth face	Dropping of the lower jaw with the mouth in oval shape; the corners of the mouth are not pulled back.
Ears pulled back	Ears flattened to the side of the head.
Lunge	Leaping or jumping towards another individual.
Chase	One individual in the running pursuit of another individual.
Stare	Prolonged gaze towards another individual.
Eyebrow raise	Raising of eyebrows.
Head bob	Rapid raising of the head and trunk.
Rubbing	Rubbing muzzle or chest on ground or tree trunk.
Ground slap	Striking of the ground with hand, often with noise.
Big yawn	The mouth is opened to expose canines and gums.

Vocalisations

Alarm bark	Harsh, short vocalisation. Often paired with head bobbing
Contact bark	Loud and tonal vocalisations, given by animals separated from the rest of the group or from particular individuals.
Grunt exchange	More than two grunts, exchanged between two animals.
Pant	Loud two-syllable vocalisation, first inhaled 'huh', second exhaled 'huh'.
Roar grunt	Deep pitch, low humming by adult males. Often preceding a wahoo bark.
Scream	Loud, high pitched, continuous vocalisation.
Wahoo bark	Loud, two-syllable call that occurs in bouts of 1-20 minutes in length. Given by adult males in response to predators, distress, or to wahoos of neighbouring groups, or may be spontaneous.

2.4.2 Female reproductive state

The reproductive state of females was recorded daily using a classification that was developed particularly for baboons at GGNP (Higham 2006). Definitions are given in Table 2.9. In this study, females in the state S0 – S3 were merged under 'cycling females'.

2.4.3 Ecological sampling

Phenology data were collected once a week (*i.e.* for each troop every two weeks), whereas the density and size of plants and trees were recorded every three months for both troop's ranges (see section 2.4.3.1 & 2.4.3.2 for details on methods). These data were combined to calculate the food availability index. Predation risk was estimated every three months (see section 2.4.3.4 for details on methods). Ecological variables are analysed in chapter 3, and results are used in the following chapters.

Table 2.9: Definitions of female reproductive states. Adapted from Higham (2006).

State	**Description**
Lactation	Presence of suckling infant
Pregnant	Inferred from continued post-cycle absence of swelling
S0	No sexual swelling but cycling
S1	Small sexual swelling of the ano-genital area
S2	Large swelling of the ano-genital area accompanied by small swelling of the para-callosal skin
S3	Large swelling of the ano-genital area and the para-callosal skin

2.4.3.1 Density and size of food plants and trees

The density and size of trees were measured every three months by plot methods (Ganzhorn 2003). The locations of plots were determined by creating random points within each habitat type using the Hawth's tool extension (Beyer 2004) for ArcGIS. These random points formed the south-western corner of the plots. The size of plots was dependent on the height of trees within that particular habitat type (Ganzhorn 2003); plots within the gallery forest, lowland forest, mango forest, and palm forest were each 200 m^2; plots in Guinea savannah and agricultural land were 100 m^2 each; plots in areas with elephant grass were 2 m^2 each. Five plots were established in each habitat type within both home ranges. A total of 100 plot measurements were taken in the home range of each troop. Within each plot, for trees with a DBH larger than 10 cm, the species and DBH was recorded. DBH of trees was measured at a height of 1.3 metres; when trees had buttresses, DBH was measured above these. For smaller plants, the diameter was measured at the middle of the stem. The density was calculated for each food species in each habitat type as the number of trees per hectare. In both troops, several species were not found in any of the plot measurements but were known to be present within the home range, as these species were monitored in the phenology walks (see below). As five specimens of each species were monitored in the phenology walk, at least five of trees of these species were known to be present in the home range. Therefore, in the cases were species were not observed in the plots, a density of five trees over the whole home range was entered (*i.e.* Gamgam 5/252 hectare = 0.198; Kwano 5/189 hectare = 0.026).

2.4.3.2 Phenology of food plants and trees

The phenology of five specimens of each tree and plant species that were previously identified (Warren 2003) as core staples for these troops (*i.e.* troops spent at least 1% of their monthly foraging time on these species), were monitored every two weeks. For the Gamgam troop, three of the species previously identified as core staples could no longer be found within the home range (*i.e. Diospyros mesiliformis*, *Ficus sycamorous*, *Xylopia* spp). In total 32 species (160 specimens) were monitored within the Gamgam home range. In the Kwano troop, 23 species were monitored, although for one species only two specimens could be found; therefore a total of 112 specimens were monitored for the Kwano troop. Every two weeks the proportions of young and mature leaves were recorded for each specimen, along with the number of flowers, ripe and unripe fruits, and the number of seeds, to determine the percentage of trees or plants that presented important food items at a given period. Throughout this thesis, when 'leaves' are discussed, this refers to 'young leaves' in which the protein-to-fibre ratio is high (Milton 1987).

2.4.3.3 Estimation of food availability

To estimate the availability of food within the home range of each troop, data collected by the methods outlined above were combined in a twice-monthly food availability index (FAI) as follows:

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

Were D_k is the tree density per hectare for species *k*, B_k is the mean diameter at breast height (DBH) for species *k* of trees >10 cm and P_{km} is the percentage of observed trees or plants of species *k* that present important food items for that period (*m*) (Chapman *et al.* 1992). The FAI was summed over all species in each habitat type and using the proportion of each habitat type within the home ranges (see section 3.2.1), a FAI value was calculated for each food item over the home range. The FAI values were then summed over food classes (*i.e.* fruit, leaves, seeds, flowers, and 'other') to give an indication of the abundance in the home range of each type of food. For between-troop comparisons, these FAI were divided by the home range areas, to give a per hectare value. Agricultural species were not entered into the FAI calculations, as the availability of these species may not be comparable to that of wild species. For the Gamgam troop, a total of 28 species were entered into the FAI. For the Kwano troop, this was a total of 23 species.

2.4.3.4 Estimation of predation risk

Predation represents a serious threat for many primates and can have a great impact on their behaviour. It has, however, been difficult to measure the threat of predation that primates experience. For example, estimating predation risk by measuring the mortality rates due to predation is not likely to give an accurate indication of the pressures primates are under, as these mortality rates only measure predation *after* anti-predator strategies (Cowlishaw 1994; Hill and Dunbar 1998). To determine how the threat of predation influences primate behaviour it is therefore important to have a measure of this full risk, including those animals that managed to avoid predation through anti-predator strategies. Predation risk has also been estimated through measuring primate anti-predator behaviour, such as vigilance. However, these behavioural measures may be problematic, as behaviours are often not specific to anti-predator behaviour (Cowlishaw 1997c; Cowlishaw 1997a). Similarly, the density of predators may be problematic as a measure of predation risk, as animals react to the conditions that facilitate predator attack, rather than the presence of predators itself (Hill and Cowlishaw 2002), and animals may still show anti-predator behaviour after a predator has become extinct (Cowlishaw 1997c). However, because of animals' reaction to environmental conditions that facilitate predation, it is possible to identify the ecological variables that underlie this perception of risk (Cowlishaw 1997c; Cowlishaw 1997b; Hill and Weingrill 2007) and characterise habitats accordingly. This method of estimating predation risk through habitat physiognomy has been developed over the past two decades (Boesch 1991; Cowlishaw 1997c; Cowlishaw 1997b; Cowlishaw 1998; Enstam 2007; Hill and Weingrill 2007).

The perceived risk of predation depends both on the likelihood of attack and on the likelihood of capture (Cowlishaw 1997c; Cowlishaw 1997b; Hill and Weingrill 2007); therefore in this study predation risk was split into the risk of attack and the risk of capture following attack (Cowlishaw 1997c). Leopards (*Panthera pardus*) are the most common predator for baboons (Altmann 1980; Cowlishaw 1994; Cowlishaw 1997c) and are found in Gashaka-Gumti National Park (Sommer and Ross 2011). During the study period, leopard footprints were found and a leopard was sighted by a researcher, suggesting that, although rare, these predators still exist in the study area.

Because leopards stalk and ambush their prey, their hunting success is dependent on their ability to get close enough to their prey without being detected (Cowlishaw 1997c). Typically, leopards need an ambush distance between 5-10 metres (Cowlishaw 1997c). Habitat types that provide more cover are thus more risky for baboons as leopards are most successful in attacking prey here (Cowlishaw 1997c). Open habitats are safer habitats for baboons, as they are more likely to detect a leopard before it reaches the distance needed for a successful ambush. The risk of attack was measured as the proportion of locations at which visibility fell below this ambush distance, which was defined as 10 metres (following Cowlishaw 1997c), thus facilitating a predator attack.

The risk of capture was determined through measuring the distance to a suitable refuge from a leopard, in relation to habitat visibility and the velocities of predator and prey (Cowlishaw 1997c). In order to remain safe, baboons need to stay within a certain distance of a refuge. This distance depends both on the visibility in a habitat and the velocities of predator (v_{pred}) and prey (v_{prey}), and is determined as follows:

$$R_{\max} = d_{vis}(k - 1)$$

Where d_{vis} is the median visibility in a habitat type, and $k = v_{pred} / (v_{pred} - v_{prey})$ (Cowlishaw 1997c). Following Cowlishaw (1997c), baboon velocity (v_{prey}) was set at 4.0 m/sec; leopard velocity (v_{pred}) was set at 8.1 m/sec. The risk of capture was estimated for each habitat type as the proportion of locations at which the distance to a refuge was equal to or greater than R_{max} (Cowlishaw 1997c).

Perceived predation risk was measured in each of the eight habitat types outlined in Table 2.2; there were six habitats types in the home ranges of each troop. For Gamgam these were gallery forest, lowland forest, Guinea savannah, burned Guinea savannah, agricultural land, and elephant grass; for Kwano these were gallery forest, lowland forest, Guinea savannah, burned Guinea savannah, mango forest and palm forest. Six random points were created in each habitat type using the Hawth's tool extension (Beyer 2004) for ArcGIS (ESRI 2011). At each of these points, habitat visibility and distance to nearest refuge were measured. Habitat visibility was measured in the four cardinal directions at baboon eye-level, using a tape measure, or range-finding binoculars for longer distances. A refuge was defined as a tree larger than 8m tall that was at least 75° inclined to the horizontal (Cowlishaw 1997c). Trees were not considered to be a safe refuge if they had a low branch that was less than 75° to the horizontal, as leopards may climb such a branch. The distance from the random point to the nearest refuge was measured using a tape measure, or range-finding binoculars. Habitat visibility and distance to nearest refuge were measured every three months and were used to estimate the risk of attack and the risk of capture in each habitat type in each season.

2.5 Social network analysis

Social networks were constructed for associations (chapter 4) and behavioural interactions (chapter 5). Association networks were based on the twice weight index (TWI) calculated from scan data as follows:

$$TWI = \frac{X}{X + Y_a + Y_b}$$

Where X is the number of times a and b were seen together, Y_a the number of times a was seen but not b, and Y_b the number of time b was seen but not a (Cairns and Schwager 1987). Behavioural networks were based on the average rate per minute a dyad engaged in the interactions, or, in the case of the grooming network, the proportion of an individual's total grooming time that an individual spent grooming another individual, which were calculated from behavioural data collected during focal observations. Only adults and subadults that were present for the entire study period were included in the networks. In Gamgam these were eight individuals and in Kwano these were 16 individuals.

These associations or dyadic interactions were used to make adjacency matrices from which networks were generated. Example datasets and networks are given in Figure 2.4. In unweighted networks, adjacency matrices are binary, where a value of 1 indicates a tie is present between individuals, and a value of 0 indicates a tie is absent.

In weighted networks, not only the presence of a relationship but also the strength of that relationship is considered. In adjacency matrices for weighted networks the strength of the relationship is measured by the frequency or duration of the interaction. Inclusion of the strengths of relationships is important, because for primates it is likely that it is the frequency or duration rather than the occurrence of a behaviour that defines a relationship. For example, the relationship between two individuals that were seen to groom each other once a week is likely to be very different from the relationship between two individuals that groom each other several times a day. The use of weighted networks is particularly important for the study of primate social groups, because these are often relatively small, closed groups in which the majority of individuals are connected to each other (Jacobs and Petit 2011; Sueur *et al.* 2011a). Using binary networks, and depending on the time frame over which the network spans, the number of cases in which two individuals do not have a relationship can be very limited (Sueur *et al.* 2011a). In these cases measuring and comparing networks may reveal little about the structure of networks. Including weights in networks allows for a differentiation of its relationships and consequently for a richer analysis of network structure.

BINARY

	A	**B**	**C**	**D**
A	-	1	1	1
B		-	0	0
C			-	1
D				-

WEIGHTED

	A	**B**	**C**	**D**
A	-	0.7	0.5	0.3
B		-	0	0
C			-	0.2
D				-

WEIGHTED & DIRECTED

	A	**B**	**C**	**D**
A	-	0.7	0.5	0.3
B	0	-	0	0
C	0	0	-	0
D	0.4	0	0.2	-

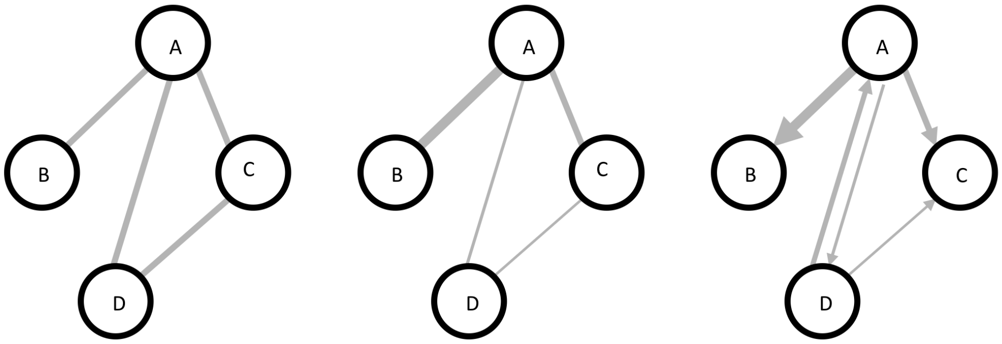


Figure 2.4: Examples of types of adjacency matrices and types of networks generated from them. In unweighted networks data are binary, and thus indicate if a tie is present (1) or absent (0). In weighted networks relationships are based on the frequency or duration of interactions and the relationship strength is indicated by the thickness of the tie. In directed networks data are asymmetric, the actors are given on the rows of the matrix, the recipient on the column, and arrows indicate the direction of the relationship.

For many social behaviours, the direction of the interaction is also important. For example, in a grooming network, if individual *a* grooms individual *b*, this is not necessarily reciprocated by individual *b*. For directed networks the data in the adjacency matrix is not symmetric, and can be weighted or unweighted. These types of networks will be discussed in greater detail in chapter 5.

All networks generated in this study are weighted networks, and depending on the type of interaction may be directed or undirected. Networks were visualised using Netdraw visualisation software (Borgatti 2002). Graphs were laid out using spring-embedding, so that nodes with more ties are at the centre of the network, and nodes with fewer ties are at the edges of the network (Croft *et al.* 2008).

2.5.1 Filtering of networks

Networks based on primate associations and behavioural interactions may contain ties that do not represent a 'relationship' as defined by Hinde (1976). Primate groups are often closed and relatively small, leading to social networks in which the majority of individuals are interconnected (Jacobs and Petit 2011). Furthermore, networks that are based on associations defined by 'the gambit of the group' (Whitehead and Dufault 1999), *i.e.* when individuals are assumed to be associated when they are found in the same group, are more likely to contain ties that are due to random events, because pairs of individuals may be found in spatial proximity due to chance. To help focus on relationships that are more likely to be biologically meaningful, networks are often filtered until non-random core elements remain (Croft *et al.* 2008). A filter is applied to a network by removing all the ties that are under a certain cut-off value, which can be set at any level (Croft *et al.* 2008; Sueur *et al.* 2011a).

In this study, the appropriate level of filtration was determined by filtering the network until it was significantly different from random. To this end, the observed network was dichotomised, and compared to 50 Erdös-Rényi random graphs (Erdös and Rényi 1959). Erdös-Rényi random graphs contain the same number of nodes and edges as the observed network, but ties are placed between two randomly chosen nodes (Erdös and Rényi 1959; Croft *et al.* 2008). The mean clustering coefficient and the mean shortest path length were calculated for the observed network and compared to the distribution of the test statistics for the 50 random networks. The mean clustering coefficient and mean shortest path length were chosen as test statistics because both metrics are a measure of the average cohesion of a network, and are complementary; the mean shortest path length is a global network measure, in that it considers paths over the whole network, whereas the clustering coefficient focuses more on local structures (Croft *et al.* 2008). The observed networks were filtered and dichotomised by increments of 0.01 until both metrics were significantly different from random. Once the appropriate level of filtration was determined, the filter was applied to the weighted network. The results of the determination of the filtering level for specific networks are given in the Methods sections in the relevant chapters.

2.5.2 Binary and weighted network metrics

Once networks are generated and filtered, the social network approach provides a series of descriptive statistics to quantify the structure of a network and the position of individuals within it. These network metrics can also be binary or weighted; with the binary version taking only the presence of ties into account, whilst the weighted versions also take into account the weights of relationships, although currently only a small set of network metrics have been redefined to take weights into account explicitly (Newman 2001; Opsahl and Panzarasa 2009; Opsahl *et al.* 2010). In this study, networks were filtered, which helps to focus on biologically meaningful relationships, and thus avoids the problem of a fully connected network. Therefore, it was possible to use a mixture of binary and weighted networks for analyses. Definitions of binary metrics used in this study are given in Table 2.10, and of weighted metrics in Table 2.11. The way that the weights of relationships are taken into account in distance measures (*i.e.* metrics that measure the distance between individuals in a network) and centrality measures (*i.e.* metrics that measure how evenly ties are distributed over the network) are discussed below.

Distance measures in binary networks are based on the assumption that all ties are equal in a network, such that the shortest path is always the most efficient path. However, in a weighted network ties are not all equal as ties have different strengths. Consequently, a longer but stronger path may be a closer relationship than a shorter but weaker path. Distance-based measures have been redefined to take this into account by introducing the notion of a tie *length* or *cost* (Opsahl 2009). To this end, the weights of the ties are inverted, so that a

Table 2.10: Definitions of binary network metrics (adapted from Wasserman and Faust 1994; Croft *et al.* 2008).

Binary network metrics	
Density (Δ)	The density of a network is a measure of the number of ties in a network, and indicates the level of cohesion. It indicates the number of ties in relation to the possible number of ties. For an undirected network: $$\Delta = \frac{E}{n(n-1)/2}$$ For a directed network: $$\Delta = \frac{E}{n(n-1)}$$ Where E is the number of ties in the network, and n the number of nodes. The value of Δ ranges between 0 (empty network) to 1 (completely connected network).
Mean clustering coefficient (C)	The mean clustering coefficient is a measure of the cliquishness of a network. It indicates the average proportion of ego's neighbours that are also connected to each other. $$C = \frac{1}{n}\sum_{i=1}^{n}\frac{2t_i}{k_i(k_i-1)}$$ Where t_i is the number of triangles of which node i is part, and k is the number of nodes i is connected to. The clustering coefficient ranges between 0-1, with large values indicating a large proportion of a node's neighbours also have ties between themselves (clustered).
Mean geodesic (L)	The average shortest path length is a measure of how close, on average, two individuals are to each other in the network. It indicates the shortest path from a node to all other nodes in the network. $$L = \frac{1}{n}\sum_{i=1}^{n} d_{ij}$$ Where n is the number of nodes in the network, and d is the shortest distance between node i and j. Larger values indicate a greater distance between individuals and thus that relationships are less direct.
Compactness	Compactness is a measure of the distance-based cohesion of a network. It indicates the average distance in a network, by taking the harmonic mean of the distances. Its value ranges between 0-1, with 0 indicating that all individuals in a network are isolates, and 1 indicating that all individuals in the network are adjacent to each other.
Mean degree (k)	The mean degree is a measure of how well connected a network is. It indicates how many ties nodes in the network have on average. $$k = \frac{1}{n}\sum_{i} k_i$$ Where k_i is the number of nodes i is connected to. To allow for comparisons the mean degree is normalised by the number of possible partners in the network. Higher values indicate that on average individuals have more relationships, or are connected to a greater proportion of their network.
Largest strong component	The largest fully connected part of a network. The normalised value is the largest fully connected component of a network as the proportion of the number of nodes in the network. Larger values indicate that a larger proportion of the network is completely interconnected.

Table 2.11: Definitions of weighted network metrics (adapted from Wasserman and Faust 1994; Croft *et al.* 2008; Opsahl and Panzarasa 2009; Opsahl *et al.* 2010).

Weighted network metrics	
Weighted mean clustering coefficient	The mean clustering coefficient is a measure of the cliquishness of a network. It indicates the average proportion of ego's neighbours that are also connected to each other. In the weighted metric, each triplet is assigned a weight, based on the weights of the edges. $$C_\omega = \frac{\sum_{r\Delta} \omega}{\sum_r \omega}$$ Where $r\Delta\omega$ *is* the total value of closed triplets, and rω the total value of triplets. The weighted mean clustering coefficient also ranges between 0-1, with large values indicating that a node's neighbours also have ties between themselves (clustered).
Weighted mean geodesic	Measures the average shortest distance from a node, to all other nodes in the network, taking the weights of ties into account, thus giving the average value of the paths with the lowest costs in the network. A higher value indicates a more distant relationship.
Weighted diameter	The weighted network diameter is the largest of the paths with the lowest costs in the network. This gives an indication of how 'wide' a network is, in other words, the maximum distance between nodes. A higher value indicates that individuals in the network may be more distant from each other.
Average tie weight	The average tie weight is a measure of how strong relationships are on average in a network. This measure does not take into account those relationships that are absent (*i.e.* have a weight of 0). This indicates the average strength of relationships in a network, when there is a relationship. A higher value indicates that relationships on average are stronger.
Weighted mean degree (mean node strength)	The weighted equivalent of the mean degree is the mean node strength. The node strength is the sum of the weights of an individual's relationships, and thus indicates individual 'effort'. The mean node strength indicates the average 'effort' of individuals in a network. This indicates how strongly connected a network is, and differs from the average tie strength in that it also takes into account when relationships are not present (*i.e.* individuals with a node strength of 0 are included in the mean measure). $$S = \frac{1}{n}\sum_i S_i$$ Where S_i is the total strength of node *i*'s ties. This metric can be directed. A higher value indicates individuals are on average more strongly connected.
Weighted Network centralisation	The network centralisation is a measure of how evenly ties are distributed over individuals in the network. It indicates the differences between the largest individual centrality score and the scores of all the other individuals in the network, and is normalised by maximum possible difference. $$C_D = \frac{\sum_{i=1}^{n}[C_D\,(n*) - C_D(n_i)]}{max\sum_{i=1}^{n}[C_D(n*) - C_D(n_i)]}$$ Where $C_D(n_i)$ is the centrality score (as proposed by Opsahl *et al.* 2010- see main text for definition) for node *i*, and $C_D(n*)$ is the largest observed value. Low values indicate ties are equally distributed over individuals, high values indicate that a few individuals have most of the ties in the network. This metric can be directed.

path with strong edges has a short length (or low cost) (Croft *et al.* 2008). Weights are accounted for in this way in analyses of the mean shortest path length, and the diameter (see Table 2.11). In the weighted version of the clustering coefficient, each triad is assigned a weight based on the weights of the edges in that triplet. In these analyses the triplet value was set to 'minimum' (default), which means each triplet was assigned the value of the lowest edge weight in that triplet (Opsahl and Panzarasa 2009).

In the weighted network centralisation metric, a measure of node centrality is used that takes into account both the number of ties a node has, as well as the weights of those ties (Opsahl *et al.* 2010). The measure takes the product of the number of nodes, and the weights of the nodes that have been adjusted according to the tuning parameter α, which determines the relative importance of the number of ties compared to the weights of the ties. This degree centrality measure is then:

$$C(i) = k_i \left(\frac{s_i}{k_i} \right)^{\alpha}$$

Where k is the node degree, s the node strength, and α is the tuning parameter (Opsahl *et al.* 2010). In these analyses the tuning parameter was set to 0.5, which means that equal weight was given to the number of ties and the strength of those ties.

For this study, six standard binary network metrics and seven weighted network metrics were used (see Table 2.10 & Table 2.11). The binary clustering coefficient, compactness and shortest path length were calculated in UCINET (Borgatti *et al.* 2002); all other metrics were calculated using the *tnet* package

(Opsahl 2009) in R (R Development Core Team 2010). When a network contains an isolate, or more than one component, the distance from one node to a node in another component is infinite (Croft *et al.* 2008). In order to avoid infinities, distance-based measures (*i.e.* weighted diameter, weighted mean geodesic and normalised weighted mean geodesic) were calculated among 'reachable pairs' (Borgatti *et al.* 2002; Croft *et al.* 2008), *i.e.* pairs of nodes that are in the largest strong component.

2.6 Statistical analysis

Before statistical analyses were carried out, data were tested for normality using Shapiro-Wilks tests, and for homogeneity of variance using Levene's tests. When the assumptions of parametric methods were violated, frequently due to a small sample size, non-parametric tests were used. All tests are two-tailed with a significance level of 0.05. Exact p-values are given wherever possible. When multiple tests were used the significance level was not adjusted for multiple comparisons, because in animal behaviour studies sample sizes are frequently small, leading to a low statistical power of significance tests (Nakagawa 2004). When a Bonferroni adjustment is applied, the statistical power is further decreased, thus inflating Type II errors (Moran 2003; Nakagawa 2004). Standard statistical analyses were done using SPSS (IBM 2010 version 19). Figures present medians or means and error bars show 95% confidence intervals. Discrete and mixture models (chapter 6) were fitted by maximum likelihood methods using the *MASS* (Ripley *et al.* 2012), *VGAM* (Yee

2010), and the *mixdist* (Macdonald and Du 2011) packages in *R* (R Development Core Team 2010).

Standard inferential statistical procedures are not appropriate for social network data as, by definition, these data are relational and thus violate the assumption of non-independence (Wasserman and Faust 1994; Hanneman and Riddle 2005). This non-independence of data not only occurs in direct connections between individuals; third-party relationships or the structure of the entire network may also influence the type and number of relationships an individual has (Lehmann and Ross 2011). This may be particularly important for primates, who recognise third-party relationships (Brent *et al.* 2011). Using standard statistical significance tests on network data would greatly inflate Type I errors (Hanneman and Riddle 2005). Instead, inferential statistics used for network data are based on permutations of the observed network, in which the test statistic is compared to a probability distribution that is generated from simulated networks (Hanneman and Riddle 2005). In this study, a range of permutation-based inferential statistics were used, t-tests, ANOVAs, correlations, contingency table tests, joint-count tests, and the Geary statistic for autocorrelation were carried out in UCINET (Borgatti *et al.* 2002), and *R* (R Development Core Team 2010) was used to carry out two-sample permutation tests in the *DAAG* package (Maindonald and Braun 2011), conditional uniform graph tests in the *sna* package (Butts 2010), and weighted random networks were created using the *tnet* package (Opsahl 2009). The default number of permutations was used for these analyses, apart from when a result had a *p*-value close to 0.05, in which case the number of permutations was increased by an order of magnitude. Further details of these permutation-based inferential statistics are given in the Methods sections of the social network chapters (chapter 4 & 5).

2.7 Ethical approval

The Ethics Committee of Roehampton University approved this study (reference BHS 08/ 010). A risk assessment was completed for fieldwork. Research permits were granted by the Nigerian National Park Service via the Gashaka Primate Project.

Chapter 3

Ecology, ranging patterns and habitat use

3.1 Introduction

For their survival, primates, like all other animals, have two major concerns (Dunbar 1988; Stanford 2002; Pollard and Blumstein 2008). Firstly, access to food is key, as primates need to obtain enough food to meet their energetic and nutritional requirements (Dunbar 1988; Stanford 2002). Secondly, primates need to stay safe from danger, such as predators (Dunbar 1988; Stanford 2002). As outlined in chapter 1, primate social groups are thought to result from an optimisation process, in which within-group competition for food is minimised, and predation risk reduced to tolerable levels. It has therefore been suggested that these environmental factors affect the degree of fission-fusion dynamics, although the way in which they do this not clear.

3.1.1 Socioecology of fission-fusion dynamics

Traditionally, ‘fission-fusion societies’ have been assumed to face ‘special’ ecological pressures (Aureli *et al.* 2008a), and the fluid grouping patterns were seen as an adaptation of larger-bodied animals to environmental conditions that are variable in space and time. Due to a lower risk of predation for larger-bodied animals, females can disperse to reduce within-group feeding competition when resources are scarce or dispersed, and form larger groups when ecological conditions permit this, thus providing the animals with flexibility in their response to ecological fluctuations (Boesch and Boesch-Achermann 2000). In support of this, strong linear relationships between party size and the abundance and distribution of food have been found in several ‘fission-fusion species’ (Symington 1988; Symington 1990; Stevenson *et al.* 1998; Kerth and König 1999; Smith *et al.* 2008). More recently it was suggested that high degrees of fission-fusion are the result of time budget constraints (Lehmann *et al.* 2007b). In marginal habitats, primates in large groups may need to compromise on time available for grooming, leading to unstable social relationships. By fissioning into smaller subgroups, individuals not only reduce travel costs (Lehmann *et al.* 2007a), but may also reduce the time needed for grooming. With a few individuals mediating between subgroups, individuals within each subgroup would need to maintain relatively few social relationships (Lehmann *et al.* 2007b).

However, the relationship between grouping patterns and ecology is not always straightforward, and over recent years the direct causal relationship between ecology and primate grouping patterns has been questioned (see section 1.2.5).

In various studies the relationship found between subgroup size and the abundance and distribution of food is complex. In several studies only part (Chapman *et al.* 1995; Anderson *et al.* 2002) or none (Henzi *et al.* 1997a; Hashimoto *et al.* 2001; Anderson *et al.* 2002) of the variation in party size is explained by food distribution. Similarly, the impact of predation risk on grouping patterns is not clear, with some studies reporting a positive relationship between group size and predation pressure (Dunbar 1988; Hill and Lee 1998), whilst others found a negative relationship (Isbell 1994) or no relationship at all (Boesch 1991). It is thus not clear how primates adjust their grouping patterns to ecological variables, what the costs and benefits are that primates trade off, and if more fluid grouping patterns indeed reflect short-term optimisations to ecological conditions.

Furthermore, it is becoming clear that a wide variety of vertebrates live in social systems similar to those of primate groups with a high degree of fission-fusion dynamics. For example, the social systems of bottlenose dolphins (Lusseau *et al.* 2006; Foley *et al.* 2010; Lewis *et al.* 2011), Galápagos sealion (Wolf *et al.* 2007), several species of bat (Kerth and König 1999; Kerth *et al.* 2006; Rhodes 2007; Popa-Lisseanu *et al.* 2008; Kerth 2010; Patriquin *et al.* 2010; Kerth *et al.* 2011), spotted hyena (Smith *et al.* 2008), Grevy's zebra (Sundaresan *et al.* 2007), onager (Sundaresan *et al.* 2007), African buffalo (Cross *et al.* 2005), and African elephants (Wittemyer *et al.* 2005) have all been labelled as ‘fission-fusion’. It seems unlikely that these, at least superficially, similar social systems in this wide range of species are due to the same set of ‘special’ ecological pressures (Aureli *et al.* 2008a). Instead, it may be that some of degree flexibility in grouping patterns is found in all animals, and that species simply differ in the extent of this flexibility.

With the proposal of the fission-fusion dynamics framework (Aureli *et al.* 2008a), it was suggested that all species exhibit fluidity of their grouping patterns to a certain extent. It is not clear how ecology affects fission-fusion dynamics and if variation in the degree of fission-fusion dynamics are adaptations to quantitatively or qualitatively different ecological pressures. Apart from fission-fusion dynamics, primates may also adjust ranging patterns and the way they use their home range, to cope with fluctuations in levels of food availability and predation risk. To gain a full understanding of how ecology affects fission-fusion dynamics, ranging patterns and habitat use should therefore also be considered.

3.1.2 Ranging patterns and habitat use

Apart from adjusting grouping patterns, primates adjust ranging patterns and the way they use their home range to cope with fluctuations in the environment and to ensure a steady supply of food (Dunbar 1988).

Ranging can be measured by the size of the home range, which is the '*area traversed by the individual in its normal activities of food gathering, mating and caring for young*' (Burt 1943: 351). The home ranges of individuals in a group overlap (Burt 1943), and together these form the group's home range. Ranging is also measured by the day journey length, which is the distance that is travelled per day (Strier 2003a). Primates adjust their ranging patterns to the quality, distribution and availability of food. Temporal variation in food availability has been found to influence home range size across the primate order (Clutton-Brock and Harvey 1977); home ranges tend to be largest when least food is available (Dunbar 1988). Similarly, day journey length tends to be longer in poor quality habitats (Dunbar 1988), and variation of day journey lengths between troops and between populations has been attributed to differences in the distribution and the predictability of food (*Cercopithecus aethiops*: (Struhsaker 1967); *Gorilla gorilla gorilla*: (Doran-Sheehy *et al.* 2004); *Papio ursinus*: (Henzi *et al.* 1992); *Papio anubis*: (Barton *et al.* 1992)) as has the seasonal variation in day range length within troops (*Cercopithecus aethiops*: (Willems *et al.* 2009); *Gorilla gorilla gorilla*: (Doran-Sheehy *et al.* 2004); *Papio ursinus*: (Anderson 1981; Henzi *et al.* 1992); *Papio hamadryas hamadryas*: (Swedell 2002)).

Ranging patterns also vary with the size of the foraging troop, because the energetic requirements of individual troop members are relatively constant (Dunbar 1988), and larger troops have to travel further to meet the nutritional and energetic requirements of all troop members (Isbell 1991; Chapman and Chapman 2000). A positive correlation was, for example, found between group size and total group home range size across 36 primate species (Milton and May 1976). Such relationships between home range size and troop size have been demonstrated in several baboon populations (Iwamoto and Dunbar 1983; Barton *et al.* 1992; Swedell 2002), as have relationships between day journey length and troop size (Anderson 1981; Sharman and Dunbar 1982; Iwamoto and Dunbar 1983; Barton *et al.* 1992; Dunbar 1992; Bettridge *et al.* 2010). Ranging patterns and the formation of small foraging subgroups are thus an inter-related set of responses to the environment.

Animals do not range in all parts of their home range equally (Dunbar 1988), as certain parts of the home range or habitats within the home range may be used preferentially, whilst others may be avoided. Access to food, and predation are factors that are thought to influence the way that primates use their habitats.

Optimal foraging theory proposes that during foraging, animals maximize the energy and nutrients obtained, in relation to the cost in terms of time and energy expended (Charnov 1976). Therefore, primates are expected to range selectively in habitats that give the highest energy returns, whilst avoiding habitats with low rates of returns. Hamadryas baboons in central Ethiopia have year-round access to a high quality food source, the doum palm fruit (Swedell 2002). These palm nuts are a preferred food (Schreier 2010), and are high-quality, fulfilling a large part of the baboons' daily energetic requirements (Swedell 2002). In this population, habitat use was largely determined by the presence of the doum palm fruit; the areas of the home range in which the bands preferentially ranged changed throughout the seasons, with bands being attracted to parts of the home range where palm nuts were available (Schreier 2010). Food availability also predicted habitat use in some chacma baboon troops, which ranged preferentially in parts of the range that were most productive (Henzi *et al.* 1992).

On the other hand, predation risk may constrain habitat use. One of the ways animals avoid being attacked by a predator is to avoid places where predators are likely to hunt (Stanford 2002). However, as food acquisition is also key for survival, many animals are forced to trade-off predator avoidance with food acquisition by using their habitats strategically (Cowlishaw 1997c). In other words, primates may forage in habitats that are sub-optimal in terms of energy returns if predation risk is low in those habitats (Cowlishaw 1997c). For example, chacma baboons in Tsaobis Leopard Park, Namibia, range non-randomly in the various habitat types within their home range (Cowlishaw 1997c). Troops were found to spend less time feeding in habitats with a high density of food, most likely because predation risk was high in these habitats. Instead, troops selected habitats that were less abundant in food, but in which they were safer from predators (Cowlishaw 1997c). Thus, primates appear to select their habitats based on a trade-off between energy returns and predation risk. Primates are thereby able to adjust to fluctuations in the environment by adjusting ranging patterns, both in terms of the distance and the location.

In summary, it is not clear if fission-fusion dynamics reflect a short-term optimisation of the costs benefits ratio of group living or if they are an intrinsic property of the animal's social structure. Moreover, it is not known if differences in the degree of fission-fusion dynamics are caused by qualitative or quantitative differences in ecological pressures.

3.1.3 Aims of this chapter

The aims of this chapter are to identify variation in food availability and predation risk across habitats, seasons, and between troops, while taking into account how these factors affect the way the study troops use their environments. Results of this chapter will be related to association networks (chapter 4), behaviour networks (chapter 5) and fission-fusion dynamics (chapter 6). The specific research questions of this chapter are as follows:

1. Do the sizes of the home ranges of the Gamgam and Kwano troops differ?
2. Day journey length
    a. Does season affect the troops' day journey length?
    b. Do the Gamgam and Kwano troops differ in day journey lengths?
3. Food availability
    a. Does season affect the availability of food in the troops' home ranges?
    b. Does the food availability in the home ranges of the Gamgam and Kwano troops differ?
4. Perceived predation risk
    a. Does perceived predation risk differ by habitat type?
    b. Does the habitat specific perceived predation risk differ by season?
    c. Do the home ranges of the Gamgam and Kwano troops differ in the level of perceived predation risk?
5. Habitat use
    a. Do the Gamgam and Kwano troops use habitats non-randomly?
    b. Does habitat use differ with food availability?
    c. Does habitat use differ with perceived predation risk?
    d. Do baboons selectively engage in or avoid particular activities in particular habitats?

3.2 Methods

Methods used to estimate food availability and predation risk are given in sections 2.4.3.3 and 2.4.3.4 respectively. Here, methods for the estimation of home ranges, habitat availability, and day journey length are described. A summary of the questions addressed in this chapter, along with the analyses and the data used, is given in Table 3.2.

3.2.1 Estimation of home ranges and availability of habitat types

Home ranges were estimated from GPS locations of the focal animal taken every 15 minutes. The overall number and the number of GPS locations per season are given in Table 3.1. These locations were imported into ArcGIS (ESRI 2011) and home ranges were estimated as minimum convex polygons (MCP) using the Hawth's Analysis Tools extension for ArcGIS (Beyer 2004). With this method, the home range is constructed around the most peripheral locations, such that all locations fall within the polygon, and the internal angles of the polygon are not greater than 180 degrees (Burgman and Fox 2003). The area of each MCP was calculated in ArcGIS to estimate home range size. Cumulative monthly home range area curves were plotted to estimate if enough GPS locations were collected to get an accurate estimate of the home range. Once the home range area no longer increases when more GPS locations are added, *i.e.* when the curve reaches asymptote, this is considered to be an accurate home range estimate (Odum and Kuenzler 1955; Bond *et al.* 2001).

The area of each of the habitat types was determined using habitat maps from a previous study (Warren 2003). These habitat maps were scanned and imported into ArcGis (ESRI 2011). GPS points were taken along rivers, streams, roads, tracks and at other landscape features and these points were used to geo-reference the habitat maps of both troops. Two habitat areas, the mango and palm forests, were added to the Kwano map. These habitats are both small areas that contain a high density of either *Mangifera indaca* (mango) or *Elaus guineansis* (oil palm) trees, and were mapped by taking GPS points around the periphery of these habitats, and importing the points into ArcGis (ESRI 2011). Polygons were created over each habitat type outlined on the habitat maps, and from the imported GPS points for the mango and palm forests. Once these new maps were created, the current home range was overlaid (Figure 3.1 & Figure 3.2). The area of each habitat polygon was measured in ArcGis (ESRI 2011) to estimate the area of each vegetation type within the home ranges. As home ranges have slightly changed since the habitat maps were made, habitat types were not known for the entire home ranges (Figure 3.1 & Figure 3.2). For the Gamgam troop, in 0.31 km^2 of their home range habitat type was not known, for the Kwano troop this was 0.56km^2.

Table 3.1: Number of GPS locations for both troops used in the estimation of home ranges and seasonal core areas.

	Number of GPS points	
	Gamgam	Kwano
BEG WET	755	1069
END WET	111	311
BEG DRY	653	785
END DRY	590	829
ALL	2109	2994

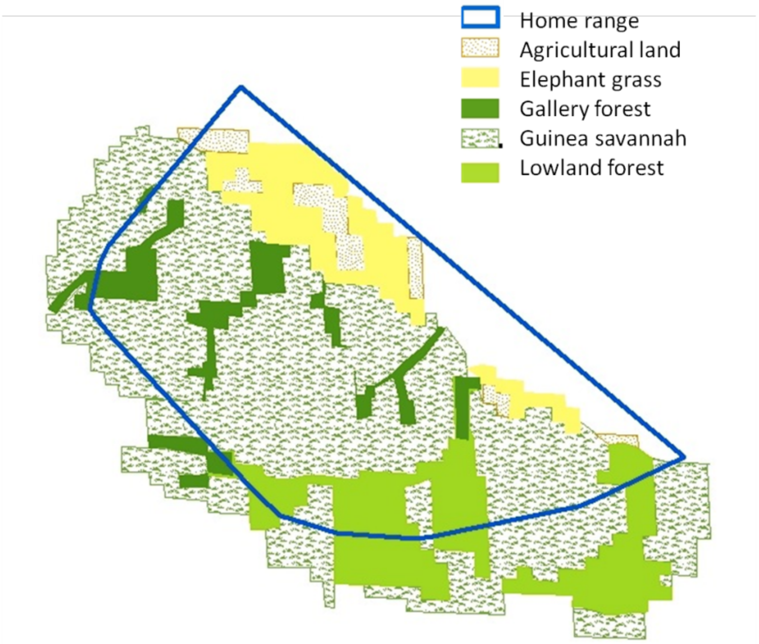


Figure 3.1: Habitat map of the Gamgam study area with the outline of home range overlaid. For estimation of the proportion of each habitat type only areas within the home range were used.

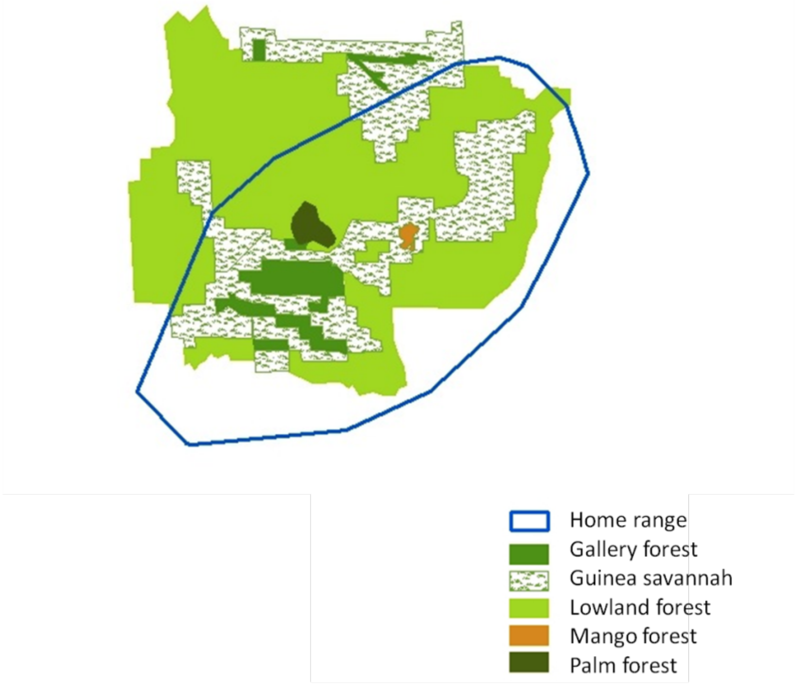


Figure 3.2: Habitat map of the Kwano study area with the outline of home range overlaid. For estimation of the proportion of each habitat type only areas within the home range were used.

3.2.2 Estimation of day journey length

Day journey lengths were estimated from GPS locations that were taken every 15 minutes during focal follows. GPS points were imported into ArcGIS (ESRI 2011), and the distance between each point and the following point was calculated using the Hawth's tool extension for ArcGIS (Beyer 2004). The times between GPS locations was not always exactly 15 minutes; however, only points that were between 12 and 18 minutes apart were used in these analyses. For each focal animal, an average distance travelled per 15-minute period was calculated per season, and these were used to estimate day journey length (*i.e.* over a 12-hour period) per focal individual per season. As such an estimate of day journey length may be influenced by the spread of sampling periods over the course of the day, an additional day journey length estimate was calculated. In this second estimate, the mean distance travelled for each 15-minute period (*e.g.* 9:00-9:10 or 15:30-15:45) was calculated for each season and for the entire study period. These mean distances were summed to give an estimate day journey length for each season and for the study period. When a particular time period did not have an average distance value in that season (*i.e.* when baboons were not observed during a particular time period), the average value for that time period taken over the entire study period was used.

3.2.3 Data analysis

The analyses used to answer each research question are outlined below. Research questions, analyses and variables are summarised at the end of this section (Table 3.2).

3.2.3.1 Does season affect the troops' day journey length?

To determine if daily travel distances varied by season, day journey estimates calculated for each season were compared via 1-way repeated measures ANOVAs. When variances were not equal between seasons, the Brown-Forsythe test of equality of means is reported instead

Only individuals for whom day journey lengths estimates were available for all four seasons were entered in these analyses (number of individuals: Gamgam *N* = 6; Kwano *N* = 7). Seasonal differences in day journey lengths were examined further through planned contrasts, in which comparisons were made between adjacent seasons (*i.e.* BEG WET & END WET, END WET & BEG DRY, BEG DRY & END DRY).

3.2.3.2 Do the Gamgam and Kwano troop differ in their day journey lengths?

Day journey lengths were estimated for each focal animal in each season. Day journey lengths may vary by sex; for example, male baboons may need to travel further in a day in order to meet their nutritional requirements due to their larger body size (Dunbar 1988). Between-troop differences in day journey length may thus be influenced by differences in the sex ratio. In order to control for this, individual day journey estimates by season were compared between troops via a 2-way ANOVA with troop and sex as fixed factors (number of day journey length estimates: Gamgam *N* = 29; Kwano *N* = 57).

3.2.3.3 Does season affect the availability of food in the troops' home ranges?

To determine if season affected the availability of food in the home ranges of each troop, comparisons were made between the twice-monthly FAIs across seasons with Kruskal-Wallis tests. *Post hoc* Mann-Whitney tests were used to make direct comparisons between all seasons. Comparisons were made between total FAIs and the FAIs per food class (*i.e.* flower, fruit, leaf, seed, 'other' that includes items such as gum and bark) (number of FAIs: Gamgam N = 19; Kwano N = 21).

3.2.3.4 Does the food availability in the home ranges of the Gamgam and Kwano troops differ?

A FAI was calculated for every two-week period both for the total food availability, and the food availability per food class. To determine if food availability differed between home ranges of the troops, these twice-monthly FAIs were compared using Mann-Whitney tests (Gamgam N = 19; Kwano N = 21).

3.2.3.5 Does predation risk differ by habitat type?

The risk of attack (R_a) and the risk of capture following attack (R_c) were measured at six locations in each habitat type in the home ranges of both troops in each season (number of predation risk estimates: gallery forest N = 47; lowland forest N = 46; Guinea savannah N = 53; burned Guinea savannah N = 50; agricultural land N = 24; elephant grass N = 22; mango forest N = 24; palm forest N = 24). First, Kruskal-Wallis tests were used to determine if R_a differed by habitat type, and results were followed up with Mann-Whitney *post hoc* tests. Based on these results, habitat types were provisionally ranked by their level of risk of attack. Second, to make a further distinction between habitats that had similar R_a scores, R_c scores were compared using pair-wise Mann-Whitney tests. Habitat types were thus ranked according to their level of predation risk sequentially, firstly on their R_a and secondly on their R_c. Habitat types that did not differ significantly in either R_a or R_c were ranked equally.

3.2.3.6 Does the habitat specific perceived predation risk differ by season?

The effect of season on habitat specific risks of attack and capture were determined with Friedman's ANOVAs. Data was pooled across troops, as habitat physiognomy is similar in the same habitat type over the two home ranges (number of sampling locations: gallery forest N = 11; lowland forest N = 11; Guinea savannah N = 11; burned Guinea savannah N = 13; agricultural land N = 6; elephant grass N = 4; mango forest N = 6; palm forest N = 6). Pair-wise Wilcoxon signed-ranks tests were used *post hoc* to make further distinctions between R_a and R_c scores of preceding and succeeding seasons if a significant effect of season was found.

3.2.3.7 Do the home ranges of the Gamgam and Kwano troops differ in the level of perceived predation risk?

Habitat specific R_a and R_c scores were weighted by the availability of habitat types within the Gamgam and Kwano home ranges, *i.e.* the area of each habitat type as a proportion of the total home range area. Weighted R_a and R_c scores were summed for each home range and compared descriptively between troops to determine if the average risk of attack and risk of capture differed between the home ranges of the troops. Further comparisons were made between the proportion of the troops' home ranges that provided safe, intermediate-risk and high-risk habitats. As the relative proportions of burned Guinea savannah and Guinea savannah that was not burned were unknown, these categories were collapsed into a single 'Guinea savannah' category.

3.2.3.8 Do the Gamgam and Kwano troops use habitats non-randomly?

To determine if troops used habitats non-randomly, the frequencies of observations in each habitat type taken from scan data were compared to expected frequencies using Chi-square goodness-of-fit tests. Expected frequencies were calculated for each habitat type by multiplying the total number of scans (for that season or overall) by the proportion of that habitat type in the home range. The total number of scan used was 420 for the Gamgam troop, and 529 for the Kwano troop.

To determine which habitat types the troops selectively ranged in or avoided, Ivlev's electivity index *E* (Jacobs 1974) was calculated for each habitat type in each season. This index considers the relative difference between the proportion of time spent in a habitat and the proportion of that habitat within the home range. *E* is defined as:

$$E = (r_i - p_i)/(r_i + p_i)$$

Where r_i is the proportion of observations in habitat i and p_i is the proportion of that habitat type in the home range (Jacobs 1974). *E* ranges between -1 and

+1, where a score of 0 indicates that habitat use is as expected, negative scores indicate avoidance of a habitat, and positive scores indicate selection of a habitat (Jacobs 1974).

3.2.3.9 Does habitat use differ with food availability?

To determine if the abundance of food in each habitat type affected habitat use, an average monthly total FAI was calculated for each habitat type from the bimonthly total FAIs (see section 2.4.3.3). Furthermore, to take account of the availability of each habitat type within the home range, Ivlev's electivity index (Jacobs 1974) was calculated for each month. Ivlev's index indicates the difference between the time a troop was observed in a habitat and the time a troop was expected to spend in a habitat, given its availability in the home range, and thus indicates a preference or avoidance of each habitat. For the Gamgam troop, the agricultural areas were not included in these analyses, as there was no FAI calculated for these areas. Furthermore, no data were collected for the Gamgam FAI during July and October, and the Kwano FAI during July, therefore, habitat use was not analysed for these months. For Gamgam N = 40 (*i.e.* four habitat, 10 months), for Kwano N = 55 (*i.e.* five habitat, 11 months). The monthly FAI and the monthly Ivlev's electivity indices were correlated using Kendall's tau-b correlations, as data were not normally distributed.

3.2.3.10 Does habitat use differ with perceived predation risk?

Correlations were used to examine the extent to which the perceived risk of predation of a habitat type influenced the use of that habitat. For each troop correlations were run between the seasonal Ivlev's electivity index and the seasonal risk of attack and risk of capture scores pooling the data across 5 habitat types across 4 seasons (N = 20). Sample sizes were too small to run correlations separately for each habitat type.

3.2.3.11 Do baboons selectively engage in or avoid particular activities in particular habitats?

To determine if habitat type influenced the troops' activities, hourly scan data were used in which both the habitat type and the activity of each individual present was recorded. For each individual in the troop (number of individual: Gamgam N = 22; Kwano N = 40) the proportion of time spent foraging, resting, socialising and travelling in each habitat type was compared to the overall proportion of time spent in each activity. The difference between the observed and expected proportion was thus calculated for each activity in each habitat type for each individual, with negative scores indicating that an individual engaged in an activity less frequently than expected in a particular habitat, and positive scores indicating the opposite. A score of zero indicates that an individual engaged in an activity in a particular habitat as expected, in other words, habitat type did not influence that activity. The 'other' behaviour category was omitted from these analyses, as sample sizes were too small. One-sample t-tests were used to determine if the deviations of activity budgets per habitat type differed significantly from zero. One-sample Wilcoxon signed-rank tests were used when data were not normally distributed.

Table 3.2: Questions addressed in this chapter, the type of analyses and the data used.

Question	**Analyses**	**Data used**
1. Do the sizes of the home ranges of the Gamgam and Kwano troops differ?	Descriptive comparison	• Home ranges estimated as minimum convex polygons from GPS location of the focal animal taken every 15 minutes
2a. Does season affect the troops' day journey length?	1-way repeated measures ANOVA Planned contrasts	• Day journey lengths estimated for each focal per season
2b. Do the Gamgam and Kwano troops differ in their day journey lengths?	2-way ANOVA	• Day journey lengths estimated for each focal per season
3a. Does season affect the availability of food in the troops' home ranges?	Kruskal-Wallis test *Post hoc* Mann-Whitney tests	• Twice-monthly FAIs for: • Total food availability • Food availability per food class
3b. Does food availability in the home ranges of the Gamgam and Kwano troops differ?	Mann-Whitney tests	• Twice-monthly FAI per food class and total twice monthly FAI
4a. Does predation risk differ by habitat type?	Kruskal-Wallis test *Post hoc* Mann-Whitney tests for provisional ranking	• R_a scores measured at 6 locations in each habitat type (6) in each season (4)
	Mann-Whitney tests for further distinction between habitats with equivalent R_a scores	• R_c scores measured at 6 locations in each habitat type (6) in each season (4)
4b. Does the habitat specific perceived predation risk differ by season?	Friedman's ANOVA *Post hoc* Wilcoxon signed-rank test	• R_a scores measured at 6 locations in each habitat type (6) in each season (4) • R_c scores measured at 6 locations in each habitat type (6) in each season (4)

Question (continued)	Analyses	Data used
4c. Do the home ranges of the Gamgam and Kwano troops differ in the level of perceived predation risk?	Descriptive comparison	• Habitat-specific R_a and R_c scores weighted by the availability of that habitat type in the home range, and summed over all habitat types
5a. Do the Gamgam and Kwano troops use habitats non-randomly?	Chi-square goodness-of-fit test	• Frequency of scans in each habitat type for the entire study period and per season • Expected frequencies based on the proportion of the habitat type within the home range
	Ivlev's electivity index	• Frequency of scans in each habitat type per season • Proportion of habitat types in the home range
5b. Does habitat use differ with food availability?	Kendall's Tau-b correlation	• Monthly Ivlev's electivity index for each habitat type • Mean monthly FAI for each habitat
5c. Does habitat use differ with perceived predation risk?	Pearson's correlation	For each season: • Habitat specific Ivlev's electivity indices • Habitat specific risks of attack or risks of capture

5d. Do baboons selectively engage in or avoid particular activities in particular habitats?	One-sample t-test / One-sample Wilcoxon signed rank test	• Deviation between observed and expected proportion of time spent in each activity in each habitat type, per individual
		  • Observed: individual activity budgets per habitat type from hourly scan data
		  • Expected: overall individual activity budgets from hourly scans

3.3 Results

3.3.1 Home ranges

Home ranges are shown in Figure 3.1 & Figure 3.2. The Gamgam troop ranged over a larger area (2.52 km^2) than did the Kwano troop (1.89 km^2).

Cumulative monthly home range size curves were plotted to determine if enough GPS locations were collected to estimate the size of the home ranges accurately (Figure 3.3). The cumulative sum of monthly home range areas had not reached asymptote for the Gamgam troop, therefore it is likely that the home range size given here is an underestimation. For the Kwano troop, the cumulative sum of monthly home range areas did reach asymptote, indicating that this is a realistic estimate of home range size.

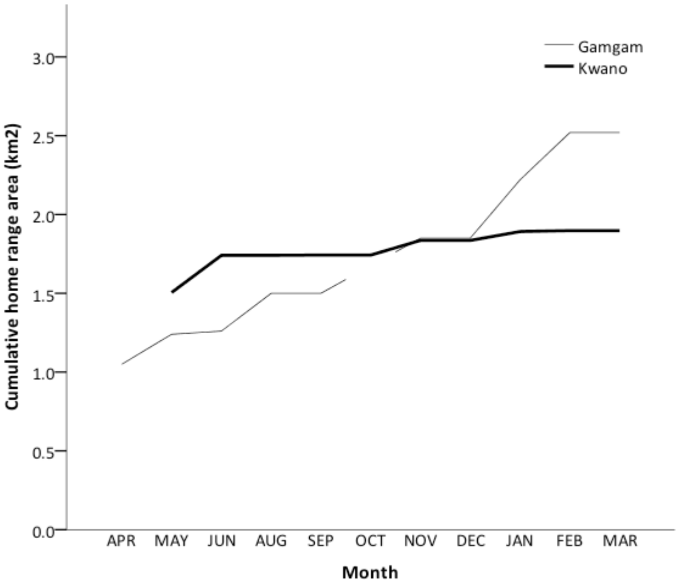


Figure 3.3: Cumulative monthly home range size for the Gamgam and Kwano troops.

In a previous study, (Warren *et al.* 2011) the home range estimates of both troops were found to be around 1.5 km^2, although in this study, the cumulative monthly home range size also did not reach asymptote . The home range of the Kwano troop on the other hand seems to be slightly larger than it was a decade ago.

3.3.2 Day journey length

3.3.2.1 Does season affect the troops' day journey length?

Season was found to have a significant effect on day journey length for individuals in both troops (Gamgam: repeated measures ANOVA: $F(3, 15) = 4.03$, $p = 0.027$; Kwano: $F(3, 18) = 4.52$, $p = 0.016$). Comparisons of the seasonal day journey lengths are given in Figure 3.4 & Figure 3.5. In both troops, day journey length was highest in the beginning of the wet season, in Gamgam this was lowest in the end of the wet season, while in Kwano day journey length was similarly low across the remaining seasons. Pairwise comparisons between seasons (planned contrasts) showed that in Gamgam mean day journey length in the end of the wet season was significantly lower than in the beginning of the wet and the beginning of the dry season (BEG WET – END WET: Gamgam: $F(1, 5) = 11.68$, $p = 0.019$; END WET-BEG DRY: $F(1, 5) = 8.23$, $p = 0.035$). Mean day journey length did not differ significantly between the beginning and the end of the dry season (BEG DRY – END DRY: ($F(1, 5) = 0.44$, $p = 0.538$). In Kwano day journey length in the beginning of the wet season was significantly longer than in the end of the wet season (BEG WET- END WET: ($F(1, 6) = 7.80$, $p = 0.031$), while during the remaining seasons this was not significantly different (END

WET-BEG DRY: *F*(1, 6) = 0.05, *p* = 0.839; BEG DRY-END DRY (*F*(1, 6) = 0.60, *p* = 0.467).

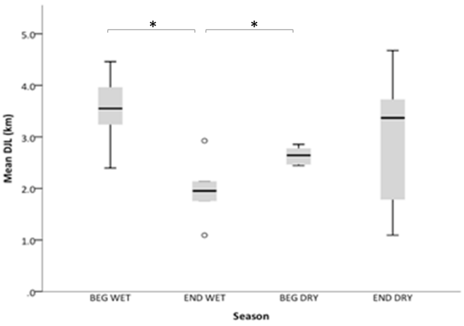


Figure 3.4: Within-troop seasonal comparison of day journey lengths (DJL) for the Gamgam troop from planned contrasts. Adjacent seasons were compared. * indicates $p < 0.05$. $N = 6$.

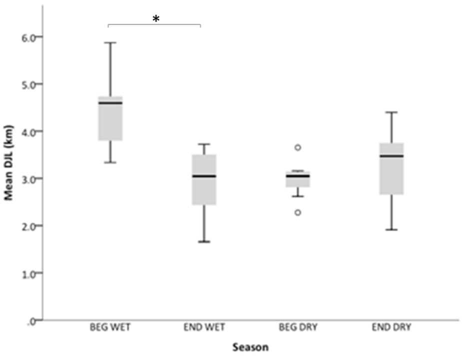


Figure 3.5: Within-troop seasonal comparison of day journey lengths (DJL) for the Kwano troop from planned contrasts. Adjacent seasons were compared. * indicates $p < 0.05$. $N = 7$.

3.3.2.2 Do the Gamgam and Kwano troop differ in their day journey lengths?

There was a significant effect of troop on the distance travelled each day (2-way ANOVA: *F*(1, 82) = 5.65, *p* = 0.020). Individuals in the Kwano troop (mean = 3.30 km, SD = 1.01) had a significantly longer day journey than individuals in the Gamgam troop (mean = 2.78 km, SD = 0.92). Sex did not affect day journey length (2-way ANOVA: *F*(1, 82) = 0.08, *p* = 0.783) and no interaction effect was found between troop and sex on day journey length (2-way ANOVA: *F*(1, 82) = 0.46, *p* = 0.498) indicating that the between-troop difference in day journey length was not due to between-troop differences in the sex ratio.

When day journey lengths were estimated from the average distance travelled during each 15-minute period, and summed to get a 12-hour day estimate, day journey lengths were similar to the results reported above, with the Gamgam troop travelling an average of 2.98 km per day, and Kwano troop and average of 3.46 km.

Both of these estimates do differ however from day journey lengths estimates from a previous study of these troops (Warren *et al.* 2011), where the Gamgam troop was found to travel 3.1 km each day, and this was significantly longer than the 2.4 km travelled by the Kwano troop each day.

3.3.3 Food availability

3.3.3.1 Does season affect the availability of food in the troops' home ranges?

Gamgam

FAIs were compared across seasons with Kruskal-Wallis tests. Results are given in Table 3.3. Season was found to affect total food availability and the availability of flowers, fruit, leaves, seeds, and 'other' food items significantly when these were considered separately. These results were followed up with pairwise Mann-Whitney tests comparing FAIs across all seasons. Results are given in Figure 3.6a-f and Table 3.4. For comparisons between the total FAI and flower FAI, none of the *post hoc* tests revealed significant differences, despite the finding of a significant overall effect of season on these FAIs. There are several possible explanations for these results; in both sets of *post hoc* comparisons a trend towards significance was found; for the total FAI this trend was found between the beginning of the dry and the end of the dry season. For the flower FAI a trend towards significance was found in the difference of the flower FAI of the beginning of the wet and the beginning of the dry season. As the sample sizes were small, the *post hoc* comparisons may have lacked the statistical power for these differences to reach significance. Alternatively, the sample sizes for some seasons may have been too small, leading to a Type I error in the Kruskal-Wallis test. Finally, the between-season differences in FAIs may have been more complex than simple comparisons between the median FAIs of seasons, *e.g.* if the median of FAIs in two seasons was larger than the median of FAIs in the other two seasons. This may lead to a significant result when the effect of season on FAIs in considered, but would not have been picked up by the seasonal comparisons in the *post hoc* tests. Thus, these results suggest that total food availability may have been low in the end of the dry season, and relatively high in the beginning of the dry season, whereas the availability of flowers may have been low in the beginning of the wet season, and high in the beginning of the dry seasons.

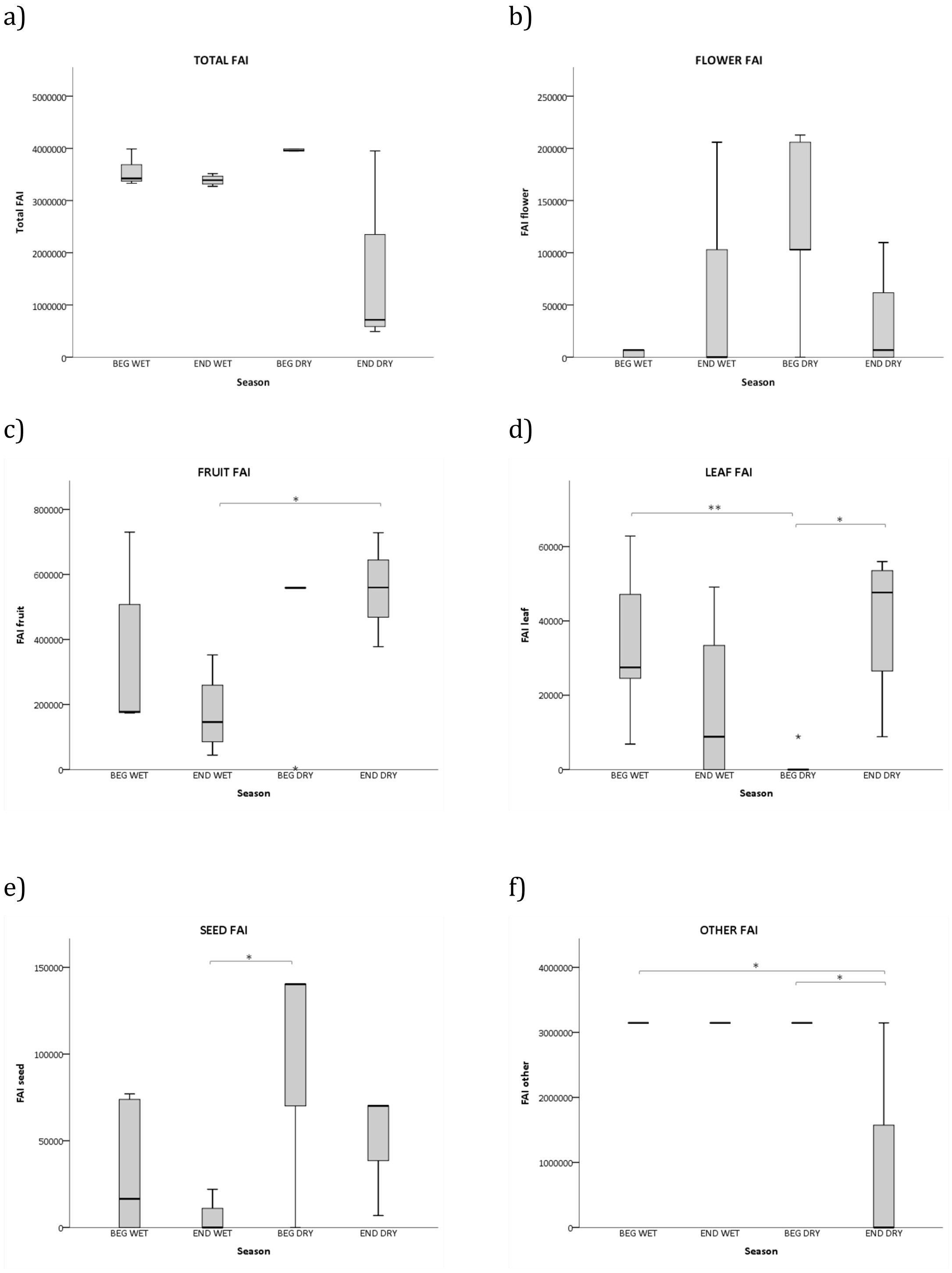


Figure 3.6a-f: Boxplot for the FAI in the Gamgam home range for a) total FAI; b) flowers; c) fruit; d) leaves; e) seeds; f) 'other' food items. ** indicates $p < 0.01$, * indicates $p < 0.05$.

Table 3.3: Results for the Kruskal-Wallis tests comparing the FAIs in the Gamgam home range across seasons for the total food availability and availability per food class. Values in bold indicate that season had a significant effect on availability of that food class. $N = 19$.

FAI	χ^2	*df*	*p*
Flower	**4.14**	**3**	**0.039**
Fruit	**7.55**	**3**	**0.002**
Leaf	**9.40**	**3**	**< 0.001**
Seed	**7.41**	**3**	**0.002**
Other	**12.57**	**3**	**0.004**
Total	**6.00**	**3**	**0.009**

Table 3.4: Results for Mann-Whitney *post hoc* tests comparing Gamgam's FAIs between seasons for each food class. Values in bold indicate a significant difference.

FAI	Seasons	*U*	*p*	FAI	Seasons	*U*	*p*
Total	BEG WET - END WET	8.00	0.476	Flower	BEG WET - END WET	9.00	0.524
	BEG WET - BEG DRY	8.00	0.247		BEG WET - BEG DRY	5.00	0.071
	BEG WET - END DRY	5.00	0.171		BEG WET - END DRY	8.00	0.433
	END WET - BEG DRY	4.00	0.190		END WET - BEG DRY	5.50	0.270
	END WET - END DRY	4.00	0.343		END WET - END DRY	4.00	0.314
	BEG DRY - END DRY	2.00	0.063		BEG DRY - END DRY	6.00	0.373
Fruit	BEG WET - END WET	4.00	0.114	Leaf	BEG WET - END WET	6.00	0.238
	BEG WET - BEG DRY	10.00	0.429		**BEG WET - BEG DRY**	**1.00**	**0.009**
	BEG WET - END DRY	5.00	0.171		BEG WET - END DRY	9.00	0.610
	END WET - BEG DRY	4.00	0.190		END WET - BEG DRY	6.00	0.286
	END WET - END DRY	**0.00**	**0.029**		END WET - END DRY	3.00	0.171
	BEG DRY - END DRY	4.00	0.190		**BEG DRY - END DRY**	**0.50**	**0.024**
Seed	BEG WET - END WET	4.50	0.124	Other	BEG WET - END WET	12.00	1.000
	BEG WET - BEG DRY	7.00	0.177		BEG WET - BEG DRY	15.00	1.000
	BEG WET - END DRY	9.00	0.576		**BEG WET - END DRY**	**3.00**	**0.033**
	END WET - BEG DRY	**1.00**	**0.032**		END WET - BEG DRY	10.00	1.000
	END WET - END DRY	1.00	0.057		END WET - END DRY	2.00	0.143
	BEG DRY - END DRY	7.00	0.508		**BEG DRY - END DRY**	**2.50**	**0.048**

Overall, these results suggest that food availability in the Gamgam home range differed by season. Although total food availability was low during the end of the dry season, this was mainly due to the low availability of 'other' food items in this season. The availability of fruit and leaves were highest in this season, and the availability of seeds was intermediate. During the beginning of the dry season food was also relatively abundant; total food availability, flower availability and seed availability all peaked in this season, however, few leaves were available. Food was less abundant in the beginning of the wet season; although leaf availability peaked, flower availability was lowest, and the availability of seed and fruit was also relatively low in the beginning of the wet season. Least food was available in the Gamgam home range during the end of the wet season; fruit and seed availability were lowest in this season, and the availability of flowers and leaves was also relatively low.

Kwano

The results for the Kruskal-Wallis test comparing seasonal FAIs in the Kwano range are given in Table 3.5. As the FAIs of 'other' food items were constant across seasons, these were omitted from the analysis. Total food availability, and the availability of flowers, leaves, and seeds were significantly affected by season, while the availability of fruit was not.

Table 3.5: Results for the Kruskal-Wallis tests comparing the FAIs in the Kwano home range across seasons for the total food availability and availability per food class. Values in bold indicate that season had a significant effect on availability of that food class. The FAIs of 'other' food items were constant across seasons; these were therefore omitted from the analysis. *N* = 21.

FAI	χ^2	*df*	*p*
Flower	**5.19**	**3**	**0.027**
Fruit	1.83	3	0.183
Leaf	**6.01**	**3**	**0.012**
Seed	**6.51**	**3**	**0.008**
Other	-	-	-
Total	**6.26**		**0.008**

Pairwise Mann-Whitney tests were conducted to compare FAIs across all seasons. Results are given in Figure 3.7a-f and Table 3.6. Total food availability was lowest in the beginning of the dry season, compared to both the beginning of the wet and the end of the wet season, while food availability was most variable in the end of the dry season. No significant differences were found in the comparisons for the flower, leaf, and seed FAIs between any seasons, despite the significant overall effect of season on the availability of these food items. However, for each of these food classes at least one pair-wise comparison showed a trend towards significance. Flower availability tended to be lower in the end of the wet season compared to the end of the dry season. The availability of leaves tended to be higher in the end of the dry season compared to the beginning of the wet season and the beginning of the dry season. Seed availability tended to be high in the beginning of the wet season compared to the end of the wet season and the beginning of the dry season.

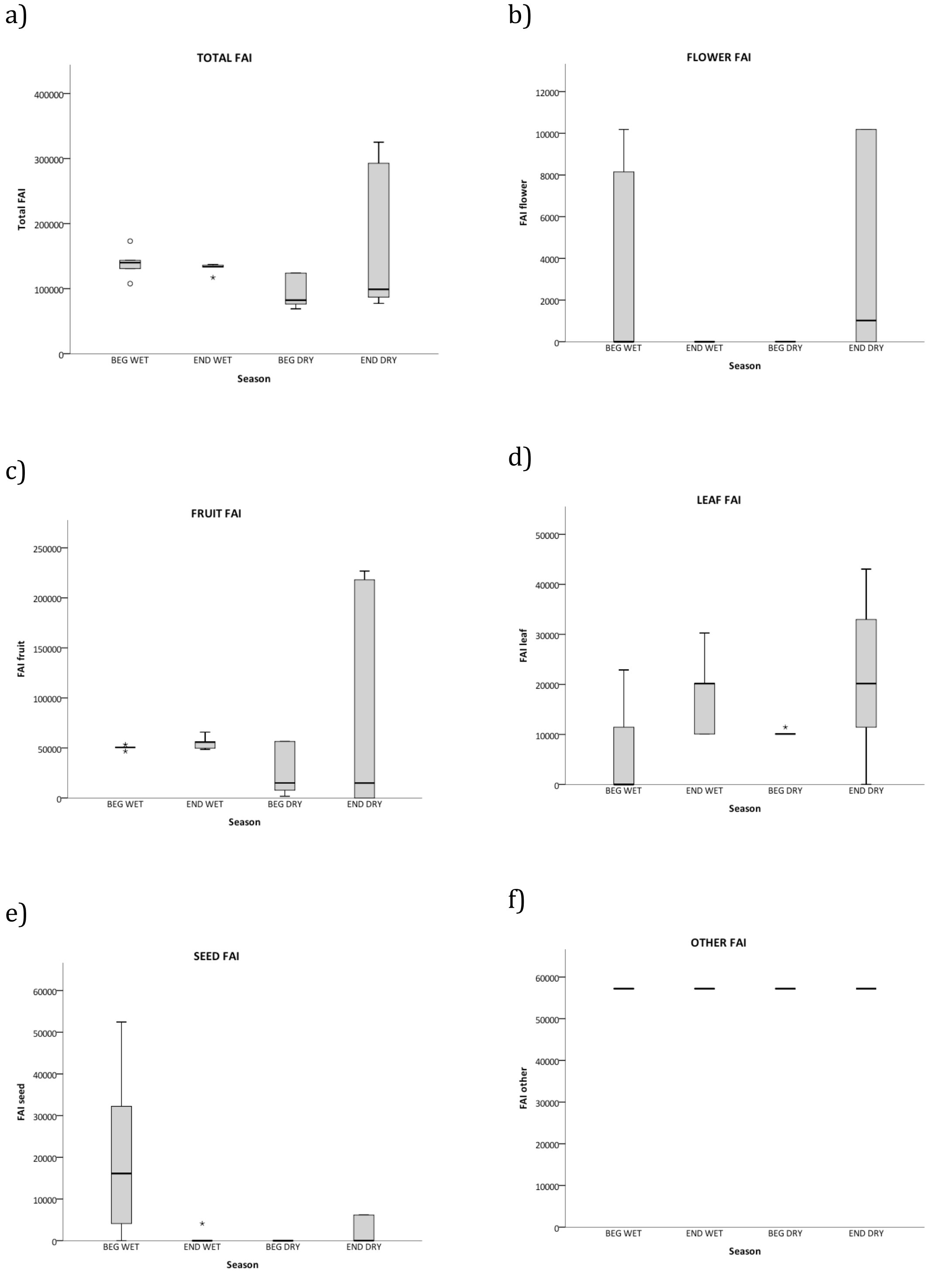


Figure 3.7a-f: Boxplot for the FAI in the Kwano home range for a) total FAI; b) flowers; c) fruit; d) leaves; e) seeds; f) 'other' food items. ** indicates $p < 0.01$, * indicates $p < 0.05$.

Table 3.6: Results for Mann-Whitney *post hoc* tests comparing Kwano's FAIs between seasons for each food class. Values in bold indicate a significant difference.

FAI	Seasons	*U*	*p*	FAI	Seasons	*U*	*p*
Total	BEG WET - END WET	9.00	0.548	Flower	BEG WET - END WET	7.50	0.444
	BEG WET - BEG DRY	**2.00**	**0.032**		BEG WET - BEG DRY	12.00	1.000
	BEG WET - END DRY	11.00	0.537		BEG WET - END DRY	11.00	0.470
	END WET - BEG DRY	**2.00**	**0.032**		END WET - BEG DRY	5.00	0.167
	END WET - END DRY	10.00	0.429		END WET - END DRY	5.00	0.061
	BEG DRY - END DRY	9.00	0.329		BEG DRY - END DRY	10.00	0.411
Fruit	BEG WET - END WET	8.00	0.421	Leaf	BEG WET - END WET	6.00	0.190
	BEG WET - BEG DRY	10.00	0.659		BEG WET - BEG DRY	9.50	0.571
	BEG WET - END DRY	10.00	0.426		BEG WET - END DRY	5.00	0.080
	END WET - BEG DRY	8.00	0.389		END WET - BEG DRY	6.00	0.167
	END WET - END DRY	10.00	0.420		END WET - END DRY	11.00	0.489
	BEG DRY - END DRY	13.00	0.755		BEG DRY - END DRY	5.00	0.061
Seed	BEG WET - END WET	3.50	0.087				
	BEG WET - BEG DRY	4.50	0.095				
	BEG WET - END DRY	7.00	0.162				
	END WET - BEG DRY	7.00	0.206				
	END WET - END DRY	8.00	0.210				
	BEG DRY - END DRY	9.00	0.284				

Overall, these results suggest that food was least abundant in the Kwano home range during the beginning of the dry season; food availability was similar across the beginning of the wet and the end of the wet season, while food availability was most variable during the end of the dry season. The availability of flowers, leaves and seeds was low in the end of the wet season and the beginning of the dry season. During the beginning of the wet season seed availability peaked, whereas in the end of the dry season there was a relatively high availability of leaves and flowers.

3.3.3.2 Does the food availability in the home ranges of the Gamgam and Kwano troops differ?

Mann-Whitney tests were used to compare the total FAI per hectare, and the FAI per hectare for each food class between troops for each season. Results are given in Table 3.7. Total food availability was higher in the Gamgam home range compared to the Kwano home range in all seasons.

In part, this between-troop difference is due to the absence of 'other' food items in the Kwano home range in three out of four seasons. Furthermore, the types of food that were more abundant in the Gamgam home range as compared to the Kwano home range, differed by season. During the beginning of the wet season, fruit, leaves and 'other' food items were more abundant in the Gamgam home range compared to the Kwano home range, whilst the availability of flowers and seeds were comparable across home ranges. By the end of the wet season, the between-troop difference in total food availability was mainly due to the higher abundance of 'other' food items in the Gamgam home range; the availability of all other food classes in the Kwano and Gamgam home ranges were not significantly different. During the beginning of the dry season significantly fewer leaves were available in the Gamgam home range compared to the Kwano home range. However, due to the higher availability of 'other' items in the Gamgam home range, the total FAI in the Gamgam home range was higher in this season. During the end of the dry season the between-troop difference in total food availability was largely due to the greater abundance of fruit and seeds in the Gamgam home range, whilst the abundance of flowers, leaves and 'other' food items were comparable in the home ranges of the troops.

Table 3.7: Comparison of the FAIs per hectare between troops separately for each season. Comparisons were made between the total FAI, and the FAI for each food class. Values in bold indicate that the troops differed significantly in the FAI.

		N		GAMGAM		KWANO			
Season	Food class	GAMGAM	KWANO	Mean FAI	SE	Mean FAI	SE	*U*	*p*
BEG WET	Flower	6	5	4537	1435	3667	2268	15.00	1.000
	Fruit	**6**	**5**	**323658**	**97724**	**50321**	**1055**	**0.00**	**0.004**
	Seed	6	5	30654	15105	20985	9659	13.50	0.840
	Leaf	**6**	**5**	**32729**	**7969**	**6866**	**4577**	**2.00**	**0.017**
	Other	**6**	**5**	**3145699**	**0**	**57216**	**0**	**0.00**	**0.002**
	TOTAL	**6**	**5**	**3537277**	**103882**	**139054**	**10560**	**0.00**	**0.004**
END WET	Flower	4	5	51465	51465	0	0	7.50	0.444
	Fruit	4	5	172299	65200	55241	3069	5.00	0.286
	Seed	4	5	5501	5501	823	823	9.00	0.722
	Leaf	4	5	16698	11579	18159	3775	7.00	0.508
	Other	**4**	**5**	**3145699**	**0**	**57216**	**0**	**0.00**	**0.008**
	TOTAL	**4**	**5**	**3391661**	**51176**	**131438**	**3660**	**0.00**	**0.016**
BEG DRY	Flower	5	5	124891	39265	0	0	4.00	0.087
	Fruit	5	5	447906	111102	27516	12029	4.00	0.079
	Seed	5	5	98225	28064	0	0	4.00	0.087
	Leaf	**5**	**5**	**1768**	**1768**	**10359**	**271**	**0.00**	**0.008**
	Other	**5**	**5**	**3145699**	**0**	**57216**	**0**	**0.00**	**0.008**
	TOTAL	**5**	**5**	**3818488**	**168297**	**95092**	**11920**	**0.00**	**0.008**
END DRY	Flower	4	6	30853	26511	3735	2065	7.00	0.319
	Fruit	**4**	**6**	**556527**	**71573**	**79098**	**45577**	**0.00**	**0.010**
	Seed	**4**	**6**	**54338**	**15822**	**2057**	**1301**	**0.00**	**0.010**
	Leaf	4	6	40026	10672	21306	6227	5.00	0.171
	Other	4	6	786425	786425	57216	0	6.00	0.129
	TOTAL	**4**	**6**	**1468170**	**829242**	**163411**	**46449**	**0.00**	**0.010**

The difference in food availability in the home ranges of troops may in part be due to the different number of species that were entered into the FAI of each troops, which was 28 for the Gamgam troop and 23 for the Kwano troop. Different numbers of species were entered into each troop's FAI calculations for two reasons; firstly, only items that were previously classified as monthly staples for a troop (Warren 2003) were monitored, and the number of staples differed between troops. Secondly, not all species were found in the home ranges of both troops. Thirteen species were found in both home ranges and had been classified as monthly staples for both troops (see Appendix A, Table A.1) and were therefore entered into the FAI of both troops. Several species (*i.e.* nine for Gamgam, six for Kwano) were found in the home ranges of both troops but were only entered into the FAI of one troop, as it was found to be a monthly staple for that troop but not the other. Six species that were entered in the Gamgam FAI were not found in the Kwano home range, whilst four species in the Kwano FAI were not found in the Gamgam home range. Thus, higher FAIs of the Gamgam troop may in part be higher because a greater number of species were entered into its calculation. However, the majority of the food items that were found in both home ranges but were only considered in the FAI of one of the troops represent relatively marginal foods. The troops spent a relatively small proportion of their feeding time, usually only one month per year, on these items (see Appendix A, Table A.2).

Overall, these results indicate that, even without the crops that were included in their home range, the Gamgam troop had more food available in their home range throughout all seasons. The type of foods that were more abundant in the Gamgam home range differed by season, although the abundance of ‘other’ food items played an important role in the between-troop differences in food availability in three out of four seasons, which is largely due to the fact that elephant grass stems were included in this index in the Gamgam home range, but not in the Kwano home range.

3.3.4 Perceived predation risk

3.3.4.1 Does perceived predation risk differ by habitat type?

Habitat specific R_a, R_{max} and R_c estimates are given in Table 3.8. The risk of capture was high in agricultural land and elephant grass areas because no trees were found in these areas. Thus, if a baboon was attacked in these habitats, a leopard was likely to outrun it before it could reach a refuge. The R_a and R_c estimates are used in the subsequent predation risk analyses.

Table 3.8: Estimates of risk of attack (R_a), maximum distance a baboon can be from a refuge in order to reach a refuge safely in case of an attack (R_{max}), and risk of capture following attack (R_c) across habitats.

Habitat	*N*	R_a	R_{max}	R_c
Gallery forest	47	0.36	10.87	0.00
Lowland forest	46	0.36	11.05	0.04
Guinea savannah	53	0.71	7.62	0.32
Burned Guinea savannah	50	0.64	11.84	0.24
Agricultural land	24	0.64	11.68	0.92
Elephant grass	22	0.70	13.92	0.64
Mango forest	24	0.53	9.59	0.08
Palm forest	24	0.25	12.78	0.00

The risk of attack varied significantly by habitat type (Kruskal-Wallis test: χ^2_7= 49.78, p < 0.001, *N* = 290). The results of pair-wise Mann-Whitney *post hoc* tests are given in Table 3.9. The risk of attack in the gallery, palm, and lowland forests did not differ significantly from each other, whilst the risk of attack in these habitat types was significantly lower than the risk of attack in all other habitats. In other words, baboons were safest from predator attack in the gallery, palm, and lowland forests because of better visibility in these habitats. The risk of attack was higher in the mango forest, burned Guinea savannah, agricultural land, elephant grass and Guinea savannah habitats. No significant differences were found in the risk of attack among these habitats, with the exception of the risk in the mango forest being lower than in the Guinea savannah.

In order to make further distinctions between habitat specific predation risks, habitat specific risk of capture following attack was compared between those habitats in which the risk of attack was comparable (*i.e.* low risk of attack in gallery, lowland, and palm forest; high risk of attack in mango forest, burned Guinea savannah, agricultural land, elephant grass and Guinea savannah). Results are given in Table 3.10. The risk of capture following attack was comparable in the gallery, palm, and lowland forests, indicating that the overall the risk of predation (*i.e.* the risk of being attacked and the risk of being captured following an attack) was similar in these habitats. Comparing the risk of capture in the habitats with a high risk of attack did allow for a further differentiation of levels of predation risk between these habitat types. The risk of capture was significantly higher in agricultural areas compared to all other habitat types, making this the most hazardous habitat for baboons. The risk of capture in the elephant grass was significantly higher than that in the mango forest, burned Guinea savannah and Guinea savannah areas, which indicates that this is the second most dangerous habitat for baboons. The differences in the risk of capture between the mango forest, burned Guinea savannah, and Guinea savannah were less clear cut; the risk of capture in the burned Guinea savannah did not differ significantly from that in either the mango forest or the Guinea savannah. Thus, in these habitats with an intermediate risk of attack, the mango forest was safest, followed by the burned Guinea savannah and the Guinea savannah.

Table 3.9: Results for the *post hoc* Mann-Whitney comparisons between the habitat specific risks of attack. U-values are given along with the p-value in brackets and the habitat type with the higher R_a score. When no habitat type is given in the cell the risk of attack was equal in the two habitats. Values in bold indicate significant differences in the risk of attack.

	Gallery forest	Lowland forest	Guinea savannah	Burned Guinea savannah	Agricultural land	Elephant grass	Mango forest	Palm forest
Gallery forest *N* = 47	-	1080.00 (0.995)	**595.500** **(< 0.001)** **GS higher**	**712.50** **(< 0.001)** **BGS higher**	**324.00** **(0.003)** **AL higher**	**255.00** **(< 0.001)** **EG higher**	**398.50** **(0.038)** **MF higher**	464.50 (0.211)
Lowland forest *N* = 46		-	**619.00** **(< 0.001)** **GS higher**	**742.00** **(0.002)** **BGS higher**	**327.00** **(0.004)** **AL higher**	**266.00** **(0.001)** **EG higher**	**382.00** **(0.029)** **MF higher**	451.00 (0.196)
Guinea savannah *N* = 53			-	1206.00 (0.389)	551.00 (0.316)	577.50 (0.949)	**455.00** **(0.034)** **GS higher**	**241.00** **(< 0.001)** **GS higher**
Burned Guinea savannah *N* = 50				-	577.50 (0.781)	513.00 (0.625)	503.00 (0.244)	**319.50** **(0.001)** **BGS higher**
Agricultural land *N* = 24					-	230.00 (0.435)	236.50 (0.267)	**128.50** **(0.001)** **AL higher**
Elephant grass *N* = 22						-	186.00 (0.074)	**109.00** **(< 0.001)** **EG higher**
Mango forest *N* = 24							-	**141.50** **(0.001)** **MF higher**
Palm forest *N* = 24								-

Table 3.10: Results for the *post hoc* Mann-Whitney comparisons between the habitat specific risks of capture for habitats in which the risk of attack was comparable. Non-shaded cells indicate comparisons between habitats with a low risk of attack; shaded cells indicate comparisons between habitats with a high risk of attack. *U*-values are given along with the *p*-value in brackets and the habitat type with the higher R_c score. When no habitat type is given in the cell, the risk of capture was equal in the two habitats. Values in bold indicate significant differences in the risk of capture.

	Gallery forest	Lowland forest	Guinea savannah	Burned Guinea savannah	Agricultural land	Elephant grass	Mango forest	Palm forest
Gallery forest *N* = 47	-	1034.00 (0.242)						564.00 (1.000)
Lowland forest *N* = 46		-						528.00 (0.543)
Guinea savannah *N* = 53			-	1218.00 (0.389)	**257.00** **(< 0.001)** **AL higher**	**399.00** **(0.019)** **EG higher**		
Burned Guinea savannah *N* = 50				-	**194.00** **(< 0.001)** **AL higher**	**332.00** **(0.002)** **EG higher**	506.00 (0.127)	
Agricultural land *N* = 24					-	**190.00** **(0.032)** **AL higher**	**48.00** **(< 0.001)** **AL higher**	
Elephant grass *N* = 22						-	**118.00** **(< 0.001)** **EG higher**	
Mango forest *N* = 24							-	
Palm forest *N* = 24								-

Taking into account both the habitat specific risk of attack and the risk of capture following attack, habitats can be ranked according to perceived predation risk as follows: the safest habitats were the palm, gallery, and lowland forests. Predation risk was intermediate in the mango forest, burned Guinea savannah and Guinea savannah. Predation risk was high in elephant grass areas, and the agricultural land was the most hazardous habitat for baboons.

3.3.4.2 Does the habitat-specific perceived predation risk differ by season?

Results for the comparison of seasonal habitat-specific risk of attack and capture are given in Table 3.11. The risk of attack was significantly affected by season in all habitat types, apart from the lowland and palm forests. As the risk of attack is measured through habitat visibility, this was expected to differ by season. For the lowland forest, the effect of season on the risk of attack was close to significance. In the palm forest season may have little effect on the risk of attack, as the majority of the trees found in this area are oil palms (*Elaus guineansis*), which are evergreen and have tall trunks without foliage. As habitat visibility was measured at baboon eye-level, habitat visibility is less likely to differ per season in the palm forest.

Table 3.11: Results for Friedman's ANOVAs comparing habitat specific risks of attack and capture across seasons. The risk of capture was constant across seasons for the gallery and palm forest, and was therefore not entered into these analyses. Values in bold indicate a significant effect of season on risk score.

			Risk of attack		Risk of capture	
Habitat	Number of sampling locations	*df*	χ^2	*p*	χ^2	*p*
Gallery forest	11	3	**8.63**	**0.029**	-	-
Lowland forest	11	3	7.15	0.063	2.00	1.000
Guinea savannah	11	3	**22.87**	**< 0.001**	**11.90**	**0.005**
Burned Guinea savannah	13	3	**30.48**	**< 0.001**	**16.13**	**< 0.001**
Agricultural land	6	3	**12.06**	**0.004**	6.00	0.250
Elephant grass	4	3	**10.80**	**0.005**	2.54	0.719
Mango forest	6	3	**7.56**	**0.048**	2.00	1.000
Palm forest	6	3	3.78	0.302	-	-

The risk of capture was not significantly affected by season in the majority of habitat types. Only in the Guinea savannah and burned Guinea savannah did the risk of capture differ by season. The risk of capture score is influenced both by the distance to a refuge and by habitat visibility, which is used in the calculation of the maximum distance a baboon can be from a refuge and still outrun a leopard in case of an attack. Seasonal differences in the risk of attack in the Guinea savannah and burned Guinea savannah habitats may thus be due to a seasonal difference in the availability of refuges. During the annual burning of the grasses in these areas, trees are often also burned. However, this would be more likely to affect risk of capture scores in the burned Guinea savannah. Instead, it may be the extreme seasonal differences in habitat visibility in these habitat types that influence the seasonal effect on the risk of capture. When habitat visibility is reduced, the maximum distance at which a baboon can be from a refuge is shorter and therefore a greater proportion of sampling points may be at a distance greater than this maximum, increasing the risk of capture.

The results of pair-wise Wilcoxon signed-ranks *post hoc* tests on the seasonal risk of attack and capture are given in Figure 3.8 and Table 3.12. The seasonal differences in the risk of attack are largely driven by a low risk of attack in the end of the dry season, when visibility was high. Conversely, the seasonal differences in the risk of capture in the Guinea savannah and burned Guinea savannah was mainly driven by a high risk in the end of the wet season, when visibility in these habitats was greatly reduced.

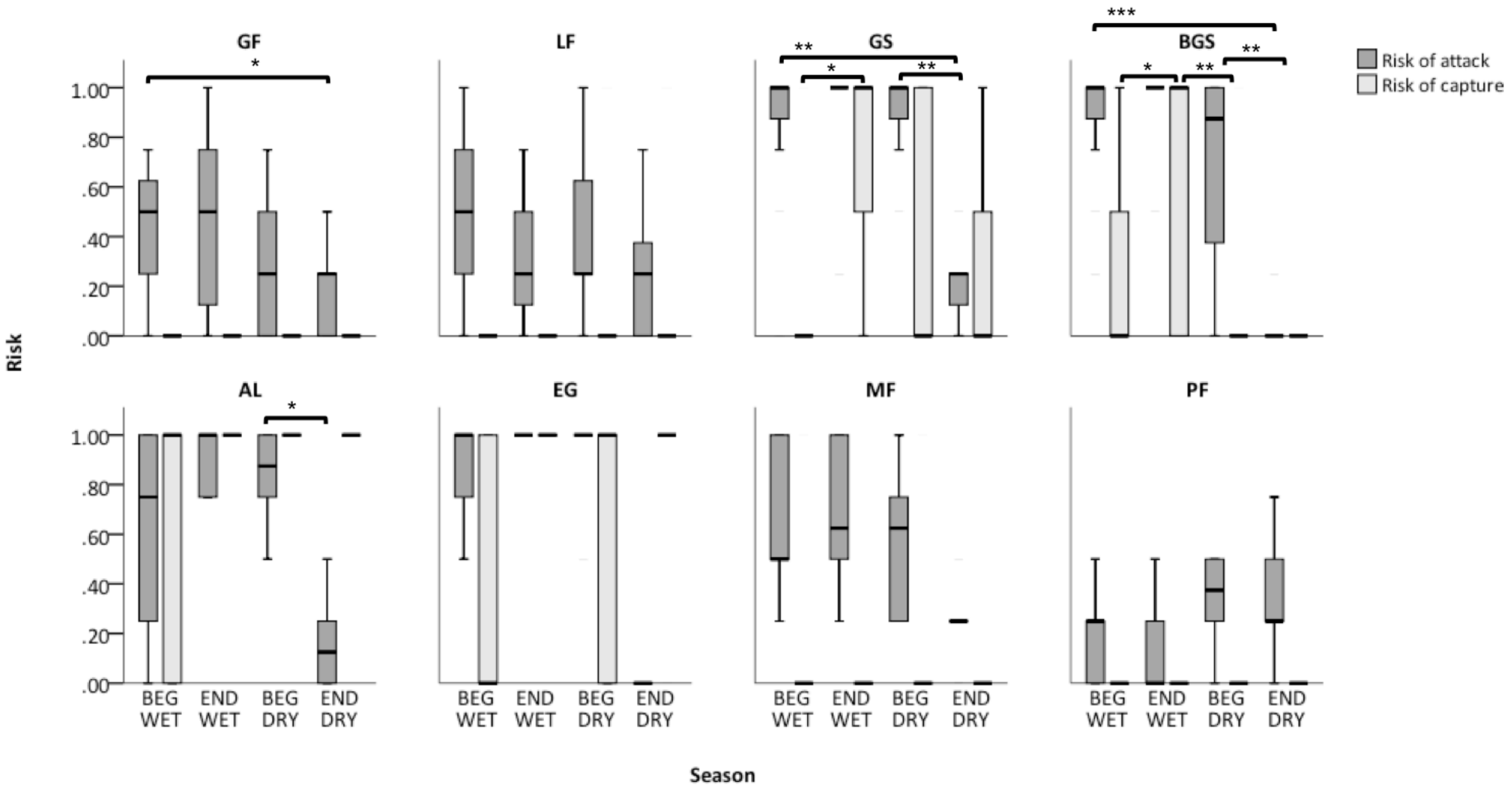


Figure 3.8: Seasonal differences in the habitat-specific risk of attack and the risk of capture for the gallery forest (GF); lowland forest (LF); Guinea savannah (GS); burned Guinea savannah (BGS); agricultural land (AL); elephant grass (EG); mango forest (MF); palm forest (PF). * indicates $p < 0.05$; ** indicates $p < 0.01$; *** indicates $p < 0.001$.

Table 3.12: Results for the Wilcoxon signed-ranks *post hoc* tests comparing the habitat-specific risk of attack (Ra) and risk of capture (Rc) across seasons. Values in bold indicate a significant difference.

		Ra		Rc	
Habitat type	Seasons	Z	p	Z	p
Gallery forest	BEG WET - END WET	-0.17	0.859	0.00	1.000
	END WET - BEG DRY	-1.29	0.227	0.00	1.000
	BEG DRY - END DRY	-1.29	0.227	0.00	1.000
	END DRY - BEG WET	**-2.40**	**0.016**	0.00	1.000
Guinea savannah	BEG WET - END WET	-1.63	0.250	**-2.65**	**0.016**
	END WET - BEG DRY	0.00	1.000	-2.00	0.125
	BEG DRY - END DRY	**-2.99**	**0.001**	-1.00	0.625
	END DRY - BEG WET	**-2.77**	**0.004**	-0.58	1.000
Agricultural land	BEG WET - END WET	-1.60	0.125	-1.41	0.500
	END WET - BEG DRY	-1.00	1.000	0.00	1.000
	BEG DRY - END DRY	**-2.23**	**0.031**	0.00	1.000
	END DRY - BEG WET	-1.63	0.188	-1.41	0.500
Mango forest	BEG WET - END WET	-0.38	1.000	-1.00	1.000
	END WET - BEG DRY	-1.00	0.625	-1.00	1.000
	BEG DRY - END DRY	-1.81	0.125	-1.00	1.000
	END DRY - BEG WET	-2.07	0.063	-1.00	1.000

		Ra		Rc	
Habitat type	Seasons	Z	p	Z	p
Lowland forest	BEG WET - END WET	-1.07	0.344	0.00	1.000
	END WET - BEG DRY	-1.03	0.354	-1.00	1.000
	BEG DRY - END DRY	-2.07	0.063	0.00	1.000
	END DRY - BEG WET	-1.72	0.113	-1.00	1.000
Burned Guinea savannah	BEG WET - END WET	-1.63	0.250	**-2.45**	**0.031**
	END WET - BEG DRY	-1.98	0.055	**-2.83**	**0.008**
	BEG DRY - END DRY	**-3.11**	**< 0.001**	0.00	1.000
	END DRY - BEG WET	**-3.30**	**< 0.001**	-1.00	0.625
Elephant grass	BEG WET - END WET	-1.34	0.500	-1.41	0.500
	END WET - BEG DRY	-1.00	1.000	-1.41	0.500
	BEG DRY - END DRY	-2.12	0.063	-0.58	1.000
	END DRY - BEG WET	-1.84	0.125	-0.58	1.000
Palm forest	BEG WET - END WET	-0.71	0.750	0.00	1.000
	END WET - BEG DRY	-1.63	0.250	0.00	1.000
	BEG DRY - END DRY	0.00	1.000	0.00	1.000
	END DRY - BEG WET	-1.13	0.500	0.00	1.000

Overall, these results suggest that perceived predation risk was lowest in the end of the dry season in the majority of habitats, because of increased visibility. Guinea savannah and burned Guinea savannah were the most variable in terms of predation risk, with these habitats being most dangerous in the end of the wet season when grasses obscured potential predators, and safest during the end of the dry season when these grasses had died off or had been burned.

3.3.4.3 Do the home ranges of the Gamgam and Kwano troop differ in the level of perceived predation risk?

Differences in the level of perceived predation risk are determined by the availability of habitat types within the home ranges of the troops. Table 3.13 shows the habitat specific mean Ra and Rc scores along with the proportion of each habitat type within the home ranges of the troops, and the habitat specific risks weighted by the proportion of the home range that habitat type represents. The mean of these weighted risks indicates the average risk of attack or capture in the home range of each troop.

Both the risk of attack and the risk of capture were higher in the Gamgam home range compared to the Kwano home range, indicating that the perceived predation risk was greater for Gamgam baboons compared to Kwano baboons. A total of 64% of the Kwano home range was low-risk habitat, compared to 19% in the Gamgam home range. This difference is largely due to differences in the proportions of low-risk lowland forest in the home ranges, which is smaller in the Gamgam home range than in the Kwano home range. Furthermore, a small area of palm forest was included in the Kwano home range, but not in the

Table 3.13: The habitat-specific mean risk of attack scores, risk of capture scores, and predation risk ranking along with the proportion of habitat types within the home ranges of each troop. Habitats with a lower predation risk ranking have a lower predation risk. The risk of attack and risk of capture within the home ranges were determined by weighting the mean risk by the proportion of each habitat type within the home range. The burned Guinea savannah and Guinea savannah categories were collapsed into a single category, as the proportion of burned Guinea savannah within the home ranges was not known.

Habitat	Mean risk of attack	Mean risk of capture	Predation risk ranking	% of habitat type in Gamgam home range	% of habitat type in Kwano home range	Risk of attack in Gamgam home range	Risk of attack in Kwano home range	Risk of capture in Gamgam home range	Risk of capture in Kwano home range
Gallery forest	0.36	0.00	low	8.36	7.35	0.03	0.03	0.00	0.00
Lowland forest	0.36	0.04	low	10.66	54.76	0.04	0.20	0.00	0.02
Guinea savannah	0.68	0.28	intermediate - high	62.98	35.88	0.43	0.24	0.18	0.10
Agricultural land	0.64	0.92	highest	5.38	-	0.03	-	0.05	-
Elephant grass	0.70	0.64	high	12.62	-	0.09	-	0.08	-
Mango forest	0.53	0.08	intermediate - low	-	0.45	-	0.00	-	0.00
Palm forest	0.25	0.00	low	-	1.57	-	0.00	-	0.00
MEAN						**0.12**	**0.09**	**0.06**	**0.02**

Gamgam range, within which baboons were relatively safe from predator attack and capture. Conversely, a larger part of the Gamgam home range (63%) consisted of Guinea savannah in which predation risk was intermediate to high. In the Kwano home range this proportion was smaller (36%). The two most hazardous habitats, elephant grass and agricultural land, were found only in the Gamgam home range, making up a total of 18% of the home range, thus increasing the overall predation risk in the Gamgam home range.

3.3.5 Habitat use

3.3.5.1 Do the Gamgam and Kwano troops use habitats non-randomly?

Both troops were most frequently observed in the gallery forest and Guinea savannah in all seasons (Figure 3.9 a-d & Figure 3.10 a-d). It was not possible to determine if the habitat use of the Gamgam troop differed from expected during the end of the wet season, as the sample size was too small for this period. Frequencies of observations of the Kwano troop in the mango and palm forest were not included in the analysis, as the sample sizes for these two habitats were too small. The time each troop spent in each habitat type was significantly different from expected given the proportion of habitat types within their home range (Table 3.14 & Table 3.15). These results suggest that both troops selectively ranged in certain habitats, whilst avoiding others and that this non-random use of habitats differed by season.

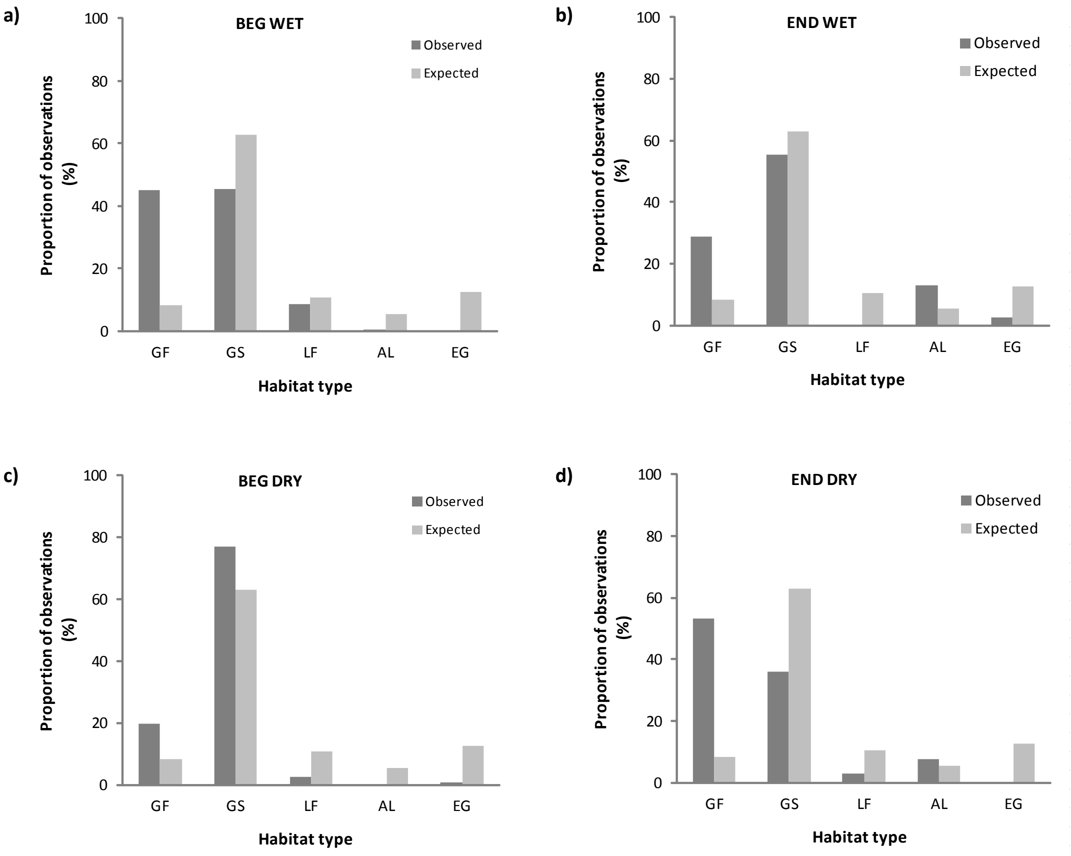


Figure 3.9 a-d: The observed and expected proportions of observations of the Gamgam troop in each habitat type for the a) beginning of the wet season; b) end of the wet season, c) beginning of the dry season; d) end of the dry season.

Table 3.14: The results for the Chi-squared test for the difference between the frequency at which the Gamgam troop was observed in each habitat type in each season, and their expected frequencies given the proportion of each habitat type within their home range. It was not possible to determine if habitat use differed from expected in the end of the wet season, as the sample size was too small for this period.

	χ^2	*df*	*p*
BEG WET	292.05	4	< 0.0001
END WET	-	-	-
BEG DRY	47.80	4	< 0.0001
END DRY	286.23	4	< 0.0001

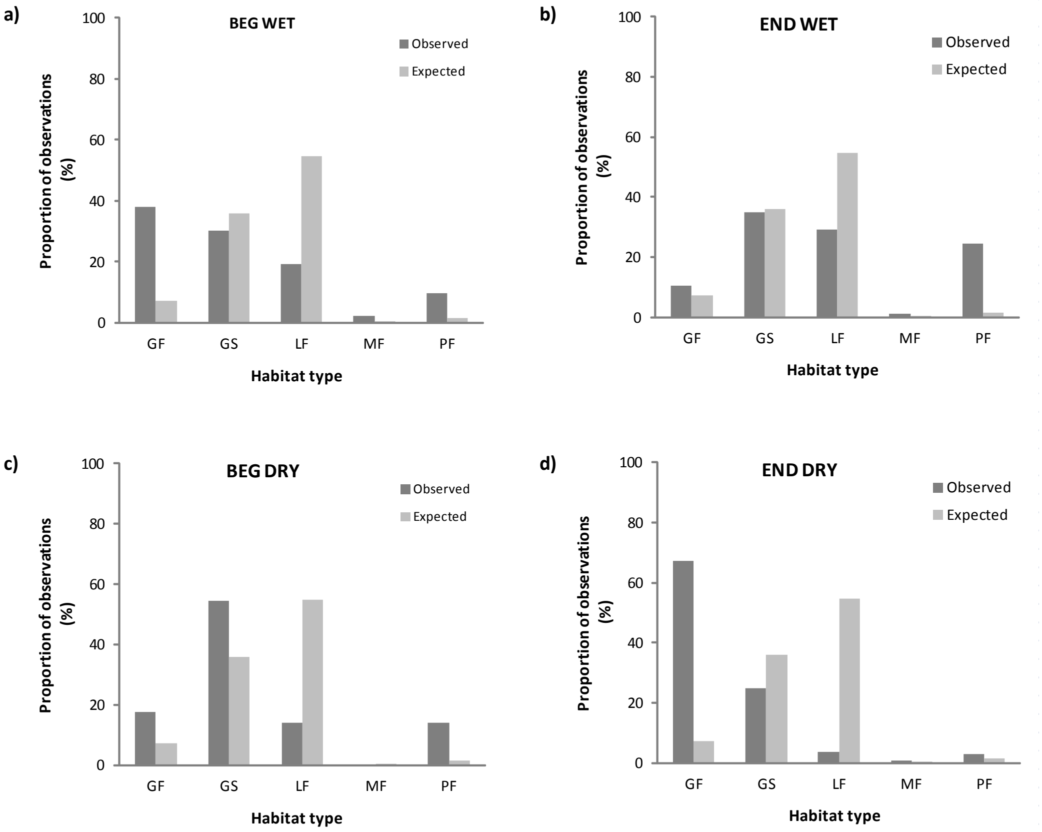


Figure 3.10 a-d: The observed and expected proportions of observations of the Kwano troop in each habitat type for the a) beginning of the wet season; b) end of the wet season; c) beginning of the dry season; d) end of the dry season.

Table 3.15: The results for the Chi-squared test for the difference between the frequency at which the Kwano troop was observed in each habitat type in each season, and their expected frequencies given the proportion of each habitat type within their home range. Frequencies in the mango forest and palm forest were not included in these analyses as sample sizes were too small.

	χ^2	*df*	*p*
BEG WET	279.78	2	< 0.0001
END WET	8.76	2	0.0125
BEG DRY	68.24	2	< 0.0001
END DRY	572.25	2	< 0.0001

These results largely confirm the findings of a previous study in which it was shown that neither troop used habitats randomly (Warren 2003), and the Gamgam troop was also most frequently observed in the Guinea savannah, whilst the Kwano troop was observed most frequently in the gallery forest.

The electivity index gives an indication of the strength of active avoidance or selection of each habitat type. This index ranges between -1 and +1, where negative scores indicate that a habitat is avoided, a positive score indicates a habitat is actively selected, and a score of zero indicates that habitat use is as expected given the proportion of that habitat type within the home range (Jacobs 1974). The seasonal Ivlev's indices for both troops are given in Table 3.16. Both troops selectively ranged in the gallery forest, whilst actively avoiding lowland forest areas. Both troops also avoided Guinea savannah areas in all seasons, apart from during the beginning of the dry season when they actively selected this habitat. Gamgam baboons avoided agricultural land during the beginning of the wet and the beginning of the dry season, whilst seeking out this habitat during the end of the wet and the end of the dry seasons. Gamgam baboons avoided elephant grass areas during all seasons. The Kwano troop selectively ranged within the palm forest in all seasons. In all but the beginning of the dry season Kwano troop selectively ranged within the mango forest.

Similar preference for the gallery forest and avoidance of the Guinea savannah was found during an earlier study of these troops (Warren 2003). Interestingly, in this previous study, both troops were found to range selectively in the lowland forest, whilst in the current study both troops were found to avoid ranging in the lowland forest. This difference is likely to be due to the fact that in the current study, the mango forest and palm forest habitat, two preferred areas, were analysed separately, whereas in the previous study, these areas may have been classed as lowland forest, thus increasing the proportions of observations in this habitat.

Table 3.16: Ivlev's electivity index for habitat selection in the Gamgam and Kwano troops by season. A score of 0 indicates random ranging in a habitat type, positive values indicate selection of a habitat type, and negative scores indicate avoidance of a habitat. Mango and palm forest habitats did not occur in the Gamgam home range; agricultural land and elephant grass did not occur in the Kwano home range.

Troop	Season	Gallery forest	Guinea savannah	Lowland forest	Agricultural land	Elephant grass	Mango forest	Palm forest
GAMGAM	BEG WET	0.687	-0.160	-0.098	-0.792	-1.000	-	-
	END WET	0.552	-0.065	-1.000	0.420	-0.655	-	-
	BEG DRY	0.403	0.100	-0.612	-1.000	-0.873	-	-
	END DRY	0.729	-0.270	-0.577	0.172	-1.000	-	-
KWANO	BEG WET	0.677	-0.084	-0.477	-	-	0.686	0.721
	END WET	0.175	-0.014	-0.306	-	-	0.440	0.879
	BEG DRY	0.517	0.164	-0.596	-	-	-1.000	0.786
	END DRY	0.811	-0.233	-0.841	-	-	0.199	0.127

3.3.5.2 Does habitat use differ with food availability?

First, to determine if food availability influenced habitat selection, the monthly Ivlev's indices for all habitat types were pooled and correlated with the monthly FAIs. In neither troop were the monthly Ivlev's indices significantly correlated with the monthly FAIs (Gamgam: $\tau = -0.18$, $p = 0.130$, $N = 40$; Kwano: $\tau = -0.04$, $p = 0.667$, $N = 55$). Thus, neither troop selected or avoided habitats solely based on the abundance of food in those habitats.

Secondly, correlations were run to determine if within habitat types, food availability was related to the strength of the selectivity or avoidance of that habitat; results are given in Table 3.17. For the Gamgam troop no significant associations were found between the monthly Ivlev's index and the monthly FAI. The Kwano troop on the other hand did select the gallery forest more often when food was more abundant in that habitat. Food availability may have also influenced the Kwano troop's ranging in the mango forest, as the monthly FAI showed a positive correlation with the monthly Ivlev's indices that was very close to significance.

Overall, for the Kwano troop, there was some indication that the troops selected the gallery and mango forest based on food availability, whilst for the Gamgam troop there was no evidence for such an effect of food on habitat selection. Thus, factors other than solely food availability seem to influence habitat use.

Table 3.17: Kendall's tau-b correlation coefficients for the correlations between monthly habitat selectivity and monthly food availability per habitat type. Values in bold indicate a significant correlation.

	GAMGAM (N = 10)		KWANO (N = 11)	
Habitat	τ	*p*	τ	*p*
Gallery forest	0.38	0.128	**0.47**	**0.048**
Lowland forest	-0.18	0.245	-0.31	0.199
Guinea savannah	0.29	0.245	-0.02	0.938
Elephant grass	0.24	0.459	-	-
Mango forest	-	-	0.50	0.056
Palm forest	-	-	-0.18	0.435

3.3.5.3 Does habitat use differ with perceived predation risk?

Correlations were run between the Ivlev's electivity indices and risk of attack and capture scores, pooling the data over all the seasons. The risk of attack and the risk of capture were not significantly correlated with habitat selection in either troop (Gamgam: R_a: $R = -0.13$, $p = 0.600$, R_c: $R = -0.30$, $p = 0.195$; Kwano: R_a: $R = -0.17$, $p = 0.477$, R_c: $R = -0.23$, $p = 0.324$). These results may be due to the small sample sizes, giving this test not enough statistical power to reach a firm conclusion. Conversely, it may be that habitat use was not determined by predation risk. Baboons are likely to be constrained in their habitat preferences by the availability of food or other resources, such as water, and are therefore unable to avoid high-risk habitats altogether. Thus, baboons may have greater choice in their habitat use for certain activities than for others. In the following section habitat use is considered per activity, to examine to what extent baboons were constrained in their habitat use, and to what extent predation risk influences habitat preference.

Correlations between the Ivlev's electivity indices and risk of attack and capture scores were not run within each habitat type, as the predation risk estimates are seasonal and sample sizes would have been too small ($N = 4$) for these tests to have sufficient statistical power.

3.3.5.4 Do baboons selectively engage in or avoid particular activities in particular habitats?

One-sample t-tests and one-sample Wilcoxon signed-rank tests were used to determine if troops preferentially performed certain activities in certain habitats. Results are given in Table 3.18.

In each habitat type, the proportion of time baboons in both troops spent foraging was not different from expected, indicating that baboons did not preferentially forage in a particular habitat.

Both troops preferred the gallery forest for social activities, whilst avoiding this habitat during travel. The Gamgam troop also rested preferentially in the gallery forest, while resting was as expected in this habitat for the Kwano troop. These results confirm the findings of an earlier study (Warren 2003), in which the Gamgam troop was, but the Kwano troop was not found to spend the majority of their resting time in the gallery forest.

Both troops travelled preferentially in the Guinea savannah, whilst avoiding this habitat for resting and social interactions. Gamgam baboons preferentially engaged in social interactions in the lowland forest, while Kwano baboons avoided social interactions there. In Kwano, resting was also avoided in this habitat and travelling preferred, while for the Gamgam troop, these behaviours were as expected.

In Gamgam, the proportions of time spent resting and travelling were not significantly different from expected in the elephant grass and agricultural land, while social interactions were avoided in these habitats.

In Kwano, resting and travelling were as expected in the mango forest, while social activities were avoided. In the palm forest, Kwano baboons preferentially rested and engaged in social interactions, while avoiding this habitat for travel.

A summary of all the results in relation to the chapter aims is given in Table 3.19.

Table 3.18: Results for one-sample t-tests and one-sample Wilcoxon signed-rank tests, testing the preference for and avoidance of activities in each habitat for both troops. For each activity in each habitat type it was determined if the difference between the proportion of time animals spent in an activity in a particular habitat and the proportion of time animals spent in an activity on average, deviated significantly from 0 (*i.e.* when habitat type and activity are not associated). Values in bold indicate a significant deviation, a positive mean / median indicates the activity occurred in that habitat more than expected, a negative mean / median indicates that activity occurred in that habitat less than expected. The level of perceived predation risk determined in section 3.3.4.1 is also given for each habitat type.

GAMGAM

			Forage			Rest			Social			Travel		
	Predation risk	*df*	Average	Test statistic	*p*	Average	Test statistic	*p*	Average	Test statistic	*p*	Average	*t*	*p*
Gallery forest	Low	21	-2.03	*W* = 81.00	0.140	**4.25**	***W* = 237.00**	**< 0.001**	**4.19**	***t* = 6.22**	**< 0.001**	**-7.65**	**W = 7.00**	**< 0.001**
Guinea savannah	Intermediate - high	21	1.41	*W* = 127.00	0.987	**-4.98**	***t* = -7.19**	**< 0.001**	**-2.18**	***t* = -4.90**	**< 0.001**	**6.09**	***W* = 252.00**	**< 0.001**
Lowland forest	Low	20	2.04	*t* = 0.40	0.696	-3.93	*W* = 94.00	0.455	**7.20**	***t* = -4.82**	**< 0.001**	3.66	*W* = 142.00	0.357
Agricultural land	Highest	21	8.59	*t* = 1.97	0.063	7.30	*t* = 1.68	0.108	**-10.63**	***W* = 0.00**	**< 0.001**	-3.80	*t* = -0.97	0.341
Elephant grass	High	6	-34.69	*W* = 7.00	0.237	56.07	*W* = 23.00	0.128	**-10.23**	***t* = -5.62**	**0.001**	-23.12	*W* = 13.00	0.866

KWANO

			Forage			Rest			Social			Travel		
	Predation risk	***df***	Average	Test statistic	*p*	Average	Test statistic	*p*	Average	Test statistic	*p*	Average	*t*	*p*
Gallery forest	Low	39	0.98	*t* = 0.64	0.528	0.86	*W* = 444.00	0.451	**0.47**	***W* = 495.00**	**0.030**	**-3.72**	***W* = 179.00**	**0.002**
Guinea savannah	Intermediate - high	39	0.74	*t* = 0.44	0.665	**-4.87**	***t* = -3.04**	**0.004**	**-2.21**	***t* = -2.94**	**0.006**	**7.10**	***W* = 661.00**	**0.001**
Lowland forest	Low	39	0.74	*t* = 0.35	0.731	**-4.97**	***t* = -2.04**	**0.048**	**-4.58**	***t* = -3.04**	**0.004**	**8.80**	***t* = 3.56**	**0.001**
Mango forest	Intermediate - low	21	-3.88	*W* = 144.00	0.570	-18.96	W = 12.00	0.833	**-8.37**	***t* = -7.73**	**< 0.001**	-21.06	*W* = 106.00	0.506
Palm forest	Low	36	**-15.34**	***W* = 145.00**	**0.002**	**16.84**	***t* = 3.78**	**0.001**	**4.58**	***W* = 459.00**	**0.048**	**-13.01**	***t* = -4.07**	**< 0.001**

Table 3.19: Summary of the questions addressed in this chapter and the result of the analyses.

Question	**Result**
1. Do the sizes of the home ranges of the Gamgam and Kwano troops differ?	Yes. The Gamgam troop ranged over a larger area (2.52 km^2) than did the Kwano troop (1.89 km^2).
2a. Does season affect the troops' day journey length?	Yes. Gamgam day journey was significantly shorter in the end of the wet season compared to the beginning of the wet and the beginning of the dry season. Kwano day journey in the end of the wet season was significantly shorter than in the beginning of the wet season.
2b. Do the Gamgam and Kwano troops differ in day journey lengths?	Yes. Day journey was significantly longer in Kwano (3.30 km) than in Gamgam (2.78 km).
3a. Does season affect the availability of food in the troops' home ranges?	Yes. In the Gamgam home range there was a peak in the abundance of leaves and fruit in the end of the dry season. During the beginning of the dry season food was relatively abundant, with a peak in the availability of fruit and seeds. In the beginning of the wet season availability was lower, but leaf availability showed a peak. Least food was available during the end of the dry season. In the Kwano home range food availability was most variable during the end of the dry season, and the availability of flowers, leaves, and fruit peaked during this season. Food availability was similar during the beginning of the wet and the end of the wet season and lowest in the beginning of the dry season.
3b. Does the food availability in the home ranges of the Gamgam and Kwano troops differ?	Yes. Food availability was higher in the Gamgam home range than in the Kwano home range in all seasons.
4a. Does perceived predation risk differ by habitat type?	Yes. The palm, gallery, and lowland forests were safest. Risk was intermediate in the mango forest, followed by the burned Guinea savannah and Guinea savannah. The elephant grass was high risk, whereas farms were most hazardous.

Question (*continued*)	**Result**
4b. Does the habitat-specific perceived predation risk differ by season?	Yes. This was lowest in the end of the dry season in the majority of habitat types. The Guinea savannah and burned Guinea savannah were most variable in predation risk; these habitats were most dangerous in the end of the wet season and safest in the end of the dry season.
4c. Do the home ranges of the Gamgam and Kwano troops differ in the level of perceived predation risk?	Yes. Higher in Gamgam home range, where 18% was high risk, 63% intermediate-high risk, and 19% was low risk. In Kwano home range 0% was high risk, 36% was intermediate-high risk, and 64% was low risk.
5a. Do the Gamgam and Kwano troops use habitats non-randomly?	Yes. Ranged selectively in gallery and palm forest, whilst avoiding the lowland forest and elephant grass in all seasons. Troops avoided the Guinea savannah in all seasons apart from the beginning of the dry season, when they selectively ranged in this habitat. Troops selected the mango forest in all seasons apart from the beginning of the dry season, when they avoided this habitat. Farms were selected in the end of the wet and dry seasons, and avoided in the beginning of the wet and dry seasons.
5b. Does habitat use differ with food availability?	Kwano troop selected gallery forest, and possibly mango forest based on food availability. No evidence for this in the Gamgam troop.
5c. Does habitat use differ with perceived predation risk?	No. No significant correlations between the risk of attack or capture and the electivity indices.
5d. Do baboons selectively engage in or avoid particular activities in particular habitats?	Yes. Troops selected low-risk habitats such as gallery, palm and lowland forest for socialising and resting. Troops enter the most hazardous habitats such as the Guinea savannah for travel. Foraging was as expected in all habitats apart from the palm forest.

3.4 Discussion

The results presented in this chapter are a first step towards understanding how ecology affects fission-fusion dynamics. In this chapter it was demonstrated that the level of both food availability and perceived predation risk was variable, with differences found across habitat types and seasons, as well as between the two troops. Furthermore, this variation appeared to affect ranging patterns of the troops and the way they used their home range. If fission-fusion dynamics indeed reflect a short-term optimisation of the cost-benefit ratio of group living, it is therefore expected that there is variation in patterns of associations (chapter 4) and fission-fusion dynamics (chapter 6) across seasons, and troops. Below, this variation in ecology across habitats, seasons, and troops, is discussed in greater detail.

3.4.1 Between-habitat differences in ecology and activities

In this chapter, the variation in the level of predation risk across habitats was investigated, as well as the influence of food availability and predation risk on the way baboons used their home range. Predation risk differed between habitat types, with the palm, gallery and lowland forests being the safest habitats, the mango forest, Guinea savannah and burned Guinea savannah having an intermediate risk, the elephant grass high risk, and farms the most dangerous. The availability of food and the level of predation risk had little influence on whether troops selected or avoided habitats, however, troops did seem to use their home range in a predator sensitive manner, selectively choosing or adjusting their activities to habitat-specific levels of predation risk.

If troops select habitats based on a trade-off between predation risk and food availability, one would expect habitat preferences to differ by activity. Surprisingly, neither troop demonstrated a preference for a habitat during foraging; foraging was not restricted to those habitats in which food was most abundant as they also foraged in habitats where food was less abundant in order to meet energetic needs. This result differs from that found for a population of chacma baboons, which foraged more frequently in safer habitats and less frequently in hazardous habitats than was expected based on food availability alone (Cowlishaw 1997c). However, the result found here does not necessarily indicate that habitat use during foraging followed an ideal free distribution, particularly as there was little evidence for a relationship between habitat use and food availability. Both troops preferred safe habitats for resting (Gamgam: gallery forest; Kwano: palm forest) and social interactions (Gamgam: gallery forest & lowland forest; Kwano: gallery forest & palm forest), whilst avoiding areas with high predation risk, such as the Guinea savannah, elephant grass, and farms. A similar result was found in four troops of chacma baboons, who avoided all habitats for resting and grooming, apart from the safest one (Cowlishaw 1997c). Nevertheless, for both troops in GGNP, the amount of resting that was seen in several habitats (*i.e.* Gamgam: lowland forest, agricultural land, elephant grass; Kwano: gallery forest, mango forest) was no different from expected, and unlike social activities, resting did therefore not occur exclusively in the safest habitats. Preferences for safe habitats for social activities are likely to be due to the reduced levels of vigilance during grooming. Rates of vigilance have been shown to be significantly reduced during grooming in blue monkeys (Cords 1995) and rhesus macaques (Maestripieri 1993).

Interestingly, these reduced levels of vigilance during grooming in blue monkeys did not affect the choice of the location for grooming (Cords 1995), whereas GGNP baboons did choose the safest habitats. Moreover, a greater degree of vigilance can also be sustained during resting compared to grooming (Cords 1995), which may have led to the greater selectivity observed in habitat type during social interactions as compared to resting.

It is not likely that the habitat preferences found in this chapter are due to an observation bias. Such a bias might occur when habitat visibility influences the likelihood of a focal animal being lost and the activity of the focal animal influences the likelihood of being located again (*i.e.* it would be more difficult to locate moving animals compared to stationary animals), leading to an increase in the instances that the troop was found to rest and engage in social interactions in the elephant grass. It was found, however, that the Gamgam troop avoided social interactions in the elephant grass, and the amount of time spent resting was as expected, suggesting that no such bias occurred. Likewise, while troops were found to avoid stationary activities, such as resting and social interactions, in Guinea savannah areas, this also occurred during the drier months when visibility was very good. This is therefore unlikely to be the result of being able to locate a stationary animal more easily. Within the gallery and lowland forest, the structure of the vegetation is similar, and therefore the likelihood of losing the troop is the same in each of these habitats. However, preferences for some activities in these habitats differed, suggesting that observer bias did not influence these results. Overall, these results seem to indicate genuine habitat preference for certain activities.

Apart from sensitivity to predation risk, the observed habitat use may also be the result of thermoregulation, the availability of water and access to safe sleeping sites (Barton *et al.* 1992). At both study sites, mornings can be cold, with minimum temperatures of 13°C at Gamgam and 15°C at Kwano, whilst over the course of the day temperatures could rise to a maximum of 46°C in Gamgam, and 39°C in Kwano. It is possible that the troops preferred certain habitats that helped to regulate their temperature. Both troops on cold mornings were frequently observed to spend some time sitting in the sun in the Guinea savannah, resting or grooming before starting to forage. The Kwano troop was also observed to sit in the crown of palm trees within the palm forest, where there was more direct sunlight. As the Kwano troop preferentially used the palm forest for resting and social interactions, it may have been chosen to help the troop warm up rather than because it was safe. This was not the case for the Gamgam troop as the Guinea savannah was avoided for both resting and social interactions.

Alternatively, forested areas may have been preferred to help avoid the sun during the hottest part of the day (Barton *et al.* 1992; Hill *et al.* 2004; Bettridge *et al.* 2010). Baboons have been observed to reduce feeding time and increase resting time and grooming when under thermal stress (Hill *et al.* 2004). Thus, the preferences for forested habitats for social activities and resting may also be due to the need to regulate temperature. Nevertheless, this is unlikely to be the sole factor influencing habitat use, as the lowland forest and mango forest were not preferred habitats for these activities, and these habitat types were similarly shady.

Finally, the location of sleeping sites might have influenced the habitat preferences of the troops. For the Gamgam troop, the majority of sleeping sites were within the lowland and gallery forest. For the Kwano troop, this was the palm forest and to a lesser extent the lowland and gallery forest. Thus, as during resting, the Gamgam troop preferred the gallery forest and the Kwano troop preferred the palm forest. This may have been partly affected by the location of suitable sleeping trees in these areas.

In summary, the level of predation risk was shown to differ between habitat types, and this was suggested to affect the way troops used their home ranges, although the presence of sleeping sites and the need for thermoregulation may partly underlie the preference for safe habitats for resting and social interactions. If fission-fusion dynamics reflect short-term optimisations of the cost-benefit ratio of group living, it is expected that grouping patterns are adjusted to the habitat. Larger, more cohesive parties are expected in higher risk habitats, such as elephant grass or farms, while smaller, more spread out parties are expected in safe habitats such as the palm, lowland, or gallery forest. Habitat-specific predation risk is related to fission-fusion dynamics in chapter 6.

3.4.2 Seasonal variation in food availability, predation risk, and ranging patterns

For both troops, the availability of food, predation risk, and ranging patterns were compared across seasons. Food availability and day journey length differed by season, although more markedly in the Gamgam troop than in the

Kwano troop. Predation risk did not vary significantly by season, apart from within the Guinea savannah and burned Guinea savannah.

Gamgam baboons seem to have adjusted their day journey length to both the availability and the quality of food. High-quality food items are those that are easy to digest and are rich in nutrients, such as carbohydrates, lipids, or proteins (Milton 1987; Strier 2003a), and include fruit, seeds, and flowers, in particular nectar. Low-quality food items are difficult to digest, providing less nutrients, and include mature leaves and grasses, which are high in fibre and cellulose (Strier 2003a). Young leaves are more attractive as a food source than mature leaves, as the protein-to-fibre ratio is higher in the former (Milton 1987). Fruit was abundant in the Gamgam home range during the beginning and the end of the dry season, when day journey lengths were relatively short. Due to the abundance of these high quality food items, baboons were able to meet their dietary needs in a smaller area in these seasons. During the end of the dry season however, an increased variability in the availability of high quality items and an increase in abundance of lower quality food items, led to a longer and a more variable day journey length. During the beginning of the wet season, the availability of seeds and fruit was low, while leaves were still relatively abundant. During this season, Gamgam baboons ranged the furthest each day. This pattern, of shorter day journeys when food was abundant and of better quality, is as predicted by socioecological theory (Byrne 2000) and has been observed in several baboon populations (Anderson 1981; Barton *et al.* 1992; Henzi *et al.* 1992).

A caveat in this relationship between food availability and day journey length is that the abundance of food in the home range does not necessarily indicate that individuals are feeding on these foods. For example, leaf abundance peaked in the Gamgam home range in the end of the dry season, but fruit was also abundant. Looking at feeding behaviours and in particular the proportion of feeding time troops spent on each food class across seasons, could give a clearer indication if the seasonal variation in the distribution of food influenced day journey lengths.

Interestingly, the relationship between day journey length and the availability of high-quality of food was reversed during the end of the wet season, when Gamgam baboons had the shortest day journey length, high quality food items were most scarce and the abundance of leaves was also relatively low. During this season Gamgam baboons also the spent least time foraging and instead used this time to rest (see Appendix A, Table A.3, Figure A.1 & A.2). It may be that the extremely high levels of rainfall at GGNP constrain the baboons in their daily activities, forcing more resting and reducing the amount of time available for foraging (Higham *et al.* 2009), thus reducing day journey length. This effect of heavy rainfall on activity patterns has also been noted in siamangs (*Symphalangus syndactylus*) (Raemakers 1980). Detailed nutritional analyses of Gamgam baboons have shown that during the wet season, both the energy intake rate and the energy expenditure rate were negatively correlated with rainfall (Lodge 2012), suggesting that Gamgam baboons were indeed constrained by high rainfall. The reduced activity during the end of the wet season may therefore be due to a combination of high rainfall and low food availability. Compared to the beginning of the wet season, mean monthly rainfall was higher in the end of the wet season (see section 2.2.1, Figure 2.3), with lower food availability. During periods of low food availability, primates may either increase their energy expenditure or settle for less or lower-quality food, and individuals may switch between these strategies (Raemakers 1980; Dunbar 1988). Whilst in the beginning of the wet season Gamgam baboons may have responded to low food availability by increasing their day journey length, the combination of additional rainfall and lower food availability may have led the baboons simply to ‘cut their losses’ and reduce energy expenditure during the end of the wet season. Similar patterns have been observed in lar gibbons (*Hylobates syndactylus*) and siamangs (*Symphakangus syndactylus*) who, during times of food scarcity, minimised day journey lengths (Raemakers 1980).

Gamgam baboons may be able to have a period of reduced foraging because they have access to relatively productive forest (Hohmann *et al.* 2006) all year round (Higham *et al.* 2009). As such, these baboons may be able to find food even when food availability is relatively low. Perhaps more importantly, Gamgam baboons had access to anthropogenic food sources, and this may have allowed the Gamgam baboons to build up a reserve on which they could draw during the end of the wet season. A previous study has shown that Gamgam baboons were at a nutritional advantage over Kwano baboons, leading to a significant difference in inter-birth intervals (Higham *et al.* 2009). Nevertheless, the reduction of activity does not come without costs; glucocorticoid levels of GGNP baboon were found to correlate positively with mean monthly rainfall (MacLarnon *et al.* 2010), indicating that during periods of high rainfall, baboons experienced higher levels of physiological stress.

Compared to Gamgam, the Kwano troop showed less seasonal variation both in day journey length, and in food availability; day journey was similar across the end of the wet, and during the beginning and end of the dry season. Differences between total food availability were mainly between the whole of the wet and dry seasons, whilst the availability of fruit did not differ significantly across seasons. Consequently, no clear relationship was found between food availability and day journey length. The tempering of seasonality in Kwano may be due to the inclusion of more forested habitat in the home range, which are less seasonal than savannah habitats (Dunbar 1988; Higham *et al.* 2009).

In short, day journey lengths of Kwano baboons showed less seasonal variation than those of Gamgam baboons, most likely because food availability varied less by season. Gamgam baboons on the other hand adjusted day journey lengths to the availability of food. A distinct pattern was found during the end of the wet season, where foraging activity and day journey lengths were reduced due to a combination of high rainfall and low food availability.

3.4.3 Between-troop variation in food availability, predation risk, and ranging patterns

The home range, day journey length, food availability and predation risk were compared between troops. Individuals in the Kwano troop travelled further each day, yet the home range of the Kwano troop was smaller. Overall, the Gamgam troop had more food available in all seasons, but this difference was mainly due to higher abundance of fruit and 'other' food items, including elephant grass stems, in the Gamgam home range. The Kwano troop had a larger proportion of low-risk habitat in their home range, while the Gamgam range also included elephant grass and farms, the two most dangerous habitats. Overall, the Kwano home range was safer than the Gamgam home range.

The between-troop difference in predation risk may, to some extent, have been underestimated here, as the effects of humans on the risk of predation were not taken into account. First, leopards may have been deterred from entering the Gamgam home range because this was close to human habitation (Boesch 1991). The Kwano research station was, however, within the home range of the Kwano troop, and therefore the deterrence of leopards by humans may have had a similar effect here. Secondly, humans may have affected between-troop differences in predation risk, as primates may perceive humans as predators, particularly when primates raid crops (Else 1991). Indeed, farmers were frequently observed to chase or even throw stones at baboons in GGNP. However, this would not alter the outcome of these analyses, but would only affect the magnitude of difference in predation risk in the home ranges of the troops.

A combination of differences in food availability and troop size may account for the variation in day journey lengths of the Gamgam and Kwano troops. Both across primate species and across baboon populations, smaller troops have been found to have shorter day journeys (Anderson 1981; Sharman and Dunbar 1982; Iwamoto and Dunbar 1983; Barton *et al.* 1996; Dunbar 1996; Bettridge *et al.* 2010). Because smaller troops have a lower total energy requirement and because they deplete patches at a slower rate, day journey length may be reduced (Dunbar 1988; Isbell 1991; Chapman and Chapman 2000).

Additionally, food was more abundant in the Gamgam home range, which may have further reduced the distance individuals needed to travel to meet their energetic requirements. Nevertheless, troop size has also been shown to affect home range size (Milton and May 1976; Iwamoto and Dunbar 1983; Barton *et al.* 1992; Swedell 2002) and the larger home range of the Gamgam troop is therefore somewhat surprising.

It may be that the quality of particular food items was higher for the Kwano troop, allowing the troop to range over a smaller area. The palm forest especially may have provided the Kwano troop with a high quality food throughout the year. However, this may have been off-set by the inclusion of anthropogenic food sources in the Gamgam diet, which are also considered to be high quality (van Doorn *et al.* 2010).

Alternatively, the spatiotemporal distribution of food patches may have affected home range sizes (Dunbar 1988; Strier 2003a). Thus, it may be that the less seasonal environment in the Kwano home range, as shown in the availability of food, allows the Kwano troop to range in the same area throughout the seasons. Furthermore, while the distribution of food patches was not measured directly, the curves of the cumulative home range size distribution give an indication that there was greater variation in the ranging areas of the Gamgam troop compared to the Kwano troop. For Kwano, the curve was near asymptote very quickly, and over the rest of the year only showed small increases in the size of the home range. This indicates that the Kwano troop ranged over the same small area throughout the year. The cumulative monthly home range size for the Gamgam troop on the other hand did not reach asymptote, but did show several plateaus during the year. This indicates that the troop ranged in the same area for a few months, before moving to another area, which suggested seasonality in ranging patterns

This is further supported by the location of seasonal core ranging areas within the home range (see Appendix A, Figure A.4 a & b). In the Gamgam troop, very little overlap was found between seasonal core areas, whereas in Kwano, core areas were less distinct over the seasons. Primate groups may migrate between distinct seasonal ranges due to seasonal variability in resource availability (Dunbar 1988). For example, vervet monkeys have similar sized core areas across seasons, but the location of these core areas varies, with areas being selected for their productivity (Willems *et al.* 2009). Thus, the home range of the Gamgam troop may have been larger because of greater seasonal variation in resource availability across areas of the home range.

In GGNP, levels of predation risk and food availability varied seasonally, which affected the ranging patterns and activity budgets of troops. Furthermore, differences were found in the seasonality of available foods between the two troops. Therefore, grouping patterns are expected to vary seasonally, and between troops. Association patterns can give a good indication of how individuals relate to conspecifics; however, with traditional dyadic analyses of association it is difficult to determine how this individual-level behaviour translates into patterns at the level of the troop. In the following chapter, a social network approach will be used to capture the spatiotemporal cohesion of troops, in order to make comparisons across seasons and troops.

3.5 Summary of chapter

- Predation risk was found to differ between habitats. The palm, gallery, and lowland forests were safest, the mango forest, Guinea savannah, and burned Guinea savannah had an intermediate risk, elephant grass had a high risk, and farms were the most dangerous.
- Both troops were found to range non-randomly in their home range, preferring gallery forest habitat, whilst avoiding lowland forest and Guinea savannah. Additionally, the Gamgam troop avoided agricultural land and elephant grass, while the Kwano troop preferentially ranged in the mango and palm forests.
- Availability and quality of food in the habitats had little influence on habitat use. Instead, troops used habitats in a predator-sensitive manner. Whereas for some activities, such as foraging and travelling, baboons were limited in habitat preferences, for social interactions and resting troops selected the safest habitats, probably because during these activities individuals are more vulnerable to predation and are less limited by the habitat type.
- For both troops, food availability and day journey length differed by season, although this was more marked in the Gamgam troop. Apart from in the Guinea savannah and burned Guinea savannah, predation risk did not vary with season.
- The Gamgam troop adjusted their day journey length to the abundance of high quality food items. However, during periods of low food availability and high rainfall, the troop altered their foraging strategy to

conserve energy. It was suggested that Gamgam baboons were able to do this due to the generally high productivity of forest habitats and the build-up of reserves from crop raiding. The higher proportion of forested habitat in the Kwano range meant that the availability of food was less seasonal here, and therefore may account for lower seasonal variation in day journey lengths.

- In the Gamgam home range, food availability and predation risk were higher than in the Kwano home range. Gamgam baboons travelled a shorter distance each day, but overall the troop had a larger home range than the Kwano troop did. A combination of a smaller troop with a greater abundance of food may have reduced the day journey of Gamgam baboons. Seasonal variation in the distribution of resources was found to affect the size of home ranges, leading to a larger home range in the Gamgam troop compared to the Kwano troop.

Chapter 4

Association networks

4.1 Introduction

Primates have relatively long lives, during which they have repeated social interactions with conspecifics that they recognise individually (Cheney and Seyfarth 1999; Silk *et al.* 1999). The majority of primates that live in social groups therefore have differentiated social relationships (Swedell 2012). The opportunities group members have for social interactions are critically affected by the spatiotemporal cohesion of their group and fluidity of grouping patterns may therefore lead to preferential associations and even the existence of cliques within a social group. Currently it is not known how the degree of fission-fusion dynamics may affect individual association preferences and how that translates to patterns at the level of the group. Furthermore, it is not known how flexible primates are in these patterns of associations, and if and how social and ecological factors affect the structure of associations.

Patterns of associations are an essential part of social organization, and consequently patterns of association have frequently been analysed in the study of primate sociality (*e.g.* to investigate the trade-offs of costs and benefits associated with group-living to individuals: (Chapman 1990; Hohmann *et al.* 1999; Newton-Fisher 1999; Shimooka 2003; Wakefield 2008; Sueur *et al.* 2011a); to identify the ecological pressures and social constraints on the order of progression during group movement (Sueur and Petit 2008); as a proxy for social structure (Ramos-Fernández *et al.* 2009); to define social groups (Sailer and Gaulin 1984); and to elucidate the sociality of a species or sex (Mitani *et al.* 1991; Wakefield 2008)). Association patterns are crucial for understanding the social cohesion of a society (Bezanson *et al.* 2008), and association networks in particular can help identify individual association preferences, subgroups or cliques in associations, and the cohesion of a group.

In this chapter, association preferences and substructures in association patterns are investigated in two olive baboon troops, using a social network approach. Furthermore, the impact of ecological and social factors on individual behaviour, and consequently on the network of associations are analysed.

4.1.1 Association preferences

While most primates have differentiated relationships, associations, because these are defined by the proximity of two individuals, may not necessarily reflect a social bond or preference. A ‘non-random social bias’ can result either from constraints by the physical environment, or from an active social preference (Lehmann and Boesch 2009). Passive associations occur when individuals are independently attracted to certain locations or resources, such as fruit trees, watering holes, or cycling females (Mitani *et al.* 1991; Newton-Fisher 1999). Individuals congregate around these resources, and are therefore in association with each other, but individuals do not necessarily choose to associate with some individuals over other individuals. This does not mean that individuals associate equally with all group members however, as individuals are likely to differ in their attraction to particular resources (Newton-Fisher 1999) or might not be tolerated near particular others. Thus, individuals with an attraction to similar resources may associate more frequently. Passive associations have been observed in orang-utans (Mitani *et al.* 1991), male chimpanzees (Pepper *et al.* 1999), female spider monkeys (Ramos-Fernández *et al.* 2009), and female chacma baboons (Henzi *et al.* 2009). Conversely, associations may be driven by the attraction to particular individuals, as pairs might actively seek each other out, whilst others avoid each other, making associations 'active' (Mitani *et al.* 1991; Newton-Fisher 1999).

While active associations have been observed in a number of primate species (mantled howler monkeys (Bezanson *et al.* 2008), chimpanzees (Newton-Fisher 1999; Pepper *et al.* 1999; Wakefield 2008), and in spider monkeys between males, and between mothers and their juvenile offspring (Ramos-Fernández *et al.* 2009)), it is not clear if baboon grouping patterns are the result of active associations or passive aggregations. Particularly, the social bonds of female chacma baboons have been the subject of some discussion (Silk *et al.* 2006; Henzi *et al.* 2009; Silk *et al.* 2010). In some studies it was found that females had strongly differentiated associations with other females (Silk *et al.* 1999) and formed strong and enduring social bonds with particular troop members (Silk *et al.* 2006; Silk *et al.* 2010). However, studies at other sites found that females did not form differentiated and stable relationships (Henzi *et al.* 2009). Instead it was suggested that associations between females were the result of increased gregariousness when food was more abundant (Henzi *et al.* 2009), which suggests these were passive associations. Moreover, the existence of social preferences for social interactions in baboons has been questioned and instead these may reflect market forces (Barrett *et al.* 1999), and evolved 'rule-of-thumb' strategies (Barrett *et al.* 2007). Thus, it is not clear to what extent baboons may show active preferences in their associations, and how that may affect grouping patterns. In order to understand the association patterns of olive baboons it is therefore crucial to determine first if individuals indeed have association preferences. Following on from this, constructing networks of associations allows for the investigation of whether cliques or substructures exist within each troop and what determines their membership.

4.1.2 Networks of associations

Societies that are fluid to some extent may have certain layers or substructures in networks of associations, of individuals that associate more frequently with each other than with the rest of their group. For example, Hamadryas baboons are known for having a multilevel social system in which individuals associate in harems, clans, and bands (Kummer 1968). While some foraging subgroups have been observed in olive baboons, it is not clear if these reflect longer term active or passive associations, and thus if there is a level of substructuring in association networks. Moreover, it is not clear how the degree of fission-fusion dynamics affects the extent of layering and substructuring of association networks through these social preferences. Association networks have proven valuable in the study of fission-fusion dynamics across animal species (Cross *et al.* 2005; Ramos-Fernández *et al.* 2006; Sundaresan *et al.* 2007; Wolf *et al.* 2007; Wolf and Trillmich 2008; Lehmann and Boesch 2009; Ramos-Fernández *et al.* 2009), particularly because they allow for the identification of layers and substructures (see section 1.5.3) in societies where these are not easily observable due to the societies' dynamic nature. The extent to which substructures are present is expected to vary with the degree of fission-fusion dynamics as follows.

In societies with a low degree of fission-fusion dynamics, there is little variation in party size, party composition, and spatial cohesion (Aureli *et al.* 2008a), and individuals thus associate frequently and simultaneously with all or the majority of the individuals in their group. In terms of the structure of the association network, this means individuals have ties with all individuals in their group, and the network is cohesive. On average, ties between individuals are strong, as all individuals are associated for the majority of time. Furthermore, in these networks no substructures are expected to appear, as individuals do not have a subset of individuals that they associate with more frequently.

Conversely, in groups with a high degree of fission-fusion dynamics, individuals associate in parties of variable size and composition. In association networks of such groups, individuals also have ties to all, or the majority of, individuals in their group, as over time individuals associate with the majority of members in their groups. However, because individuals are not always associated with all group members, on average, associations between individuals are weaker than in association networks of groups with a low degree of fission-fusion dynamics. This was for example seen in two species that are thought to have a high degree of fission-fusion dynamics, spider monkeys (Ramos-Fernández *et al.* 2009) and chimpanzee (Lehmann and Boesch 2009) association networks were dense when all associations were considered. Some structuring of the association network may appear; for example, chimpanzees were found to have long-term preferences in association partners (Lehmann and Boesch 2009), whereas the association networks of spider monkeys were segregated by sex (Ramos-Fernández *et al.* 2009). Nevertheless, substructures are not overly pronounced in the association networks of these types of groups, as individuals are less consistent in their association partners. For example, in the chimpanzee communities only about 14% of associations were more frequent than would be expected by chance, and in these networks of preferential associations, no distinct subgroups were found (Lehmann and Boesch 2009). Similarly, in the preferential association networks of spider monkeys all individuals were connected to a single network structure, and no substructures were found (Ramos-Fernández *et al.* 2009).

In groups with an intermediate level of fission-fusion dynamics, the structure of the association networks may be more difficult to predict as it may either be that all three aspects of fission-fusion dynamics have an intermediate level, or it may be that a group shows variation in some aspects of fission-fusion dynamics but not in others. Nevertheless, the extent of variation in the composition of parties may have the greatest influence on the structure of the association network. Variation in the size of parties does not affect association patterns much, apart from the secondary effect that a change in party size also indicates a change in party composition. Variation in spatial cohesion only affects association patterns if at times cohesion is so low that individuals are considered to be in different parties. Thus, it seems that it is largely the variation in party composition that affects the structure of association networks. In groups that fragment into set subgroups (*i.e.* subtroops), associations between individuals within subtroops are strong, whilst bonds between individuals in different subtroops are weak. In association networks of these groups, the strength of relationships would be differentiated and substructures would be clearly apparent.

Association networks in general, and the investigation into substructures in particular, can thus give us greater insights into the spatiotemporal cohesion of a society, and can help to identify if individuals have social preferences. Subsequently, it is possible to identify the ecological and social factors that may regulate these patterns of associations.

4.1.3 Ecological influences on associations

Socioecological theory outlines the way that the distribution of food and the risk of predation affect primate social organisation. The socioecological model has been extended to account for differences between baboon subspecies (Barton *et al.* 1996). In this model, variations in both the level of predation risk and the distribution of food are thought to account for the different social organisations and social structures observed in the baboon subspecies; the level of predation pressure is said to determine the potential for within-group competition and the distribution of food determines its form (Barton *et al.* 1996). Following this model, high levels of predation pressure lead to large groups or aggregations, thus increasing the potential for within-group contest competition. In these conditions, males would often cooperate (Figure 4.1 b & c). The cohesiveness of the group and the strength of female social bonds are further determined by the strength of within-group food competition (Barton *et al.* 1996). When food is dispersed, within-group competition is low, and females are thought to have relatively weak bonds with each other, but strong bonds with males (Figure 4.1b). When predation pressure is high, and food is clumped, troops are large and cohesive; females form strong bonds with each other, and may have special relationships with certain males (Figure 4.1c). Conversely, when predation risk is low, is it suggested that the potential for within-group competition is much lower, as groups or aggregations can be smaller. In this case, males may actively avoid each other (Figure 4.1a).

Following the recent shift of viewing the spatiotemporal flexibility of primate social organisations as differing in a scalar rather than a categorical manner (Aureli *et al.* 2008a), it is crucial to determine how flexible primate grouping patterns are, and if the socioecological model can account for these differences. For example, it is not clear if the socioecological model can account for more small-scale differences, such as between troops within a single population. Moreover, if primate grouping patterns are highly flexible, it is expected that individuals adjust their associations to seasonal fluctuations in their environment. Seasonal changes in food availability and distribution, and levels of predation risk (*i.e.* through changes in visibility or cover) alter the balance between the cost and benefits of associations to individuals and may consequently influence their patterns of associations.

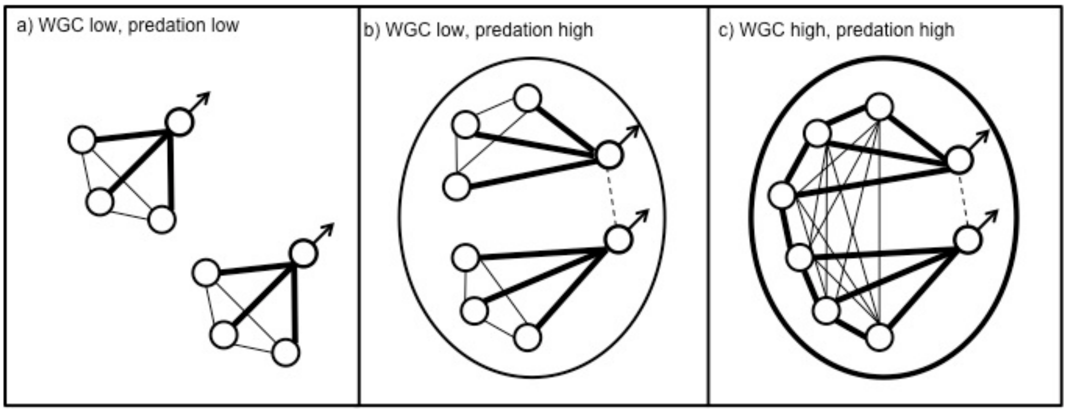


Figure 4.1: Diagram representing the baboon socioecological model (adapted from Barton *et al.* 1996). WGC = Within-Group Competition. Circles represent females, circles with arrows represent males. Strong bonds are indicated by thick lines, weak bonds by thin lines. Dotted lines represent coalitions between males. Ellipses represent group cohesion.

Some evidence for this level of flexibility has been found in long-haired spider monkeys, where the strength of associations was found to fluctuate seasonally, albeit differently for males and females (Shimooka 2003). Female spider monkeys' associations were influenced by both ecological (*i.e.* fruit abundance) and social (*i.e.* dependent offspring, reproductive state) factors; females associated in larger parties in the fruit abundant season, and nursing females were more gregarious than non-nursing females. Male associations were more stable throughout the seasons due to males being the philopatric sex (Shimooka 2003). Some indications that baboons may adjust their association to seasonal ecological conditions have also been found, as the associations of female chacma baboons were stronger, less differentiated, and more cliquey in seasons of food scarcity compared to when food was more abundant (Henzi *et al.* 2009). However, apart from these studies, the way seasonal changes in the environment affect association patterns has rarely been tested.

In this chapter, the flexibility of olive baboons' association patterns is investigated. In the previous chapter (chapter 3), it was shown that food availability and predation risk differed between troops and seasonally. Therefore the patterns of associations are expected to differ between troops and across seasons. Between-troop and seasonal comparisons of association networks can elucidate whether there are small-scaled differences between troops, and seasonal difference within troops, and if the socioecological model can account for those differences. However, over the last decade the impact of social strategies on primate grouping patterns has become apparent, and social influences on associations should therefore also be considered.

4.1.4 Social influences on associations

Fitness not only depends on survival, it also depends on reproduction; finding mates and protecting offspring are crucial to an individual's reproductive success (Chapman 1990). Whilst ecological pressures set an upper and lower limit to group size, (van Schaik and van Hooff 1983) and thus the number of conspecifics an individual associates with, social pressures may influence with *whom* individuals associate (Chapman 1990; Aureli *et al.* 2008a). Individuals therefore have both 'ecological' and 'social' fitness considerations that influence association patterns, and consequently social organization (Aureli *et al.* 2008a; Kummer 2008). A number of studies have identified the importance of social strategies for shaping individual association preferences in primates (Chapman 1990; Sakura 1994; Matsumoto-Oda *et al.* 1998), and sex, reproductive state, kinship, and dominance are thought to be key organising principles in primates societies (Gouzoules 1984). However, it is not yet known how these individual-level strategies affect the structure of associations at the level of the troop. Looking at social strategies across animal taxa can inform theories about the social factors that influence the troop-level structure of associations.

4.1.4.1 Age and sex

Social strategies may involve preferentially associating with troop members of the same age or sex. Age may be used as a context-dependent proxy for paternal relatedness in baboons (Silk 2002b; Boyd and Silk 2006). Because high-ranking males often monopolize access to receptive females for some time, individuals of a similar age are therefore more likely to be paternal half-siblings (Silk *et al.* 2006). There are some indications that age is used as a proxy for paternal relatedness in baboons; female yellow baboons that were not maternally related were shown to have stronger grooming and proximity bonds with females that were close in age (Silk *et al.* 2006).

Individuals may preferentially associate with individuals of the same sex to reduce the costs of compromising their time budgets. Behavioural synchronisation occurs when individuals within a group engage in identical activities, and it is a common feature of animal groups (Rands *et al.* 2008; King and Cowlishaw 2009). Maintaining behavioural synchrony can be costly to individuals, as individuals differ in their metabolic requirements, energetic gains, and vulnerability to predation, particularly in sexually dimorphic species (Chapman 1990; Rands *et al.* 2008; King and Cowlishaw 2009). When the costs of synchronisation become too high, groups fragment (Conradt and Roper 2000; Conradt and Roper 2005), leading to a social segregation of a group (Conradt and Roper 2000). While, sexual dimorphism is relatively high in baboons (Swedell 2011), it is not yet known if sex is an important organising factor baboon associations.

Sexual-segregation of primate groups may also occur due to a sex difference in predation risk or a sex difference in foraging preferences (Ruckstuhl and Neuhaus 2000). Females may be more vulnerable to predation (Rands *et al.* 2008), and may therefore be more gregarious in order to reduce levels of predation risk, or prefer habitats that have a lower predation risk, leading to spatial segregation of the sexes (Ruckstuhl and Neuhaus 2000). Furthermore, if males and females differ in their feeding preferences, the sexes may select different habitats that differ in food abundance and consequently the sexes may segregate (Ruckstuhl and Neuhaus 2000).

4.1.4.2 Dominance rank

Dominance rank has been identified as one of the key principles that organise primate groups (Hinde 1976; Gouzoules 1984). Interactions between individuals of different rank are often characterised by low-level threats or overt aggression, and individuals that are low ranking may be anxious about associating with higher-ranking troop members. For example, female olive baboons show higher levels of self-directed behaviours, a measure of stress, when they are near more dominant individuals (Castles *et al.* 1999). Thus, if low-ranking individuals avoid associating with higher-ranking individuals, association patterns will be influenced by patterns of dominance. For example, in yellow baboons, among unrelated individuals, females tended to have stronger proximity and grooming bonds with females that were closer in rank (Silk *et al.* 1999; Silk *et al.* 2006). While it is clear that dominance rank is important in shaping individual social strategies, it is not clear if this also affects associations, and group-level patterns of associations.

4.1.4.3 Female gregariousness and dependent offspring

Individual social strategies of females may vary with the presence of dependent offspring (Fairbanks 1976; Collins 1984; Chapman 1990; Shimooka 2003; Nguyen *et al.* 2009). Firstly, mothers with dependent infants may be more prone to predation than females without dependant offspring, as predators are more likely to target infants (Shimooka 2003; Barrett and Henzi 2006), and because baboon mothers carry their infants they may be slower in fleeing from a predator (Barrett *et al.* 2006). Nursing chacma baboons have been shown to be more vigilant than non-nursing females (Barrett *et al.* 2006), suggesting that females with dependent offspring perceive the risk of predation to be higher.

Secondly, as in many other primate species, new-born infants are a source of great attraction to baboons. Troop members try to touch, sniff, nuzzle, and inspect the infant whilst being in contact with the mother of the infant (Altmann 1980; Silk 1999; Henzi and Barrett 2002; Silk *et al.* 2003a). Mothers receive a lot of attention, as they are approached and groomed at high rates, especially when their infants are very young (Henzi and Barrett 2002; Silk *et al.* 2003b). In a captive group of yellow baboons, the birth of a new infant increased the mother's associations with both males and females, and affected the composition of proximity-based subgroups (Fairbanks 1976). Yellow baboon mothers of young offspring are more gregarious than females without young offspring (Collins 1984). Consequently, the association patterns of females are expected to vary with presence of dependent offspring, either because new mothers themselves become more gregarious, or because troop members are attracted to her infant. These individual fitness considerations may further affect the troop-level structure of associations.

4.1.4.4 Female reproductive state and friendships

When the reproductive state of females in a group changes, the balance of the costs and benefits of group living for both male and female troop members shifts. For males, one of the benefits of group living is access to mates, and therefore males' associations may be influenced by female reproductive state. Party composition and size are affected by the number of cycling females in chimpanzees (Sakura 1994; Matsumoto-Oda *et al.* 1998; Newton-Fisher 1999), where oestrous females are more frequently found in mixed-sex association than anoestrous females (Pepper *et al.* 1999), and males associate more frequently with oestrus females compared to anoestrous females (Pepper *et al.* 1999). Similarly, in orang-utans female reproductive state has a crucial influence on association patterns; inter-population differences in association patterns are largely accounted for by differences in female reproductive state; a population with more cycling females was found to have longer associations, males associated with each other more frequently, and females were more gregarious, compared to a population with fewer cycling females (Mitani *et al.* 1991).

For females, the balance between the costs and benefits of group living also changes with reproductive state. Female baboons become less gregarious when they are pregnant; they stay more on the periphery of their troop (Collins 1984; Barrett and Henzi 2002), and generally become less social (Barrett and Henzi 2002). It has been suggested that the asociality of pregnant females is a strategy to avoid conflict and reduce aggression by conspecifics, in order to protect their future offspring (Barrett and Henzi 2002), through avoidance of injury or a reduction in stress. Psychosocial stress has been shown to be the cause of miscarriages in several mammal species (Friebe and Arck 2008).

Lactation may also influence female association patterns; in spider monkeys, nursing females associated more with both males and females compared to non-nursing females (Shimooka 2003). This increase in female gregariousness during lactation may be due to an increase in predation pressure for females with young infants (Shimooka 2003), which has also been suggested to occur in baboons (Barrett *et al.* 2006). However, in yellow baboons, the spatial position of lactating females was not found to differ from that of cycling females (Collins 1984).

Overall, females' reproductive success may influence association patterns; males may be more attracted to cycling females than to non-cycling females, pregnant females may avoid troop members, whereas lactating females may be more gregarious.

In addition to female reproductive state, associations between males and females may also be influenced by friendships that are formed between adult males and females with young offspring. Friendships in baboons are characterised by high rates of association and grooming, and low rates of submissive and aggressive behaviours (Cheney and Seyfarth 2007; Nguyen *et al.* 2009; Moscovice *et al.* 2010), and often end once the infant is weaned or dies (Cheney and Seyfarth 2007). Consequently, association networks may be assorted around strong associations between lactating females and adult males.

4.1.4.5 Individual social strategies and troop-level association patterns

Apart from the strategies outlined above, matrilineal kinship is also likely to have a great influence on the structure of associations of olive baboons; females may associate preferentially to cooperatively defend resources against members of other matrilines (van Schaik 1989), and to receive higher rates of support in agonistic contests (Silk *et al.* 2004). For example, it has been observed that maternal relatives in savannah baboon troops have a tendency to associate, forming kin-based subgroups within the wider troop (Smuts 1985). However, in this study, the kin relationships that were known were mainly between mother and offspring. Therefore it was not possible to determine the influence of matrilineal membership on the structure of association networks.

Overall, the evidence for individual fitness considerations relating to, for example, mating strategies or the optimisation of time budgets, is rapidly growing. But despite this growing evidence for the influence of social factors on individual association patterns, it has been difficult to understand how complex decisions at the level of the individual shape patterns at the level of the group. The social network approach is particularly beneficial in this respect, as it allows for analysis at the individual, subgroup, and group-level, and can therefore help to understand how each of these levels affect each other.

4.1.5 Aims of this chapter

The aims of this chapter are to test if olive baboons have preferential associations, to investigate if olive baboons show flexibility in their grouping patterns, and to investigate if baboons adjust association patterns to ecological and social factors. To this end, association networks are analysed, focusing on how these association patterns differ between seasons and between troops, and investigating the influence of social factors, such as age, sex, the presence of dependent offspring, female reproductive state, and dominance, on such patterns. The research questions of this chapter are as follows:

1. Do GGNP baboons have preferential associations?
2. Do GGNP baboons show substructures in their association networks?
3. Do the association patterns of GGNP baboons differ by season?
4. Do the association patterns of the Gamgam and Kwano troop differ?
5. Are association patterns influenced by social factors?
    a. Are association networks assorted by age or sex?
    b. Are the associations of females affected by the presence of dependent offspring or reproductive state?
    c. Are associations between females affected by dominance relationships?

d. Are associations between females and males affected by lactation or cycling?

4.2 Methods

A summary of the questions addressed in this chapter, along with the analyses and the data used, is given in Table 4.7.

4.2.1 Association networks

All individuals that were seen during a scan were considered to be associated (see section 2.4.1 for details on scan sampling). As five minutes before each scan researchers walked around the area to locate baboons, this definition of an association is somewhat broader than a purely visual one, and may thus give a more accurate estimate of associations in habitats where visibility is frequently low, due to vegetation or an uneven terrain. The TWI was calculated for each dyad from scan data (see section 2.5), and association networks were generated from these data.

To help focus on biologically important relationships (Croft *et al.* 2008; Franks *et al.* 2010), association networks were filtered. Results of the comparison with random networks for determining the appropriate level of filtration are given in Table 4.1 (see section 2.5.1 for a full description of this method). The level of filtration was set at TWI = 0.16 for the Gamgam network, and TWI = 0.08 for the Kwano network. These filtration levels have a similar relation to the mean association index values in the Gamgam and Kwano troops (Gamgam

0.16/0.252 = 0.64; Kwano 0.08/ 0.117=0.68). Network filters were applied to weighted networks; thus in Gamgam associations weaker than 0.16 were excluded, in Kwano associations weaker than 0.08 were excluded. The filtered networks were used in all analyses unless stated otherwise.

Table 4.1: Results for the significance calculations of filtration levels. Metrics marked * are significantly different from mean of the metrics for the random networks. Bold values indicate when the association network was found to be different from random, *i.e.* where both metrics were significantly different from random.

			Mean clustering coefficient			**Mean shortest path length**		
Troop	**Filtration level**	**Density**	**Observed**	**Random**	**SD**	**Observed**	**Random**	**SD**
GAMGAM	Unfiltered	1.000	1.000	1.000	0.000	1.000	1.000	0.000
	0.01	1.000	1.000	1.000	0.000	1.000	1.000	0.000
	0.02	1.000	1.000	1.000	0.000	1.000	1.000	0.000
	0.03	1.000	1.000	1.000	0.000	1.000	1.000	0.000
	0.04	1.000	1.000	1.000	0.000	1.000	1.000	0.000
	0.05	1.000	1.000	1.000	0.000	1.000	1.000	0.000
	0.06	1.000	1.000	1.000	0.000	1.000	1.000	0.000
	0.07	0.964	0.964	0.964	0.000	1.036	1.036	0.000
	0.08	0.893	0.929	0.899	0.019	1.107	1.107	0.000
	0.09	0.857	0.929*	0.861	0.031	1.143	1.143	0.000
	0.10	0.857	0.929*	0.856	0.025	1.143	1.143	0.000
	0.11	0.821	0.940*	0.825	0.039	1.179	1.179	0.000
	0.12	0.786	0.959*	0.781	0.046	1.214	1.214	0.000
	0.13	0.786	0.959*	0.788	0.053	1.214	1.214	0.000
	0.14	0.786	0.959*	0.789	0.046	1.214	1.214	0.000
	0.15	0.786	0.959*	0.789	0.047	1.214	1.214	0.000
	0.16	**0.750**	**1.000***	**0.762**	**0.059**	**1.000***	**1.250**	**0.000**
KWANO	Unfiltered	0.992	0.992	0.992	0.000	1.008	1.008	0.000
	0.01	0.992	0.992	0.992	0.000	1.008	1.008	0.000
	0.02	0.975	0.979*	0.975	0.001	1.025	1.025	0.000
	0.03	0.933	0.967*	0.934	0.004	1.067	1.067	0.000
	0.04	0.900	0.946*	0.900	0.005	1.100	1.100	0.000
	0.05	0.867	0.943*	0.867	0.008	1.133	1.133	0.000
	0.06	0.842	0.920*	0.843	0.009	1.158	1.158	0.000
	0.07	0.792	0.900*	0.791	0.013	1.208	1.208	0.000
	0.08	**0.700**	**0.885***	**0.700**	**0.021**	**1.308***	**1.300**	**0.000**

Seasonal association networks were constructed for each of the 3-month periods outlined in section 2.2.1. These seasonal networks were filtered to the same level as the overall association networks.

4.2.2 Estimation of dominance hierarchy

The dominance rank of the study subjects was determined from aggressive and submissive interactions between dyads recorded *ad libitum* (Altmann 1974) and during focal observations. These data were entered into a matrix and Landau's linearity index correcting for the number of unknown relationships (h') was calculated using MatMan software (Noldus Information Technology 2003). Landau's h' is more appropriate when some relationships are tied.

In Gamgam females formed a strong linear hierarchy (Landau's index h': 1.000, $\chi^2_{30} = 52$, $p = 0.008$ – see Appendix B, Table B.1). Females of one matriline (MMK, KAN, GLO) ranked above all other females. Within this matriline, the mother was ranked highest (MMK), followed by her older daughter (KAN), and then her younger daughter (GLO). It was not possible to calculate a linear dominance hierarchy for the Gamgam males due to the low number of aggressive and submissive interactions between males. Kwano females also formed a linear hierarchy (Landau's index h': 0.647, $\chi^2_{20.63} = 47.88$, $p = 0.0007$ – see Appendix B, Table B.2). No linear hierarchy was found for the Kwano males (Landau's index h': 0.333, $\chi^2_{20.16} = 14.16$, $p = 0.822$), which again may be due to the low number of interactions between males.

As no dominance hierarchy was found for the males of either troop, in subsequent analyses only females' dominance was entered into analyses.

4.2.3 Data analysis

The analyses used to answer each research question are outlined below. Research questions, analyses and variables are summarised at the end of this section (Table 4.7).

4.2.3.1 Do GGNP baboons have preferential associations?

Baboons were considered to be preferred associates when they associated significantly more frequently than expected by chance (Bejder *et al.* 1998; Whitehead *et al.* 2005). Therefore, for each dyad it was determined if TWI was significantly different from random. To this end, the TWI of each dyad was compared to the distribution of the TWI between those individuals after 10000 permutations of the association network. If the observed TWI value fell within the outer 5 % of the frequency distribution, it was considered to be significantly different from random. In these permutations the TWI values were assigned to randomly chosen dyads, using the 'rg_reshuffling_w' function in tnet (Opsahl 2009). For these analyses unfiltered networks were used.

4.2.3.2 Do GGNP baboons show substructures in their association networks?

A clique analysis was performed in UCINET (Borgatti *et al.* 2002) to test whether there were substructures in the association networks. A clique is defined as group of individuals between which all possible relationships exist, or in other words, that form a 'maximal complete sub-graph' (Hanneman and Riddle 2005). The clique analysis in UCINET finds cliques by first looking at the most basic subgraph, the *minimum set*, and then adding individuals who have ties to all the existing members in the subgraph, thus indicating how the larger network is built up from its smaller components (Hanneman and Riddle 2005). In these analyses the *minimum set* was set at three, as this is the smallest clique possible above a dyad.

When spatial associations are cohesive in a troop, a single clique should emerge, in which all individuals are connected to each other. When troops have more fragmented spatial associations, several cliques should emerge. When these cliques do not overlap, *i.e.* no individual is a member of more than one clique; this indicates that individuals consistently associate with the same troop members in subgroups (*i.e*. subtroops). When there is overlap between cliques, the formation of subgroups may be more fluid, so that the composition of these subgroups varies over time (*i.e.* parties).

Substructures in networks may not only be due to the presence or absence of relationships between individuals; the strength of those associations is also important. Therefore, in addition to the presence of cliques, the association networks were tested for the presence of weighted network cliques, or *weighted network modules*. Weighted network modules are subgraphs that contain a specified minimum number of individuals (k-clique) (Palla *et al.* 2005), and that have a mean strength of relationships above a specified threshold (Onnela *et al.* 2005). This threshold is the *subgraph intensity*, which is denoted by I. K-cliques are maximal complete subgraphs of size k, and I is the geometric mean of the weights of the ties in a subgraph:

$$I(c) = \left(\prod_{i<j} w_{ij} \right)^{2/k(k-1)}$$

Where ω_{ij} is the weight of the tie between node *i* and node *j*, and *k* is the size of the subgraph (Farkas *et al.* 2007). A weighted network module is then a maximal group of *k*-cliques, with a value of *I* above a set threshold (Farkas *et al.* 2007).

Weighted network modules were found using CFinder software (Palla *et al.* 2005; Palla *et al.* 2010), which uses the Clique Percolation Method (CPM) (Palla *et al.* 2005) to find cliques. For this analysis, first the optimal values for *I* and *k* were found. When the intensity threshold *I* is set at a low value, a wide range of *k* values can be found, because when the intensity threshold is lower, more individuals can be included in the maximal complete subgraphs, thus increasing the range at the higher end. However, at low intensity thresholds the weighted network module is likely to contain the entire, or the majority of the network, thus concealing some of the community structure. At high values of *I*, on the other hand, more substructures may be found in the networks, however, the range of *k* values is much narrower. Therefore, to find the richest network structure, the optimal value of *I* should be found. This optimal value is just above 'the critical point', which is low enough to allow for a wide range of *k* values, but high enough to stop a giant component emerging (Farkas *et al.* 2007). For each level of *k*, the value for *I* is lowered by increments of 0.01, and the CFinder program is rerun. In small networks the critical point is determined using the ratio between the size of the second largest module and the smaller modules, following:

$$\chi = \sum_{n_\alpha \neq n_{max}} n_\alpha^2 / (\sum_\beta n_\beta)^2$$

(Farkas *et al.* 2007) where n is a network module. For each k the optimal I is the one that gives the greatest χ. Then the optimal k parameter is selected as the one that gives the broadest size distribution of modules.

However, in the Gamgam and Kwano association networks, at any levels of I and k, never more than two modules were found, making it impossible to calculate χ for these networks. Therefore, instead of using the ratio between the modules, the optimal I was chosen for each fixed k value as the threshold that gave the broadest range of community sizes. Subsequently, the k parameter with the broadest size distribution at its optimal I was selected (Farkas *et al.* 2007). For Kwano this was $I = 0.18$, $k = 5$. At all varying parameters the Gamgam network always had just one module, with individuals dropping out of the module as the clique intensity threshold increased. It was therefore not possible to determine the optimal parameters for the Gamgam network. Instead, the parameters used for the Gamgam network were based on the Kwano parameters. The clique intensity threshold for Gamgam was determined by taking the same ratio of I to the mean association value as for the Kwano troop, making these thresholds comparable across troops. K was kept at 5. At $k = 5$, the ratio from I to the mean association value in Kwano was 1.54 (I / mean TWI = 0.180000/0.116875 = 1.540107), and therefore, to maintain the same ratio, the I for Gamgam was set at 0.39 (I / mean TWI = 0.387435/0.251564 = 1.540107). Additionally, these analyses were run with $k = 3$, as three individuals is the minimum definition of a clique above a dyad. In Kwano, with $k = 3$, the broadest range of modules was found at $I = 0.20$. The ratio of I to the mean association value was 1.71123 in

Kwano (*I* / mean TWI = 0.200000/0.116875 = 1.71123), and therefore the *I* for Gamgam was set at 0.43, so that the ratio of the *I* to the mean TWI was the same as in Kwano (*I* / mean TWI = 0.430484/0.251564 = 1.71123).

4.2.3.3 Do the association patterns of GGNP baboons differ by season?

Seasonal association patterns were quantified using social network analysis; to quantify the structure of the association networks, ten network metrics were calculated and compared descriptively; the largest strong component, density, weighted diameter, weighted mean geodesic, mean degree, weighted mean degree, average tie strength, weighted mean clustering coefficient, weighted network centralisation (see section 2.5.2 for definitions) were calculated in *tnet* (Opsahl 2009), and compactness was calculated in UCINET (Borgatti *et al.* 2002). Networks were tested for significant difference in density using permutations tests in UCINET (Borgatti *et al.* 2002). To determine if associations were stable over time, the seasonal networks were correlated using a QAP correlation (Borgatti *et al.* 2002; Hanneman and Riddle 2005).

4.2.3.4 Do the association patterns of the Gamgam and Kwano troop differ?

Association networks were constructed for the entire study period, and ten network metrics were calculated (see section 2.5.2) and compared qualitatively. To allow for a better comparison between networks of different sizes, for the degree and largest strong component, normalised measures were also calculated, and the weighted mean geodesic was divided by the weighted diameter.

Nevertheless, comparing networks of different sizes is not without difficulties as the surface structure of a network, such as its size, can have a considerable influence on the calculated network metrics (Anderson *et al.* 1999), and normalising metrics by network size may not always control sufficiently for the size of a network. For example, the mean score and variance of degree centralisation have been found to be lower in larger networks, despite this being a size-normalised metric (Anderson *et al.* 1999). The effect of surface structure on metrics is due to the constraints on the number of networks that are possible given the number of nodes. The size of a network affects both the range of values possible and the value that is most common for a given network metric. In other words, networks of a certain size may be 'predisposed' to a certain distribution of a network metric (Anderson *et al.* 1999). By controlling for the size of the network it is possible to determine if the difference seen between two networks is due to a difference in the social interactions in a troop, or if this is a secondary effect due to the difference in the size of the troops.

Whilst this is a well-known issue within the social network approach (e.g. Faust and Skvoretz 2002; Faust 2006; Croft *et al.* 2008), controlling for surface structures when making comparisons between networks of different sizes remains difficult. Although some attempts have been made to overcome such issues (Faust and Skvoretz 2002; Faust 2006), these methods are not without flaws (pers. comm. Faust 2011). One way to control for the size of a network is to compare the absolute difference between the metrics of two observed networks to a baseline model, using conditional uniform graph tests (Butts 2011). The baseline model is generated from the differences in metrics between two random networks with identical number of nodes as the observed networks. Using a Monte Carlo procedure, the likelihood of the observed difference between network metrics is estimated. Here, the p-value for a two-tailed test was determined by:

$$pr\left(t(H) \geq t(G)\right) \text{ or } pr\left(t(H) \leq t(G)\right)$$

Where $t(H)$ is the difference in a metric for a random set of networks, and $t(G)$ is the difference in a metric for the observed networks (Butts 2011).

Here, the conditional uniform graph test procedure was used to determine if there was a difference in the density of ties between the association networks of the two troops, irrespective of their difference in size, using the SNA package (Butts 2010) for R (R Development Core Team 2010). Currently it is only possible to test for difference in binary metrics using this procedure, thus the results indicate a difference in the number of ties, not taking into account the weight of those ties. Therefore, dichotomised networks were used in these analyses, in which dyads that had a tie in the filtered network, had a tie of 1 in the dichotomised network, and dyads without a tie in the filtered network had a tie of 0 in the dichotomised network (*i.e.* no tie). The number of replications was set to 20000.

4.2.3.5 Are association patterns influenced by social factors?

4.2.3.5.1 Are association networks assorted by age or sex?

To test if individuals associated more with troop members of the same sex or age class, the density of ties within and between each category was compared to the distribution of ties in 10000 random permutations, using a ‘joint-count’ analysis. The densities of ties were compared between males and females, and between adults and subadults. The number of individuals in each age and sex class is given in Table 4.2.

Table 4.2: Sample sizes of age and sex classes in Gamgam and Kwano troops.

GAMGAM

	Adult	Subadult	Total
Female	5	0	5
Male	1	2	3
Total	6	2	

KWANO

	Adult	Subadult	Total
Female	9	1	10
Male	5	1	6
Total	14	2	

4.2.3.5.2 Are the associations of females affected by the presence of dependent offspring or reproductive state?

The effect of dependent offspring on female associations was tested with a node-level t-test (Borgatti *et al.* 2002). To this end, the node strength, *i.e.* the sum of the strength of an individual's relationships, was calculated for each female, and the average node strength of females with dependent offspring was compared to that of females without dependent offspring. For these analyses dependent offspring was defined as infants up to 8 months old (*i.e.* black infants). The number of females in each category is given in Table 4.3. Node strength scores were randomly permuted between categories to create a sampling distribution against which the statistical significance of the difference between means was determined. The number of permutations was set to

10000. For these analyses the seasonal association networks were used, as the dependency of offspring changes rapidly over a year (*e.g*. maturing and births).

In order to test if female association patterns were influenced by their reproductive state, a node-level ANOVA was run (Borgatti *et al.* 2002), in which the average node strength of females was compared across three categories; cycling females, lactating females, and pregnant females (for definitions see chapter 2). The number of females in each category is given in Table 4.4. Females that had anovulatory cycles (*i.e.* not pregnant, lactating, and no sexual swellings) were grouped with cycling females. The node strength scores were randomly permuted (5000 permutations) to determine statistical significance of the difference between means. Seasonal association networks were used for this analysis.

Table 4.3: Number of females with and without dependent offspring in the Gamgam and Kwano troops. Dependent offspring is defined here as infants up to 8 months old.

	GAMGAM		KWANO	
Season	Without dependent offspring (*n*)	With dependent offspring (*n*)	Without dependent offspring (*n*)	With dependent offspring (*n*)
BEG WET	3	2	9	1
END WET	4	1	8	2
BEG DRY	4	1	8	2
END DRY	4	1	6	4

Table 4.4: Number of females in each reproductive category in the Gamgam and Kwano troop.

	GAMGAM			KWANO		
Season	Cycling (*n*)	Lactating (*n*)	Pregnant (*n*)	Cycling (*n*)	Lactating (*n*)	Pregnant (*n*)
BEG WET	2	2	1	3	4	3
END WET	2	2	1	2	4	4
BEG DRY	3	2	-	6	3	1
END DRY	3	2	-	6	4	-

4.2.3.5.3 Are associations between females affected by dominance relationships?

To determine if association patterns were influenced by dominance rank, a relational contingency-table analysis was performed in UCINET (Borgatti *et al.* 2002). For this analysis, females were grouped according to rank as calculated for all females in the troop (*i.e.* also females not included in the networks), such that the highest ranking third of females were labelled as 'high-ranking', the third of females with intermediate ranks as 'middle-ranking', and the lowest ranking third of females as 'low-ranking' (Table 4.5).

Furthermore, to determine if baboons that were more similar in dominance rank were closer in the association network, the Geary statistic for autocorrelation was calculated in UCINET (Borgatti *et al.* 2002). Difference in dominance rank was calculated for each pair of baboons, and correlated to their weighted distance in the association network, which also takes the strength of the associations into account. A Geary statistic of 1 indicates no association between the attribute and the distance in the network, values below 1 indicate a positive association, and above 1 a negative association. The autocorrelation score was compared to the average calculated for 1000 random permutations to determine if this association was significantly different from random. For both troops, there was only a clear dominance hierarchy for the females; therefore males were excluded from these analyses.

Table 4.5: Number of females in each rank category in Gamgam and Kwano troops.

Rank	GAMGAM (*n*)	KWANO (*n*)
High	2	4
Middle	1	3
Low	2	3

4.2.3.5.4 Are associations between females and males affected by lactation or cycling?

To test if lactation or cycling influenced the association between males and females, two-sample permutation tests (10000 permutations) were performed on the TWI of males and lactating females versus the TWI of males and non-lactating females and on the TWI of males and cycling females versus the TWI of males and non-cycling females, in R (R Development Core Team 2010; Maindonald and Braun 2011). In both analyses seasonal association networks were used as reproductive state of females changes frequently. When females changed reproductive state during a season, which would move them from one category into another (*i.e.* resuming cycling after lactation, conception or miscarriage) the state that the female was in for the majority of days in that season was used.

Non-lactating females are cycling and pregnant females (See Table 4.4 for the number of females in each category). Non-cycling females were defined as females that were lactating, pregnant, giving birth, and ‘non-cycling’ (*i.e.* females that were not lactating or pregnant, but also showed no sexual swellings); cycling females were defined as both cycling and nulliparous cycling females (in both cases females had sexual swellings). The number of females in each of these categories is given in Table 4.6 .

Table 4.6: Sample sizes for two-sample permutation test of male - female associations, comparing the relationships of cycling females with males to the relationships between non-cycling females and males.

	GAMGAM		KWANO	
Season	Cycling (*n*)	Non-cycling (*n*)	Cycling (*n*)	Non-cycling (*n*)
BEG WET	2	3	3	7
END WET	2	3	2	8
BEG DRY	3	2	5	5
END DRY	3	2	5	5

Table 4.7: Questions addressed in this chapter, the type of analyses and the data used.

Question	Analysis	Data used
1. Do GGNP baboons have preferential associations?	Randomisation tests	• Unfiltered TWI over the whole study period
2. Do GGNP baboons show substructures in their association networks?	Clique analysis	• Association network over the whole study period • Minimum set = 3
	Weighted network module analysis	• Association network over the whole study period • *K* = 5; *I* =0.39 (Gamgam), *I* =0.18 (Kwano) • *K* = 3; *I* =0.20 (Gamgam), *I* =0.43 (Kwano)
3. Do the association patterns of GGNP baboons differ by season?	Network metrics	• Seasonal association networks
	Density permutation tests	• Density of seasonal association networks
	QAP correlation	• Seasonal association networks
4. Do the association patterns of the Gamgam and Kwano troop differ?	Network metrics	• Association network over the whole study period
	Conditional uniform graph tests	• Density of association networks over the whole study period • Density of seasonal association networks
5a. Are association networks assorted by age or sex?	Joint count tests	• Association network over the whole study period • Age & sex class for each individual

Question (*continued*)	**Analysis**	**Data used**
5b. Are the associations of females affected by the presence of dependent offspring or reproductive state?	Node-level t-tests	• Female node strength per season for females: • with dependent offspring • without dependent offspring
	Node-level ANOVA	• Female node strength per season for females that were: • cycling • pregnant • lactating
5c. Are associations between females affected by dominance relationships?	Geary analysis for autocorrelation	• Weighted distance between females in the association network over the whole study period • Differences in dominance rank between females
5d. Are associations between females and males affected by lactation or cycling?	Two-sample permutation tests	• TWI between males & females per season, grouping these by whether female was: • lactating or non-lactating • cycling or non-cycling

4.3 Results

In the association network of the Gamgam troop there was one isolate, DRW (Figure 4.2 a), who did not associate frequently enough with troop members to be included in the giant component of the network. DRW immigrated into the Gamgam troop at the beginning of the study period (see section 2.3). In the association network of the Kwano troop all individuals were connected to a single component (Figure 4.2 b).

4.3.1 Do GGNP baboons have preferential associations?

In both troops only about 4% of dyads associated preferentially (Gamgam 3.6%; Kwano 4.2%). In the Gamgam troop one dyad associated more frequently than was expected by chance (Table 4.8); MMW and STR, both adult females, were associated just over half the times they were seen during the entire study period. In the Kwano troop five dyads were associated preferentially (Table 4.9). There was one cluster of an adult male (KSA) and two adult females (SAD and YMK) that all associated with each other preferentially. The two remaining preferentially associating dyads were both between an adult male (SND or DLI) and an adult female (FDI or MOM).

Thus, there is little evidence that GGNP baboons actively associated with specific troop members, suggesting instead that most associations were passive aggregations.

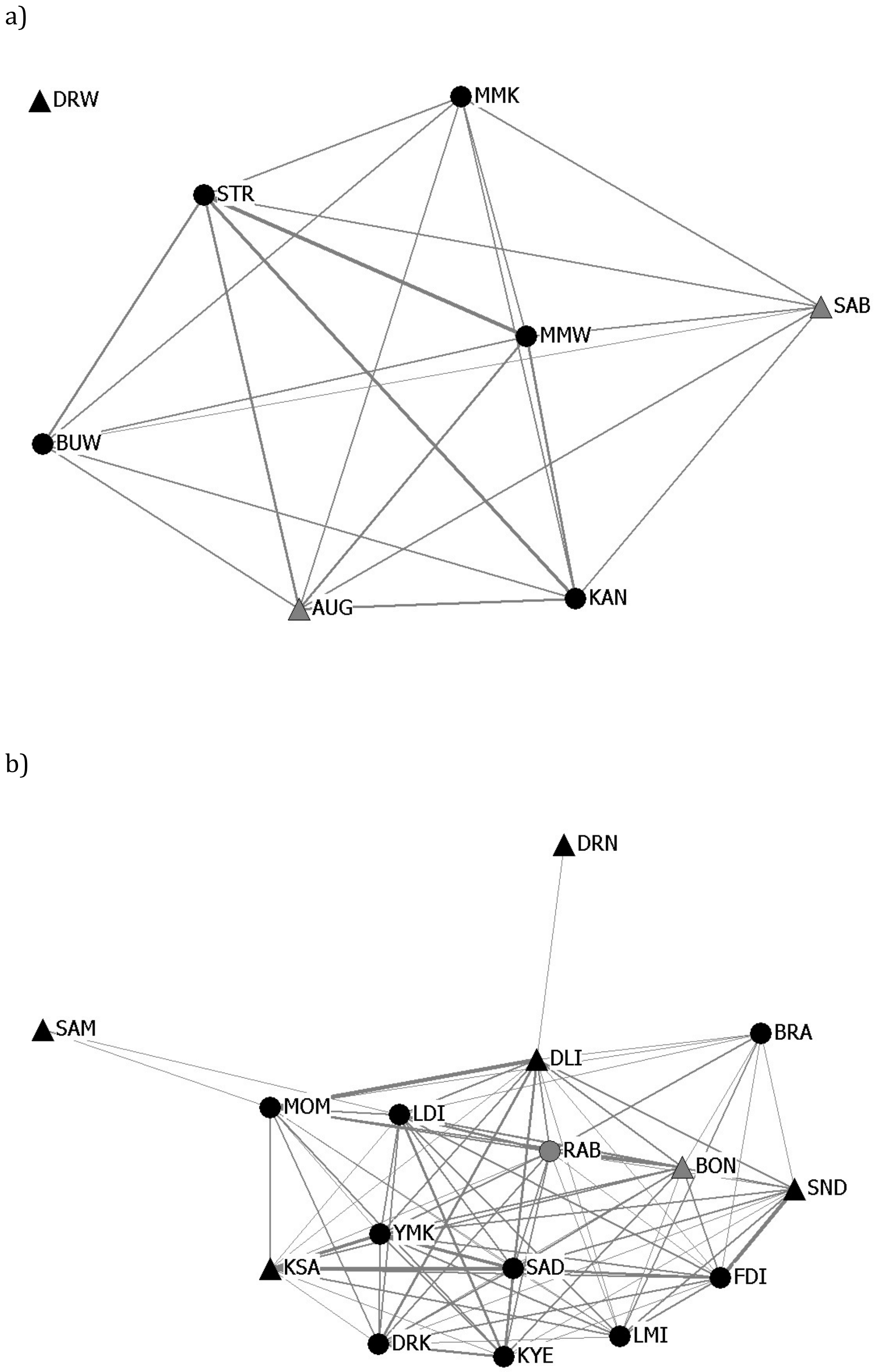


Figure 4.2: Association network of a) Gamgam; b) Kwano. Networks are laid-out using spring-embedding. Line thickness indicates tie strength. Circles are females, triangles males. Black nodes are adults, grey nodes are subadults.

Table 4.8: Unfiltered TWI matrix of Gamgam troop. Values in bold indicate that the association was greater than expected by chance, and thus a preferential association.

	AUG	BUW	DRW	KAN	MMK	MMW	SAB	STR
AUG	*	0.275	0.112	0.368	0.227	0.339	0.270	0.354
BUW		*	0.068	0.254	0.234	0.302	0.174	0.313
DRW			*	0.087	0.107	0.071	0.154	0.077
KAN				*	0.306	0.345	0.287	0.430
MMK					*	0.309	0.255	0.291
MMW						*	0.224	**0.537***
SAB							*	0.272
STR								*

Table 4.9: Unfiltered TWI matrix of Kwano troop. Values in bold indicate that the association was greater than expected by chance, and thus a preferential association.

	BRA	BON	DLI	DRN	DRK	FDI	KYE	KSA	LDI	LMI	MOM	RAB	SAD	SAM	SDA	YMK
BRA	*	0.109	0.094	0.028	0.060	0.092	0.073	0.075	0.106	0.134	0.089	0.123	0.066	0.063	0.085	0.073
BON		*	0.144	0.073	0.109	0.121	0.120	0.157	0.151	0.112	0.144	0.246	0.146	0.035	0.067	0.160
DLI			*	0.085	0.228	0.083	0.195	0.110	0.131	0.115	**0.327***	0.185	0.099	0.048	0.116	0.124
DRN				*	0.027	0.018	0.044	0.024	0.079	0.017	0.063	0.047	0.025	0.036	0.000	0.022
DRK					*	0.128	0.196	0.109	0.169	0.094	0.131	0.166	0.130	0.077	0.098	0.149
FDI						*	0.101	0.166	0.160	0.155	0.083	0.103	0.207	0.049	**0.362***	0.189
KYE							*	0.107	0.214	0.058	0.127	0.170	0.216	0.034	0.091	0.149
KSA								*	0.114	0.187	0.116	0.104	**0.335***	0.073	0.067	**0.289***
LDI									*	0.131	0.132	0.209	0.159	0.101	0.159	0.154
LMI										*	0.079	0.111	0.115	0.077	0.144	0.181
MOM											*	0.132	0.085	0.102	0.077	0.107
RAB												*	0.167	0.072	0.107	0.164
SAD													*	0.056	0.128	**0.255***
SAM														*	0.031	0.061
SDA															*	0.132
YMK																*

4.3.2 Do GGNP baboons show substructures in their association networks?

In the Gamgam association network, a single clique was found. This clique was the same as the largest strong component, and included seven of the eight baboons in the troop. Furthermore, no weighted modules were found in the Gamgam association network with either set of parameters, indicating that the network did not contain groups of strongly associated individuals.

The lack of modules in Gamgam can be due to a definition of k that is too large; when using the same definition of k, in smaller troops this means that a larger proportion of the troop has to have strong ties with each other for them to be included as a network module. Nevertheless, even with $k = 3$, the minimum definition of a clique, no modules were found in the Gamgam association network. Alternatively, the intensity threshold may be too high for individuals to be included in a network module. In absolute terms, the intensity threshold was set higher for the Gamgam troop, which may be the reason for the lack of network modules. However, relative to the mean association index, the intensity threshold was set at the same level in both troops. Thus, these results indicate that the Gamgam may not have cliques in their associations.

Conversely, associations in the Kwano troop were fragmented; a total of ten cliques was found in the association network (Table 4.10). The weighted network module analysis also showed the Kwano associations to be more fragmented; with the parameters set to $I = 0.18$ and $k = 5$ two overlapping modules were found (Figure 4.3). With the parameters set to $I = 0.20$ and $k = 3$, again two modules were found (Figure 4.4).

These results show that the troops differed in patterns of associations. The lack of cliques and modules in the Gamgam network indicates either that troop members frequently associated simultaneously with all troop members, and was thus cohesive, or that the troop may have fragmented into smaller subgroups, but the membership of subgroups varied, so that each individual has a tie to all troop members. The Kwano troop showed greater fragmentation of their association as indicated by the number of cliques and network modules that were found, suggesting that there were clusters of baboons that associated with each other more frequently than with the rest of the troop.

Table 4.10: Cliques found in Kwano association network.

Clique number	Clique members									
1	BON	DLI	DRK	KSA	LDI	LMI	MOM	RAB	SAD	YMK
2	BON	DLI	DRK	FDI	KSA	LDI	LMI	RAB	SAD	YMK
3	BON	DLI	DRK	FDI	KYE	KSA	LDI	RAB	SAD	YMK
4	BON	DLI	DRK	KYE	KSA	LDI	MOM	RAB	SAD	YMK
5	DLI	DRK	FDI	LDI	LMI	RAB	SAD	SDA	YMK	
6	DLI	DRK	FDI	KYE	LDI	RAB	SAD	SDA	YMK	
7	BRA	BON	DLI	LDI	LMI	MOM	RAB			
8	BRA	BON	DLI	FDI	LDI	LMI	RAB			
9	BRA	DLI	FDI	LDI	LMI	RAB	SDA			
10	LDI	MOM	SAM							

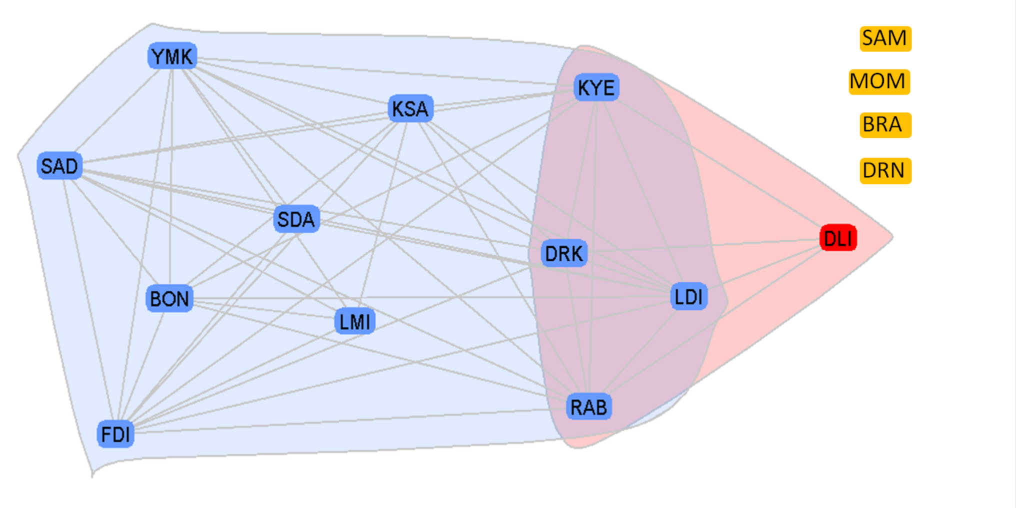


Figure 4.3: Weighted network modules of Kwano association network with $I = 0.18$ and $k = 5$. Two overlapping modules were found (red and blue nodes), with KYE, DRK, LDI, and RAB being members of both modules. Orange nodes were not part of any module.

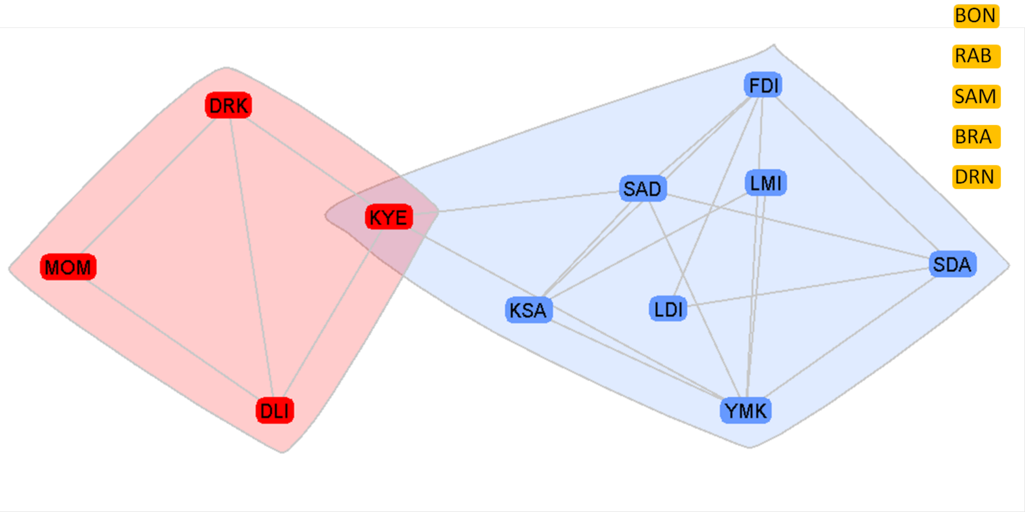


Figure 4.4: Weighted network modules of Kwano association network with $I = 0.20$ and $k = 3$. Two overlapping modules were found (red and blue nodes); KYE is member of both modules. Orange nodes were not part of any module

4.3.3 Do the association patterns of GGNP baboons differ by season?

Gamgam seasonal association networks are shown in Figure 4.5, and Kwano seasonal association networks are shown in Figure 4.6. Network metrics for the seasonal networks of both troops are given in Figure 4.7. In both troops, the associations were most cohesive at the end of the dry season; in this season, *weighted mean clustering coefficient* and *compactness* were highest, individuals associated most frequently (*mean node strength* & *average tie weight*) and with the highest number of troop members (*mean degree* & *normalised mean degree*), and the *weighted geodesic* was low. Relationships were also least differentiated (*weighted network centralisation*) in terms of number and strength during this season. Furthermore, in both troops the network was the densest (*density*) at the end of the dry season, and was significantly denser than the networks in all other seasons (Table 4.11 & Table 4.12).

In the Gamgam troop density was also significantly different between the remaining seasons (Table 4.11); with density decreasing from the beginning of the wet season, the end of the wet season, to the beginning of the dry season Figure 4.7). The associations of the Gamgam troop were least cohesive during the beginning of the dry season. In this season, only half of the possible ties were observed (*density*) and the lowest values for the *weighted mean clustering coefficient*, *mean degree*, *mean node strength*, and *compactness* were found. The *mean weighted geodesic* was longest in this season, and associations were most differentiated. Associations during the beginning and the end of the wet season were in between these two extremes; with associations being more cohesive in the beginning of the wet season compared to the end of the wet season. In the

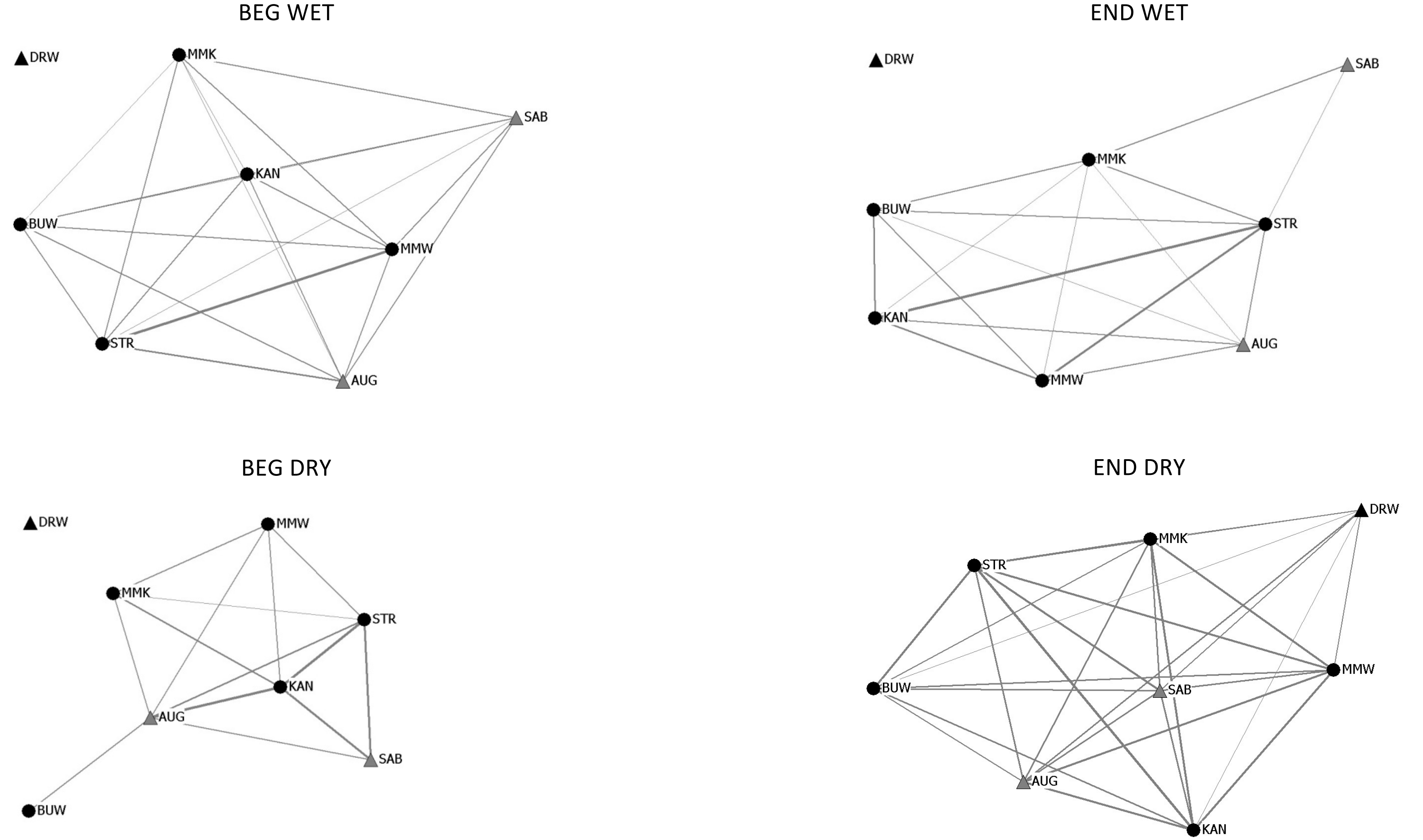


Figure 4.5: Seasonal association networks of the Gamgam troop. Networks are laid-out using spring-embedding. Line thickness indicates tie strength. Circles are females, triangles males. Black nodes are adults, grey nodes are subadults.

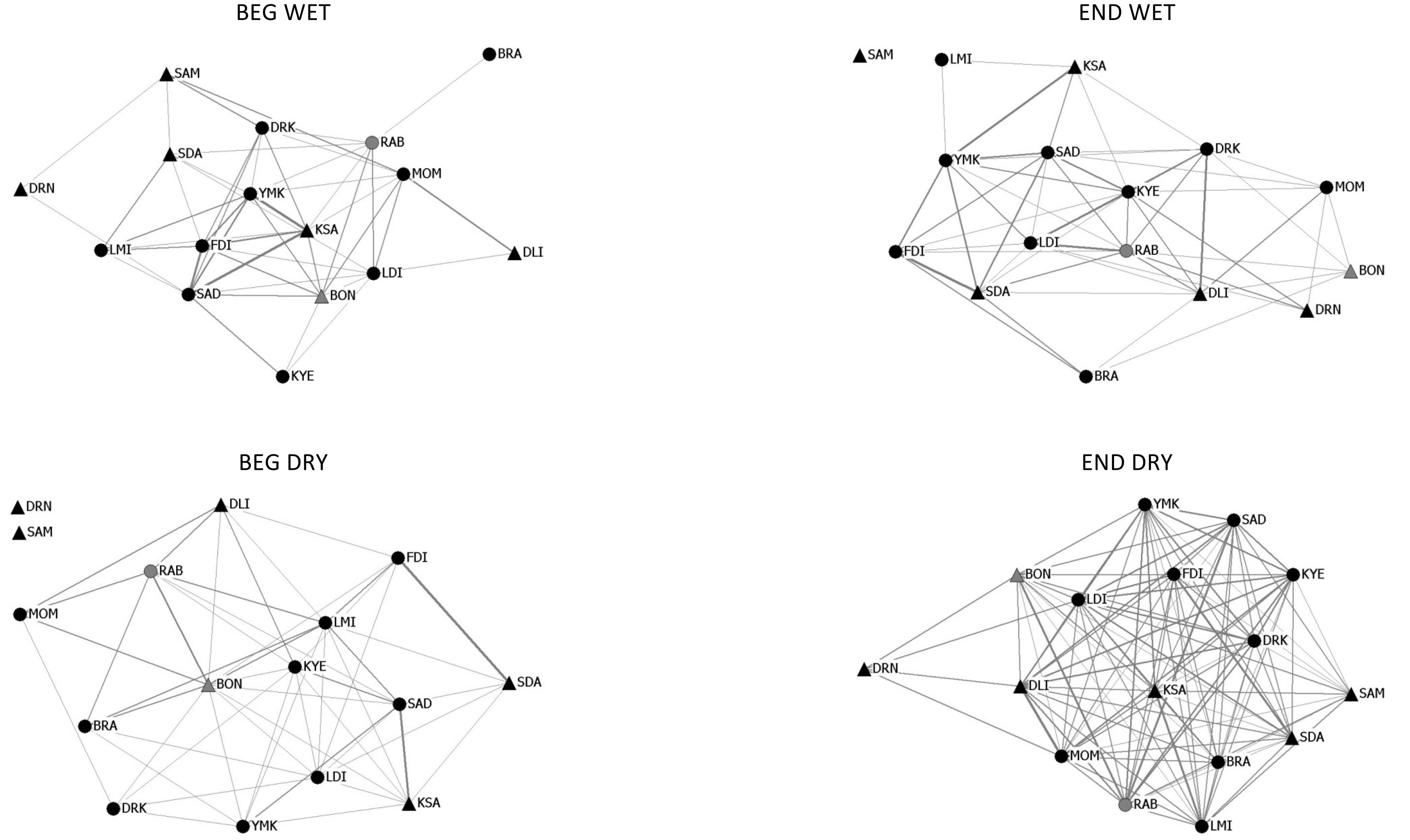


Figure 4.6: Seasonal association networks of the Kwano troop. Networks are laid-out using spring-embedding. Line thickness indicates tie strength. Circles are females, triangles males. Black nodes are adults, grey nodes are subadults.

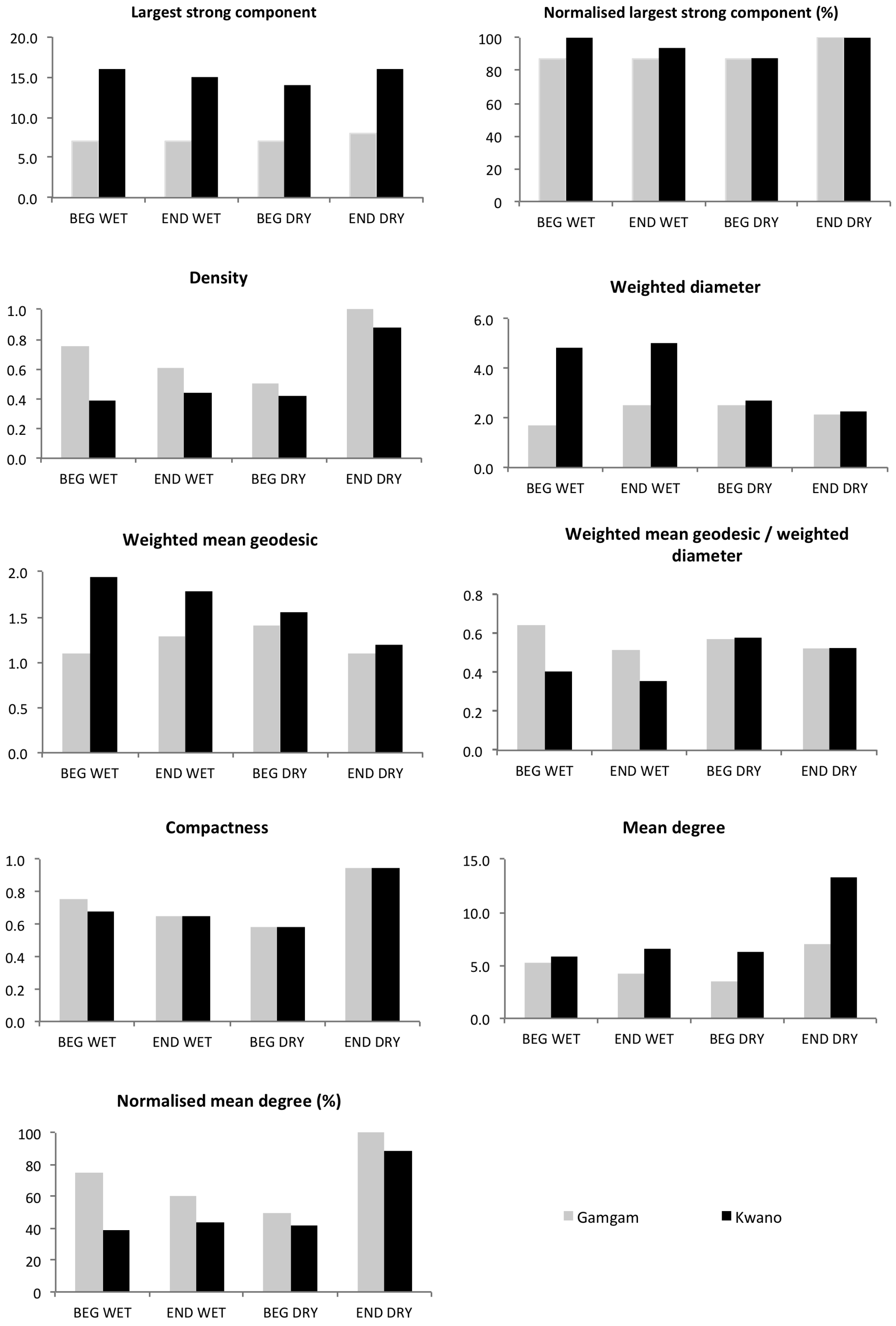


Figure 4.7: Network metrics for the seasonal association networks of the Gamgam and Kwano troops.

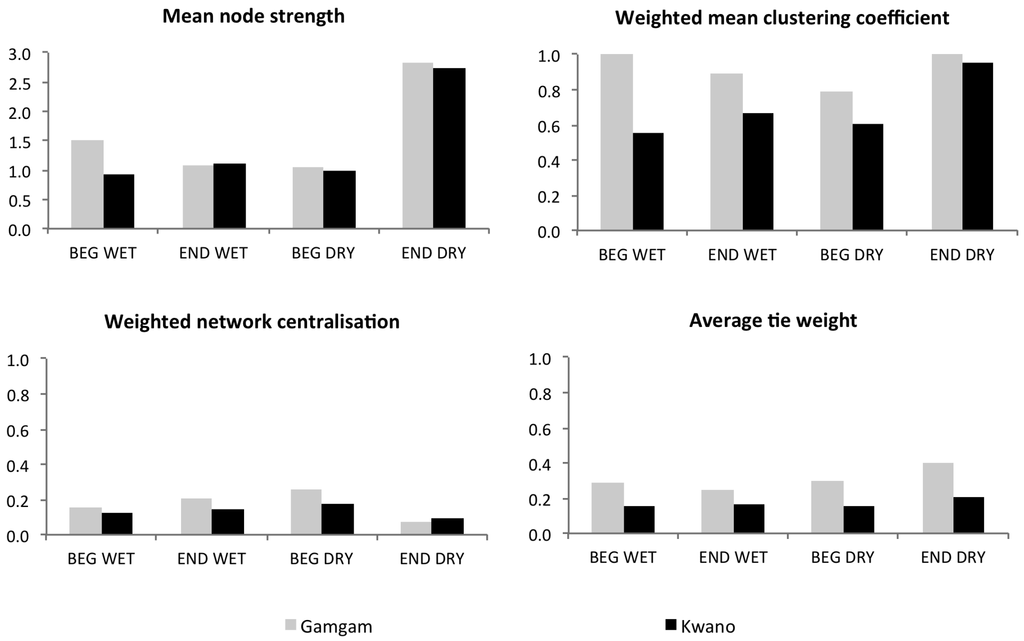


Figure 4.7 (*continued*): Network metrics for the seasonal association networks of the Gamgam and Kwano troops.

Table 4.11: Results t-test density Gamgam seasonal association networks. Bold t-values indicate a significant difference in densities, * p < 0.05, ** p < 0.01.

	BEG WET	END WET	BEG DRY	END DRY
BEG WET	-	**1.889***	**5.986****	**3.586****
END WET		-	**4.398****	**2.081***
BEG DRY			-	**-10.520****
END DRY				-

beginning of the wet season the *density*, *clustering coefficient*, *mean degree*, *compactness* and *average tie strength* were all higher, and the *mean weighted geodesic* was lower than at the end of the wet season. During the beginning of the wet season associations were also less differentiated compared to the end of the dry season (*weighted network centralisation*).

For the remaining seasons in the Kwano troop, no consistent pattern was found in the differences of cohesion of the networks. For example, *compactness* was highest in the beginning of the wet season, followed by end of the wet season and the beginning of the dry season, whereas clustering (*weighted mean clustering coefficient*) was highest at the end of the wet season, followed by the beginning of the dry season and the beginning of the wet season. Conversely, the *weighted mean geodesic* was shortest in the beginning of the dry season, followed by the end of the wet season, and the beginning of the wet season. What is more, none of these seasonal networks differed significantly in terms of *density* (Table 4.12).

In short, seasons affected the associations in both troops, but more markedly so in the Gamgam troop. Nevertheless, in both troops the seasonal association networks were all strongly correlated, indicating that there was some stability in association patterns throughout the seasons (Table 4.13 & Table 4.14), and the correlations between seasonal networks were stronger in the Gamgam troop compared to the Kwano troop. This suggests that in Kwano, associations were similar in cohesion, and the number of relationships based on associations was similar across seasons, but that the individuals changed with whom they associated by season, as indicated by the weaker correlations between seasonal networks. Conversely, while in Gamgam the strength and density of associations differed by season, individuals were more consistent in their association partners.

Table 4.12: Results t-test density of Kwano seasonal association networks. Bold t-values indicate a significant difference in densities, * p < 0.05, ** p < 0.01.

	BEG WET	END WET	BEG DRY	END DRY
BEG WET	-	-0.695	-0.366	**-8.160****
END WET		-	0.341	**-6.599****
BEG DRY			-	**-8.627****
END DRY				-

Table 4.13: Results QAP correlation of Gamgam seasonal association networks. Bold r-values indicate a significant correlation, * QAP p < 0.05, ** QAP p < 0.01

	BEG WET	END WET	BEG DRY	END DRY
BEG WET	-	**0.790****	**0.521***	**0.707***
END WET		-	**0.479***	**0.702***
BEG DRY			-	**0.706****
END DRY				-

Table 4.14: Results QAP correlation of Kwano seasonal association networks. Bold r-values indicate a significant correlation, * QAP p < 0.05, ** QAP p < 0.01

	BEG WET	END WET	BEG DRY	END DRY
BEG WET	-	**0.332****	**0.343****	**0.255****
END WET		-	**0.345****	**0.465****
BEG DRY			-	**0.459****
END DRY				-

4.3.4 Do the association patterns of the Gamgam and Kwano troop differ?

Network metrics of the Gamgam and Kwano association networks are given in Table 4.15. The patterns of associations differed between the two troops; the associations of the Gamgam troop were stronger and more cohesive than the associations of the Kwano troop. In Gamgam the association network was denser (*density*), more clustered (*weighted mean clustering coefficient*), and the average weight of association (*average tie weight*) was higher. Gamgam baboons associated with fewer individuals than Kwano baboons (*mean degree*), but this was a larger proportion of their troop (*density*). Nevertheless, Kwano baboons did have relatively direct relationships with their troop members; although the *weighted mean geodesic* was lower in the Gamgam network, when the *geodesic* was normalised by the maximum path length (*weighted diameter*), average path lengths were shorter in Kwano (*weighted mean geodesic / weighted diameter*). Thus, in relative terms, Kwano baboons had more direct connections with each other than Gamgam baboons.

Both troops had relatively high *weighted mean clustering coefficien*t. This measure gives an indication of the proportion of tie weights between individuals that are interconnected, and is thus different from the general notion of clustering as a tendency to form exclusive groups. High levels of clustering can be due to a high density of ties (Croft *et al.* 2008), as when the number of ties increases, a greater number of individuals are interconnected, and consequently the *clustering coefficient* may increase. Furthermore, Gamgam's *clustering coefficient* of 1 is a result of the way this coefficient is calculated; as only nodes in the *largest strong component* are considered for this measure, the isolate DRW was not taken into account. The remainder of the troop was all connected and therefore the troop has a clustering coefficient of 1. *Compactness* on the other hand, is a binary measure of cohesion, and indicates the proportion of troop members that are adjacent to each other. As opposed to the *weighted clustering coefficient*, this measure is calculated on the entire network, which explains the higher value for the Kwano metric in this case. In Gamgam, all individuals apart from DRW are adjacent to each other. However, because DRW was not included in the network the overall value is lower than for the Kwano network.

Table 4.15: Structural network properties of Gamgam and Kwano association network.

Network metric	GAMGAM (N = 8)	KWANO (N = 16)
Largest strong component	7	16
Normalised largest strong component (%)	88	100
Density	0.750	0.700
Weighted mean geodesic	1.058	1.506
Weighted diameter	1.739	3.691
Weighted mean geodesic / weighted diameter	0.608	0.408
Compactness	0.750	0.849
Mean degree	5.250	10.500
Mean node strength	1.592	1.528
Average tie weight	0.142	0.104
Weighted mean clustering coefficient	1.000	0.880
Weighted network centralisation	0.142	0.104

The observed difference in the *density* of association networks between troops may be due to a surface difference, such as troop size, rather than a structural difference; the conditional uniform graph tests indicate that the between-troop difference in the *density* of the association networks did not significantly deviate from the difference between random networks of the same size (Table 4.16 - ALL). This suggests that the difference in density of the Gamgam and Kwano association networks may be due to a difference in troop size. When broken down into seasonal networks, Gamgam association networks were significantly denser in 2 out of 4 seasons, the beginning and the end of the wet season (Table 4.16). A similar result was found in the end of the dry season, and this was close to significance. In the beginning of the dry season the *density* of Gamgam and Kwano associations did not differ significantly. Thus, in at least half of the seasons there was a structural difference in associations, over and above the difference due to differences in troop size.

Table 4.16: Results for the conditional uniform graph tests comparing the density of association networks between troops. Observed between-troop differences in densities were compared to that of 20000 random networks of the same sizes as the observed networks. Significant differences are given in bold.

Season	Difference in density (Gamgam - Kwano)	*p*
BEG WET	**0.358**	**< 0.001**
END WET	**0.165**	**0.013**
BEG DRY	0.083	0.133
END DRY	0.117	0.059
ALL	0.050	0.251

In short, the Gamgam troop had a better-connected, stronger-connected, more cohesive association network than the Kwano troop. Nevertheless, the Kwano baboons did have relatively direct ties between individuals. In at least half of the seasons, associations differed between troops beyond surface differences.

4.3.5 Are association patterns influenced by social factors?

4.3.5.1 Are association networks assorted by age or sex?

To investigate if association networks were assorted by age or sex, joint count tests were run to determine if baboons were more likely to associate with individuals of the same age or sex class. In neither troop was the density of ties within and between age groups significantly different from expected (Table 4.17), indicating that associations were not segregated by age.

Table 4.17: Results for the joint-count test comparing the density of ties between and within age classes to the expected density of ties for Gamgam and Kwano association networks.

	GAMGAM			KWANO		
	Density of ties			Density of ties		
Associations between	Expected	Observed	*p*	Expected	Observed	*p*
Adult - adult	11.25	10.00	0.756	63.70	60.00	0.247
Adult - subadult	9.00	10.00	0.756	19.60	23.00	0.254
Subadult - subadult	0.75	1.00	0.756	0.70	1.00	0.700

In Gamgam, associations were also not segregated by sex (Table 4.18). In Kwano, whilst female-female and female-male associations were not significantly different from random, Kwano males did have significantly fewer ties with other males than expected. This indicates that female-male and female-female associations were as expected, but that males avoided each other.

Table 4.18: Results for the joint-count test comparing the density of ties between and within sexes to the expected density of ties for Gamgam and Kwano association networks. Bold values indicate a significant difference in the density of ties.

	GAMGAM			KWANO		
	Density of ties			Density of ties		
Associations between	Expected	Observed	*p*	Expected	Observed	*p*
Female - female	7.50	10.00	0.374	31.50	39.00	0.928
Female - male	11.25	10.00	0.374	42.00	40.00	0.264
Male - male	2.25	1.00	0.374	**10.50**	**5.00**	**0.031**

4.3.5.2 Are the associations of females affected by the presence of dependent offspring or reproductive state?

To test if females with dependent offspring associated more frequently with troop members than females without dependent offspring, node-level t-tests were run. Results are given in Table 4.19. In neither troop in any season was there a significant difference in the node strength of females with dependent offspring and females without dependent offspring. Thus, the presence of dependent offspring did not appear to influence the associations of females.

Node-level ANOVAs were run to test if the association patterns of females were influenced by their reproductive state. Results are given in Table 4.20. Female node strength did not differ significantly as a function of reproductive state in either troop in any season, indicating that female reproductive state did not influence female gregariousness.

Table 4.19: Results for node-level t-tests, comparing the total strength of relationships of females without dependent offspring to that of females with dependent offspring in each season.

	GAMGAM		KWANO	
	t	*p*	*t*	*p*
BEG WET	-0.598	0.100	-0.609	0.471
END WET	-0.421	0.201	-0.501	0.297
BEG DRY	-0.860	0.354	-0.035	0.955
END DRY	-0.185	0.800	-0.283	0.329

Table 4.20: Results of node-level ANOVAs, comparing female node strength across cycling, lactating, and pregnant females in each season.

	GAMGAM			KWANO		
	F	*df* (effect, error)	*p*	*F*	*df* (effect, error)	*p*
BEG WET	27.46	2, 2	0.199	2.30	2, 7	0.178
END WET	1.67	2, 2	0.476	0.67	2, 7	0.545
BEG DRY	0.77	1, 3	0.414	0.90	2, 7	0.474
END DRY	0.66	1, 3	0.599	0.02	1, 8	0.893

4.3.5.3 Are associations between females affected by dominance relationships?

Relational contingency tests were run to test if baboons associated more frequently with troop members that were similar in rank.

In neither troop did the number of ties within and between rank categories differ significantly from expected (Relational contingency test: Gamgam: χ2 = 1.333, p = 1.000; Kwano: χ2 = 11.010, p = 0.107). Furthermore, the weighted distance in the association network was not correlated with rank differences in either troop (Table 4.21). Overall, these results suggest that the association patterns of females were not influenced by dominance rank.

Table 4.21: Results of the Geary analysis for autocorrelation between females' weighted distance in the association network and their dominance rank. A Geary statistic (C) of 1 indicates that there was no correlation; below 1 indicates a positive correlation, while above 1 indicates a negative correlation. The observed statistic was compared to the distribution of the statistic for 1000 random permutations.

	C *Observed*	Mean C *random*	SE C *random*	*p*
Gamgam	1.02	1.00	0.06	0.328
Kwano	0.94	1.00	0.06	0.152

4.3.5.4 Are associations between females and males affected by lactation or cycling?

The TWI of males and lactating females were compared to that of males and non-lactating females to test if males associated more with lactating females than with non-lactating females. Similarly, the TWIs of males and cycling females were compared to that of males and non-cycling females to test if males associated more with cycling females than with non-cycling females. Comparisons were made with two-sample permutation tests.

The TWI of males and lactating females did not differ significantly from the TWI of males and non-lactating females in either troop during any season (Table 4.22), suggesting that lactating females did not have stronger associations with males than non-lactating females.

Males' association with cycling females was also not significantly different from their association with non-cycling females in either troop in any season (Table 4.23).

A summary of all the results discussed in this chapter is given in Table 4.24.

Table 4.22: Results of two-sample permutation test of male - female TWI, comparing the associations of males with lactating females to that of males and non-lactating females.

	GAMGAM		KWANO	
	t	*p*	*t*	*p*
BEG WET	-0.03	0.626	-0.02	0.243
END WET	0.03	0.532	-0.01	0.694
BEG DRY	-0.05	0.452	0.00	0.833
END DRY	-0.03	0.472	0.01	0.811

Table 4.23: Results of two-sample permutation test of male - female TWI, comparing the associations of cycling females with males to the relationships between non-cycling females and males.

	GAMGAM		KWANO	
	t	*p*	*t*	*p*
BEG WET	-0.03	0.560	-0.02	0.27
END WET	0.00	0.937	-0.02	0.518
BEG DRY	-0.05	0.448	0.02	0.297
END DRY	-0.03	0.475	0.03	0.146

Table 4.24: Summary of the questions addressed in this chapter and the result of the analyses.

Question	Result
1. Do GGNP baboons have preferential associations?	Only c. 4% of dyads associated preferentially, giving little evidence for active associations. Instead, associations seem mainly to be passive aggregations.
2. Do GGNP baboons show substructures in their association networks?	In the Gamgam association networks, no substructures were found; the network contained a single clique including nearly all troop members, and no weighted network modules were found, suggesting the troop had cohesive associations or highly fluid subgroup membership. Kwano associations did show substructures. Several overlapping cliques and network modules were found, suggesting that the troop at times was fragmented, but overlap shows there was some fluidity in subgroup composition
3. Do the association patterns of GGNP baboons differ by season?	Yes. Association networks of both troops were most cohesive at the end of the dry season. In Gamgam, season had a marked effect on the association network in the remaining seasons, with cohesion decreasing from the beginning of the wet, to the end of the wet, and the beginning of the dry season. Kwano association patterns did not vary systematically over the beginning of the wet, to the end of the wet, and the beginning of the dry season. Seasonal networks were however strongly correlated, indicating that there was some stability in associations between individuals.
4. Do the association patterns of the Gamgam and Kwano troop differ?	Yes, associations were stronger, networks more cohesive, and individuals better connected in the Gamgam networks compared to Kwano. However, Kwano baboons did have relatively direct ties. In half of seasonal networks, these differences were over and above the effects of troop size differences.
5a. Are association networks assorted by age or sex?	In neither troop were associations assorted by age. In Gamgam, sex had no influence on association patterns, while in Kwano, males avoided each other.

Question (*continued*)	**Result**
5b. Are the associations of females affected by the presence of dependent offspring or reproductive state?	Neither the presence of dependent offspring, nor female reproductive state influenced the association patterns of females in either troop.
5c. Are associations between females affected by dominance relationships?	Dominance rank did not affect associations of females in either troop; networks were not assorted by rank class and the distance in rank was not associated with the distance in the networks.
5d. Are associations between females and males affected by lactation or cycling?	The associations between males and females did not differ as a function of lactation or cycling, indicating that these did not affect association patterns between males and females.

4.4 Discussion

In this chapter, the association patterns of two troops of olive baboons were analysed using a social network approach. Troops were found to differ in the cohesion and level of sub-structuring of their spatial associations, and for both troops season was found to influence association patterns. Here, the implications of these findings for fission-fusion dynamics will be discussed, along with between-troop and seasonal differences with reference to socioecological theory, and the influence of individual social strategies and preferences on patterns of associations.

4.4.1 Structure of association networks and implications for fission-fusion dynamics

Considerable differences were found in the structure of association networks between the Gamgam and Kwano troop; the Gamgam troop had a cohesive network of associations, in which individuals were well- and strongly-connected to troop members, and in which no substructures were found. Associations in the Kwano troop were more fragmented; the association network had less and weaker connections, and a greater number of cliques and weighted network modules were found.

These differences in the structure of association networks suggest that troops differed in their degree of fission-fusion dynamics. The cohesive network in the Gamgam troop indicates that Gamgam baboons had strong associative ties with all troop members. Combined with the lack of substructures, this indicates that Gamgam baboons frequently associated as a troop, and therefore suggests that the Gamgam troop had a relatively low degree of fission-fusion dynamics. A higher degree of fission-fusion dynamics was seen in the Kwano troop, where the weaker ties and substructures indicate that individuals did not associate equally with all troop members. In other words, the Kwano troop fragmented at times. The fission-fusion dynamics of the Kwano troop are, however, likely to be of intermediate rather than a high degree, as some substructures were found indicating that there were small groups of individuals that associated more frequently with each other than with the rest of the troop. In societies with a high degree of fission-fusion dynamics, networks are expected to show little substructuring as individuals' associates vary frequently, rather than being a set group. Nevertheless, the composition of these subgroups was somewhat fluid, as overlap was found between cliques and between weighted networks modules. The spatial cohesion of troops, and the size and composition of subgroups will be discussed in chapter 6 to investigate further the formation of these smaller subgroups.

Furthermore, the definition of who is considered to be associated is likely to affect the structure of association networks and the estimation of the degree of fission-fusion dynamics. In this study, individuals were considered to be associated when they were seen during a scan. However, because researchers spent five minutes before each scan locating animals by walking around the party, this definition goes beyond a purely visual one and is fairly broad. Defining associations as individuals who are in closest proximity to each other, or within a particular distance of each other may have produced a different, less cohesive network of associations. As these definitions of associations are central to the definitions of who is considered to be in the same party, definitions are discussed further in chapter 6, where a statistical analysis of the cut-off distance at which two individuals are no-longer considered to be associated is also presented.

Some limitations to the social network approach should be noted here. First, it may be difficult to capture the full extent of the *temporal variation* of patterns of associations using a social network approach. Social networks are constructed from data collected over some period of time, in order to ensure enough information has been collected on all individuals in a group. Rather than being a snapshot, like a scan sample might be, association networks in this study were built over a three-month period or a year. Consequently, any substructures that are found in association networks do not necessarily represent subgroups or parties. In fact, individuals within a clique or weighted network module may never have all been seen together at the same time, and instead associated with the same set of individuals at various times. In terms of understanding fission-fusion dynamics, it is not only important to look at the social preferences and relationships of individuals and the resulting structure, as was done in this chapter, but also to consider the size of parties, how frequently parties change in composition, how spread out individuals are within their party and within the troop as a whole, and the temporal variation of each of these factors, to understand how flexible the grouping patterns of a group are. These kinds of questions will be discussed in chapter 6.

Secondly, it is important to reiterate that the association networks in this analysis are not equivalent to social structure, as these networks considered just one dimension of social bonds. Social relationships are defined by the content, quality and patterning of social interactions between individuals (Hinde 1976), and thus aspects other than associations, such as grooming or aggression, are important for measuring social relationships between individuals (Pepper *et al.* 1999). An analysis of multiple behavioural dimensions as a measure of social relationships would give a more accurate description of a troop's social structure (Ramos-Fernández *et al.* 2009), and how individuals are embedded in it (Lehmann and Ross 2011). Therefore, in chapter 5 this analysis will be expanded with networks based on several different behaviours.

Thirdly, in the analysis of the social networks of small groups, as is often the case in primates, the density of ties can be high because most individuals will interact with all troop members, leading to a network in which all nodes are interconnected. In order to analyse meaningful relationships between individuals, a filter was applied to the network. By filtering out weak ties those interactions that help to maintain the cohesion of a network may be lost. Chance events can be very important for the cohesion of a network as weak ties have a greater likelihood of being bridges between the different segments of a network (Granovetter 1973; Granovetter 1983). Furthermore, when individuals in a network have strong links with a few individuals and weak links with many, filtering out of weaker ties can strongly bias network metrics and the number of substructures found in a network (Lehmann and Ross 2011). Here, networks were filtered until they were significantly different from random and the filters applied to the networks of the two troops were similar in relation to the average value of TWI for that troop, allowing for between-troop comparisons.

Despite the limitations highlighted here, social network analysis is a valuable tool for the analysis of primate social groups, and the structure of social relationships; in this study, association networks have given an indication of differences in fission-fusion dynamics, and importantly, have helped to identify substructures that were not readily apparent.

4.4.2 Ecological influences on associations

Despite the general acceptance of the fission-fusion dynamics framework over the past few years, it was not yet clear how flexible primate association patterns are, and if small-scale variations in these patterns can be accounted for by the socioecological model. In this chapter, networks of association were compared between two troops in a single population and within each troop across four seasons. Differences in the structure of associations were found between troops, and, to some extent, across seasons.

Between-troop differences in association patterns are in line with between-troop differences in food competition and predation risk. As the Gamgam troop was smaller, and generally more food was available in the home range, there may have been less within group competition for food allowing Gamgam individuals to stay cohesive as a troop. Furthermore, as the risk of predation was higher in the Gamgam range, the benefits of a cohesive, large troop may have outweighed the cost of food competition. Conversely, in Kwano less food was available while the troop was larger, making the potential for within-group competition greater. As the Kwano range was relatively safe, the troop was able to fragment into subgroups at certain parts of the year. During the end of the dry season, because leaves were highly abundant, there was less need to reduce feeding competition, and accordingly, the troop had more cohesive associations. The socioecological model therefore also seems to account for more small-scale differences.

Some evidence was also found that troops were flexible in their patterns of associations; in the Gamgam troop, the structure of the association network differed across all four seasons, while in the Kwano troop, associations were similar across three out of four seasons. Troops seemed to adjust their associations to local fluctuations in the availability of food; in chapter 3 it was found that the Gamgam home range was more seasonal than the Kwano home range. Accordingly, the Gamgam troop showed greater variability in their associations than the Kwano troop. Troops seemed to adjust association patterns to the availability of fruit and leaves.

In both troops associations were most cohesive and strongest during the end of the dry season, when there was a peak in the availability of both young leaves and fruit. In Kwano, the availability of young leaves and fruit was similar across the remaining seasons, and accordingly, association networks were similar across these seasons but differed from the end of the dry season. In Gamgam, associations were *least* cohesive during the beginning of the dry season, when few young leaves were available. Interestingly, during this season, the availability of fruit is, however, also high, which is the opposite of what would be expected if it was the availability of fruit alone that influenced association patterns. Instead, it seems to be a combination of the availability of fruit and leaves that seem to influence patterns of associations in GGNP baboons. This suggests that fissioning may be a way to deal with within-group competition. Fruit is a high quality food that occurs in patches that can be depleted and for which competition in high (Strier 2003a). Leaves on the other hand are a lower quality food that is widely distributed and for which there is little competition. Thus, when both fruit and young leaves were abundant, the Gamgam troop remained cohesive, as within-group competition was low. In a previous study of the GGNP baboons it was found that during the end of the dry season, both troops spent a large proportion of their foraging time feeding on fruit; this was around 50% in Gamgam and 30-65% in Kwano (Warren 2003). Furthermore, in both troops, the main peak in foraging on young leaves was in this season

(Warren 2003). When fruit was abundant, but young leaves were scarce, associations may have been less cohesive because individuals mainly feed on fruit that occurs in clumps, forcing individuals apart, and because there are no young leaves available, there is no counteracting movement of bringing individuals together. When fruit was scarce, but young leaves showed a small peak, there may have been little competition for food, therefore allowing the troop to be relatively cohesive. Conversely, when both fruit and young leaves were scarce, the associations of the Gamgam troop were relatively fragmented. In this season, the end of the wet season, baboons were suggested to 'cut their losses' and minimising energy expenditure because of high rainfall and low food availability, by reducing the time spent foraging and increasing the time spent resting.

However, it is not clear why Kwano associations were more cohesive at the end of the dry season, as predation risk is generally low in this range and shows little variation per season. In fact, the habitat types that do vary in predation risk were safest during the end of the dry season. Moreover, during the end of the dry season the troop selectively ranged in the gallery forest, mango forest, and palm forest, all three safe habitats, totalling 73% of observations. The troop only spent 22% of observations in the intermediate risk Guinea savannah, which they actively avoided during this season. It may be that the increased cohesion of associations in both troops during the late dry season could be a population-level effect in response to wider changes in resource availability. When water is a spatially restricted resource baboons may aggregate at places where water is available (Rowell 1972; Altmann and Altmann 1970; Kummer 1968). Even though GGNP is one of the wettest baboon study sites (Higham et al. 2009), during the end of the dry season, water does seem a limiting factor (see Appendix B, Figure B.1a-d and Figure B.2a-d). In this season, the core ranging areas centre on the larger rivers, and the vast majority of drinking sites fall within these core areas.

It is possible that the observed levels of troop cohesion differ by season due to differences in the visibility for the observer, *i.e.* when there is less vegetation, more individuals can be observed, and thus more baboons are seen to be in association. This may explain why during the end of the dry season, when visibility was highest, both troops were found to be most cohesive. However, the annual burning of grasses also takes place in the beginning of the dry season. Whilst visibility may still not be as high as in the end of the dry season, it is higher than in the beginning and end of the wet season. Consequently, if visibility to the observer influenced association patterns, we would expect association also to be cohesive during the beginning of the dry season. Instead, associations are most fragmented during this time. To explore this possibility further, mean party sizes for the different habitat types were compared between the end of the dry season and all other seasons (Table 4.25). In both troops observed party sizes in the guinea savannah habitat were significantly larger in the end of the dry season compared to the other seasons. However, observed party sizes were also significantly larger during the end of the dry season in gallery and lowland forest habitats, which are not affected by the annual burning of grass. Therefore, seasonal variation in visibility to the observer is unlikely to have affected the frequency of associations.

Table 4.25: Results for t-tests on the difference in mean party size between the beginning of the dry season and the other seasons for different habitat types. GS = guinea savannah, GF = gallery forest, LF = lowland forest, AL = agricultural land, PF = palm forest. Bold t-values indicate significant differences, * $p < 0.05$, ** $p < 0.01$.

	GAMGAM				KWANO			
	GS	GF	LF	AL	GS	GF	LF	AL
END DRY - BEG WET	**2.29***	**3.83****	1.29	0.00	**2.82***	**3.13****	1.41	**-2.21****
END DRY - BEG DRY	**2.30***	**4.90****	-2.00	-	**3.92****	**4.47****	0.69	**-3.52****
END DRY - END WET	**3.32****	2.60	-	0.40	**3.78****	**4.33****	1.23	**-2.57****

Thus, the associations of baboons in GGNP seem to be largely influenced by the abundance of various food types, the need to reduce resource competition, and aggregation around water sources, and less by predation risk.

4.4.3 Social preferences in associations

Non-random associations, or social preferences, occur when individuals are attracted to certain features in their physical environment (Lehmann and Boesch 2009), or to particular troop members (Mitani *et al.* 1991; Newton-Fisher 1999). In this study, little evidence was found for active associations in olive baboons, as in both troops just 4% of dyads associated with each other more frequently than expected.

Does this mean that GGNP baboons do not differentiate between association partners? It may be that rather than GGNP baboons not having social preferences, that they are not able to express these because of their particular degree of fission-fusion dynamics. In this case, the relatively low, or intermediate degree of fission-fusion dynamics means that troops are more cohesive and that individuals thus have less choice in whom they associate with. This would result in relatively high TWI values across all dyads. Because the random association value is the mean TWI calculated over 10000 random networks, high TWI values across all dyads would make the random value to which TWIs are compared high, and each dyad may thus be less likely to deviate significantly from random associations, as the definition of a preferential association in more stringent. Higher proportions of preferential associations would be expected with higher degrees of fission-fusion dynamics. There is some evidence for this; the associations of female chimpanzees, thought to have a high degree of fission-fusion dynamics, were all significantly different from random (Wakefield 2008). Likewise, non-random associations were found in 65% of male spider monkey dyads (Ramos-Fernández *et al.* 2009). Nevertheless, in other studies of species that are thought to have a high degree of fission-fusion dynamics, a much lower proportion of associations were preferential: in female spider monkeys 4% of dyads associated more than expected (Ramos-Fernández *et al.* 2009), bonobos 8% (Hohmann *et al.* 1999), chimpanzees 6% & 10% (Lehmann and Boesch 2009).

Furthermore, individual social strategies seem to have little effect on shaping GGNP baboon association networks; in neither troop did age or sex, presence of dependent offspring, female reproductive state, or dominance rank, influence patterns of association. The impact of one social factor, maternal kinship, on structuring grouping patterns was not tested here, because too few maternal relationships were known. Maternal kinship, particularly in female-philopatric baboons, may have an important effect on the structuring of association networks. However, none of the remaining social factors were found to influence association patterns, which supports the finding that baboons differentiate little between association partners. Nevertheless, as sample sizes were small, some caution is needed with the interpretation of these results. Low statistical power as a result of a small sample may mean that the size of the effect has to be very large, in order reach significance. The lack of influence of individual social strategies on association patterns could thus be due to small samples. Additionally, small samples mean that further research is needed before generalisation about the influence of individual social strategies on olive baboon association patterns can be made.

Investigation of the composition of weighted network modules however suggests that there may be some influence of individual social strategies on association patterns; at both parameter settings two network modules were found in Kwano association networks. The largest module contained several adult females, along with subadult and adult males who had been resident in the troop for more than two years. The smaller module contained several adult females and one newly immigrant (see section 2.3) adult male (DLI). One female in the smaller module (MOM) did not have any young offspring, and was seen in consortships with DLI. The females in the smaller module that did have small infants, all gave birth at least six months (the average gestation period for olive baboons - Smuts and Nicolson 1989; Higham *et al.* 2009), after DLI first appeared in the troop and DLI thus had a probability of having fathered their offspring. The females in the larger module on the other hand all gave birth before, or soon after, DLI arrived, and he could thus not be the father of their offspring. These females may have avoided DLI because he might have been a threat to their offspring, and instead associated with males who did have some probability of having fathered their offspring. Moreover, females were only part of modules that just contained males that could be the father of their offspring, and were not part of modules that contained males for whom it was impossible to have fathered their offspring.

Thus, infanticide avoidance may have had some influence on association patterns. Female chacma baboons have also been found to be very wary of new immigrant males, as most immigrant males that reach alpha position commit infanticide (Palombit et al. 2000; Cheney et al. 2004). This is also indicated by the elevated glucocorticoid levels of lactating females with the arrival of a new male, which is not seen in females who are pregnant or cycling (Beehner et al. 2005; Engh et al. 2006). Although infanticide is rarer in olive baboons (Lemasson *et al.* 2008), due to the high costs that infanticide imposes lactating females may avoid newly immigrant males.

Nevertheless, overall the majority of TWIs were not significantly different from random. If GGNP baboon troops have a relatively low degree of fission-fusion dynamics, and for example need to be in a group of a certain size to reduce the risk of predation, this may give individuals little choice about whom they associate with. As opposed to chimpanzees (Symington 1990; Sakura 1994) or spider monkeys (Symington 1990; Ramos-Fernández *et al.* 2009), olive baboons may have little flexibility in their associations due to the need to maintain a group of a certain size. This may be the reason that in the larger Kwano troop, associations can be more fragmented; with a lower risk of predation, less abundant food resources, and a larger troop, the troop fragments to reduce within-group competition, and individuals have some choice in their associates, and consequently in some seasons males can choose to avoid each other. Because the Gamgam troop is smaller, and predation risk was higher, Gamgam individuals are ‘forced’ together and therefore have little choice in their associates. A comparison of the party sizes of both troops will shed further light on the constraints on the choice of association partners and will be discussed in chapter 6.

Within a particular aggregation, individuals may show preferences for interacting with certain individuals; for example, individuals may choose to remain in close proximity to a particular troop member. For example, within a group of yellow baboons that are associated, individuals form spatial clusters; this spatial distribution was found to reflect their age, rank, and reproductive state (Collins 1984), indicating that within the set of troop members an individual associates with, baboons may show further social preferences for their interactions. Association patterns may be too crude a measure to indicate social preference; sitting associations (Fairbanks 1976), nearest neighbour associations (Weingrill 2000; Nguyen *et al.* 2009) and affiliative behaviours may be more appropriate measures of social choice. In chapter 5, the influence of social strategies on networks of social interactions will be investigated.

4.5 Summary of chapter

- Gamgam had a cohesive association network in which individuals were well and strongly connected to troop members, and no substructures were found, suggesting that the Gamgam troop had a relatively low degree of fission-fusion dynamics. The association network of the Kwano troop was less cohesive, and individuals had fewer and weaker connections, and some substructures were found. This shows that the Kwano troop had a high degree of fission-fusion dynamics relative to Gamgam, with the troop at times fragmenting into subgroups that were somewhat fluid in composition.

- Association networks varied between troops and seasons, which may be due to local variations in ecology. It was suggested that the availability of young leaves and fruit may drive the association patterns; troops were found to be relatively cohesive when leaves were abundant, particularly in the end of the dry season. While fruit increases within-group competition, troops may fragment to reduce this competition. When leaves are abundant, within-group competition is low, allowing troops to remain cohesive. Additionally, limited availability of water during the end of the dry season may have played a role in the cohesive associations in this season.
- Because the Gamgam troop was smaller and had more food available, within-group competition was probably lower and consequently there was less need to adjust association patterns to reduce competition. In Gamgam the association network was better and stronger connected and there was little sub-grouping. In Kwano less food was available and the troop was larger, increasing within-group resource competition. In response to this, and because predation risk was low, the Kwano

association network was more fragmented, with fewer and weaker ties and more sub-grouping.

- The majority of dyadic associations were not significantly different from random associations, and association patterns were not influenced by social factors such as age or sex, presence of dependent offspring, female reproductive state, matrilineal kinship, or dominance rank, although there was some suggestion that infanticide avoidance may have influenced associations. Overall, however, association patterns appear to reflect a passive aggregation of troop members, in which individuals differentiated little between association partners.
- This lack of differentiation may be due to the degree of fission-fusion dynamics. In Gamgam individuals may be ‘forced’ to be cohesive as a troop, and individuals may therefore have less choice in their associates. With a relatively higher degree of fission-fusion dynamics, Kwano individuals had somewhat more choice in their associates, as was seen by the males that avoided each other.

Chapter 5

Behavioural networks

5.1 Introduction

Social organisation may have an important effect on the nature and maintenance of social relationships within primate societies. For example, in groups with high levels of fission-fusion dynamics, changes in hierarchy or coalitions may take place whilst part of the group is out of sight. In order to monitor their social marketplace effectively, individuals need to update their social information after a period of no contact (Schaffner and Aureli 2005; Aureli *et al.* 2008a). In more cohesive groups, social relationships may focus more on maintaining cohesion and avoiding conflict (Aureli *et al.* 2008a). In chapter 4 it was shown that the spatial associations of two troops of baboons within a population varied, and it was suggested that this reflected different degrees of fission-fusion dynamics. In this chapter the impact of variation in association patterns on the nature of social relationships is examined by investigating behavioural networks.

In this introduction, first the multiple dimensions of primate relationships are considered. Next the social and ecological factors that may shape social relationships are explored. Finally, the way the resulting social structure relates to the social organisation is discussed.

5.1.1 Multiple dimensions of social relationships

Social relationships are described by ‘the content, quality and patterning of interactions’ (Hinde 1976). However, defining a ‘social relationship’ may be difficult because of the range in behavioural interactions that can be considered. Primates have a diverse array of behavioural interactions. Interactions may, for example, be vocal or gestural, and can be friendly, aggressive, or neutral. In the past, proximity and grooming data have frequently been the focus for defining social relationships in studies of baboon sociality (Silk *et al.* 2003a). However, social relationships based on these two types of measurements do not necessarily coincide (Henzi *et al.* 2009; Lehmann and Boesch 2009). Moreover, interactions other than grooming or proximity, such as vocal exchanges, embraces, sitting in contact, greetings, and aggression (Silk 2002c), are also likely to be important. This was highlighted in a study of social networks in olive baboons in which grooming and aggression networks were found to differ from displacement, mounting and presenting networks, whereas these latter three were similar to each other (Lehmann and Ross 2011). It has been suggested that a species’ social complexity determines the number of behavioural dimensions needed to capture an individual’s social environment (Lehmann *et al.* 2010). Currently, however, it is not clear how many dimensions are needed, or whether other behavioural interactions, such as vocalisations or affiliative behaviours other than grooming, would add another, until now unknown, dimension to social relationships. Therefore, there is a clear need for considering the multiple dimensions of social relationships (Barrett *et al.* 2012), and data on how relationships may differ or overlap over a wide range of behaviours (Lehmann and Ross 2011). It is particularly important to consider not only socio-positive interactions in the study of sociality, but also aggressive interactions, as these may also confer fitness benefits to the individual (Lea *et al.* 2010). Comparing the network positions of individuals within networks of different behaviours can give a further indication of how various behavioural dimensions may overlap. Furthermore, to understand the full complexity of primate social relationships and social structure, it is important to consider that behavioural dimensions are not independent of each other (Barrett *et al.* 2012). For example, by grooming a group member, an individual may reduce the aggression it receives from that group member.

In this chapter, the multiple dimensions of social relationships are investigated; a social network approach is used to test whether the structures of relationships differ with the behaviours that are considered, whether these different dimensions of social relationships are independent, and whether individuals have similar network positions across behavioural networks.

5.1.1.1 Social network analysis and multidimensional social relationships

The social network approach is a particularly useful tool in the multidimensional study of primate sociality because it allows for the comparison of the structure of relationships and the social roles of individuals across multiple behaviours.

Social networks can be constructed for the same set of individuals based on a number of different behaviours, and comparisons can be made between them. Recent studies of social relationships in several mammalian taxa using this approach found that different behaviours produced different network structures, highlighting the importance of using multiple behavioural measures in the study of sociality, and exemplifying the use of social network analysis in this area (Madden *et al.* 2009; Crofoot *et al.* 2011; Lehmann and Ross 2011; Tiddi *et al.* 2011). For example, Madden *et al*. (2009) constructed and compared social networks based on grooming, dominance, and foraging competition in meerkats, and found that each of these networks were independent of each other. Crofoot *et al*. (2011) compared proximity, aggression, and affiliative networks of three groups of white-faced capuchins, and found that the type of behaviour influenced network structures more than the differences between groups (Crofoot *et al.* 2011). Grooming and proximity networks were found to be similar in structure, and were found to influence each other, whereas the aggression networks had more complex substructures (Crofoot *et al.* 2011).

In addition to global network comparisons, the social network approach also offers measures of the positions of individuals in a network. Centrality measures indicate how central an individual is to their network, and can thus indicate the social roles individuals have in their group (Lehmann and Ross 2011). These measures do not just take the local neighbourhood of an individual in a network into account; instead they consider the entire network structure (Crofoot *et al.* 2011), thus moving beyond the traditional dyadic measures of interaction (Brent *et al.* 2011; Sueur *et al.* 2011a). These types of measures may be especially important because integration into a social network and network position, in both affiliative (Silk 2007; Lea *et al.* 2010) and agonistic (Lea *et al.* 2010) networks, influence individual fitness. Individual network positions can be compared across networks of different behaviours to determine whether individuals have similar roles across networks (Lehmann and Ross 2011). For example, Tiddi *et al.* (2011) compared the network positions of wild tufted capuchin monkeys in grooming and spatial proximity networks. They found that the alpha male was central to the proximity network, but not the grooming network, indicating that females seek the proximity of the alpha male to gain access to resources and protection (Tiddi *et al.* 2011). Furthermore, because females that were central in the female proximity network also had stronger proximity ties to the alpha male, females seem to compete by excluding others females from associating with the alpha male (Tiddi *et al.* 2011). Lehmann & Ross (2011) found that in olive baboons, although central individuals tended to be central in all networks, individual network positions varied across five different behavioural networks. This was particularly the case for more indirect centrality measures, that take into account the entire network structure rather than mere direct relationships. Most notably, individual positions in grooming networks were distinct from those in other behavioural networks (Lehmann and Ross 2011), highlighting again the importance of considering behaviours other than grooming in the study of primate sociality.

Despite these clear advantages of the social network approach for the multidimensional study of primate sociality, few studies have considered networks based on different behavioural measures within one study group. In several studies, while different behavioural networks were analysed, these were not compared directly. For example, McCowen *et al.* (2008) examined how the composition of captive groups of rhesus macaques affected dominance, affiliative, and submission networks, to investigate how aggression can be reduced in a captive setting. Direct comparisons between networks based on different behaviours have been made in just a handful of studies: meerkats (Madden *et al.* 2009); yellow-bellied marmots (Wey and Blumstein 2010); pigtailed macaques (Flack *et al.* 2006); white-faced capuchins (Crofoot *et al.* 2011); and olive baboons (Lehmann and Ross 2011).

5.1.2 Factors shaping social relationships

Social relationships are the result of repeated social interactions between individuals (Hinde 1976) and because these social interactions are influenced by individual behavioural strategies that are adjusted to the social and ecological environment, social and ecological factors influence social relationships (Kappeler and van Schaik 2002; Aureli *et al.* 2008a; Kummer 2008). The distribution of food, predation risk, sex, kinship, dominance, and reproductive state are important factors in shaping social relationships (Gouzoules 1984), but because the two sexes are limited by different considerations (Trivers 1972), factors affect the relationships between females, between males, and intersexual relationships differently. In the following sections, the factors that have been suggested to influence primate social relationships are discussed, and their potential effects on the social relationships of olive baboons are explored. This is followed by a discussion of the possible interactions between social structure and social organisation.

5.1.2.1 Relationships between females

Relationships between female primates are largely determined by access to resources, and in particular the competition for access to food. Following socioecological theory, it is suggested that females are 'forced' to live in groups due to predation risk or risk of infanticide (van Schaik 1996; Sterck *et al.* 1997) and as a result may compete over food. The social relationships that form between females in a group depend on the type of food competition (van Schaik 1989; Sterck *et al.* 1997), which is largely influenced by the distribution of food.

When food occurs in clumps that can be monopolised, and competition within groups occurs via contests (*i.e.* overt agonistic interactions), hierarchical relationships develop between females in the form of a dominance hierarchy, and females form strong alliances with their female kin (Sterck *et al.* 1997). However, when there is also strong contest competition between groups, within group dominance relations may be somewhat relaxed to ensure the cooperation of all females in the contests with neighbouring groups (Sterck *et al.* 1997). When competition within groups is mainly by scramble (*i.e.* no overt agonistic interactions), when food is uniformly distributed, females do not form strong hierarchies, and relationships may be weak. When between-group contest competition is also low, females have little need for alliances with their kin, whereas when between-group contest competition is high, females may compete alongside their kin against other groups (Sterck *et al.* 1997).

The baboon socioecological model was extended to include the effect of levels of predation risk on group size and the resulting within group competition (Barton *et al.* 1996). When predation pressure and within group contest competition are both high, large groups are expected in which females have strong bonds. When within-group contest competition is low, groups are still large, but the relationships between females are less strong (Barton *et al.* 1996). Whereas when predation risk and within-group competition are both low, small groups are formed in which the relationships of females are weak (Barton *et al.* 1996).

In baboons, much of the social behaviour is regulated by maternal kinship; females are known to direct their behaviour towards their maternal kin (Smith *et al.* 2003), and to form strong bonds with them (Silk *et al.* 2006). More specifically, females are more affiliative towards their maternal relatives than towards non-kin (Smith *et al.* 2008), for example, females mostly concentrate their grooming on kin (Seyfarth 1977; Schino 2001; Smith *et al.* 2003). Other cooperative behaviours may similarly be directed preferentially towards maternal kin. However, as too few maternal kin relations were known for the individuals in this study, it was not possible to determine the influence of maternal kinship on regulating social relationships.

Dominance rank has also been shown to regulate social relationships, particularly grooming relationships, in baboons. For example, it has been argued that baboons most frequently groom individuals that are adjacent in ranks, because individuals trade grooming for support in agonistic encounters and therefore compete over access to grooming the highest ranked individuals (Seyfarth 1977). This competition results in females grooming others that are close in rank. However, other studies found that females with adjacent rank were groomed equally to females non-adjacent in rank when maternal kinship was controlled for (Silk *et al.* 1999; Schino 2001). Therefore, Seyfarth's model may not adequately explain the distribution of grooming relationships in olive baboons (Sambrook *et al.* 1995).

Conversely, rank may influence social relationships because it influences the market value of commodities traded in a biological market. According to the biological market theory (Noë and Hammerstein 1995), grooming is a commodity that can be traded (Barrett and Henzi 2006). Primates may exchange grooming for other commodities, such as agonistic support, tolerance at feeding or drinking sites, mating, or access to infants (Barrett *et al.* 1999; Barrett and Henzi 2001; Barrett and Henzi 2006). The forces of supply and demand govern this trading and individuals choose their trading partners based on the latter's market value in order to maximize their benefits (Barrett and Henzi 2006). Barrett *et al*. (2002) found that when food competition was high, female chacma baboons could trade grooming for other commodities, such as tolerance, and that grooming reciprocity was more strongly influenced by the effects of rank. Lower-ranking females groomed higher-ranking females more, the more distant individuals were in rank, the less equal the reciprocation of grooming was (Barrett *et al.* 2002). When food competition was lower, the effect of rank on patterns of grooming disappeared; because grooming could not be traded for other commodities, grooming became more reciprocal (Barrett *et al.* 2002).

Apart from these behavioural responses to ecological factors, female social relationships may also be shaped by social factors, such as attraction to newborn infants (Altmann 1980; Silk 1999; Henzi and Barrett 2002; Silk *et al.* 2003a), sexual conflict (Kappeler and van Schaik 2002), or the relationships females have with males (Wrangham 1979). For example, the presence of a dependent infant can affect a female's social interactions; as outlined in section 4.1.3.3, baboons are greatly attracted to new-born infants and attempt to interact with them. As this infant handling can be quite rough, mothers are often reluctant to allow other females access to their infants (Henzi and Barrett 2002; Frank and Silk 2009). Grooming of the mother helps to facilitate access to the infant, and it is thought that grooming is 'traded' for infant handling (Henzi and Barrett 2002; Frank and Silk 2009). Thus, baboon mothers are approached and groomed at high rates (Seyfarth 1977; Henzi and Barrett 2002; Silk *et al.* 2003b) and females preferentially groom mothers (Frank and Silk 2009). The mothers of new infants on the other hand have been observed to reduce their amount of grooming, and the grooming relationships are thought to be asymmetric because the mother repays the groomer by allowing access to her infant (Frank and Silk 2009). This trade of grooming for infant handling has been shown to be subject to laws of supply and demand (Henzi and Barrett 2002). Thus, particularly for grooming relationships it is important to consider the presence of dependent offspring (Seyfarth 1977). This may further affect affiliative behaviours other than grooming; thus, grooming, affiliative and unidirectional grunt relationships are expected to be influenced by the presence of dependent offspring. For example, in baboons, lactating females receive less aggression (Seyfarth 1976), and more friendly approaches by other females (Rowell 1969) as well as more friendly gestures than non-lactating females (Seyfarth 1976).

Female reproductive state has been shown to affect the relationships between females; pregnant baboons have been observed to engage less frequently in any type of social interaction (Rowell 1969), whereas females with sexual swellings reduce their friendly interactions with other females (Rowell 1969).

5.1.2.2 Relationships between males

Relationships between male primates are largely determined by the spatial and temporal distribution of females (van Schaik 1996), and the resulting competition for access to those females. The strength and nature of this competition determine the costs and benefits of cooperating with other males, and thus the relationships between males. The grouping patterns of females, along with the degree of synchrony in female reproductive state determine whether males are able to monopolise a group of females, and thus the strength of competition over access to females (Strier 2003a). When competition over females is strong, relationships between males are hierarchical and intolerant (Kappeler and van Schaik 2002); males may be able to form uni-male groups by keeping other males out, or form strong dominance hierarchies in which high ranking males father more offspring than do low ranking males (Altmann *et al.* 1996; Strier 2003a). Competition for females is more indirect when females choose males based on certain characteristics (*i.e.* female choice), or when sexual selection takes place *after* the mating, through, for example, sperm competition (Strier 2001). In these cases, males may be more tolerant of each other, and have less hierarchical relationships. Additionally, unrelated males may form opportunistic or longer-term alliances if this increases their access to fertile females, for example by bypassing dominance rank (Chapais 1995).

Among baboons however, it has been suggested that predation risk is the primary factor shaping the relationships between males (Barton *et al.* 1996). When predation risk is low, small units with a single male can forage alone, allowing males to avoid each other. When predation risk is higher, groups are either permanently cohesive, or aggregate frequently, and in this case males may form alliances to gain access to fertile females (Whiten *et al.* 1991).

5.1.2.3 Relationships between males and females

Sexual selection and sexual conflict have been suggested to shape the relationships between males and females (Kappeler and van Schaik 2002). Males may selectively interact with cycling females to increase their mating opportunities, and therefore social interactions between males and females may be influenced by female reproductive state. For example, male baboons are known to groom females with sexual swellings more than females without swellings (Rowell 1968). Moreover, females change their pattern of grooming over their cycle; females replace their grooming of other females by grooming of males when they have sexual swellings (Rowell 1968). This pattern of interactions may be extended to other forms of affiliative behaviours.

Grunting facilitates social interactions, and the distribution of male grunts to females may reflect their interests in interacting with a female, which changes with her reproductive state (Palombit, Cheney, and Seyfarth 1999). For example, chacma baboon males are known to grunt more frequently to cycling females (Palombit *et al.* 1999), which may increase their opportunities for mating. Male interaction with lactating females can also be beneficial to the males; for example, if through repeated interactions with an infant the male is able to use that infant in agonistic buffering in conflicts with higher-ranking males (Palombit *et al.* 1999). Because female baboons with small infants are reluctant to interact with non-friend males, frequent grunting by males is needed to indicate their good intentions. For example, chacma baboon males most frequently grunt at lactating females, especially when these males are not a friend of that female (Palombit *et al.* 1999). Additionally, males grunt less frequently at pregnant females (Palombit *et al.* 1999), which may be because males are not interested in mating with these females.

Infanticide risk is an important factor shaping the relationships between males and females (van Schaik 1996), and is determined by, amongst other factors, the degree of sexual dimorphism in a species, the paternity certainty, and the time a male has been resident in the group (Weingrill 2000; Kappeler and van Schaik 2002). Through associating with a male, females have a protector that can help prevent infanticide by unfamiliar males (van Schaik 1996). As outlined in section 4.1.3.4, friendships between adult males and females have been observed in olive baboons, and are thought to be protection against non-lethal harassment of offspring (Lemasson *et al.* 2008). Males and females that have this type of bond engage more frequently in grooming bouts, and show low rates of submissive and aggressive behaviours (Cheney and Seyfarth 2007; Nguyen *et al.* 2009; Moscovice *et al.* 2010). Therefore, these strong bonds between particular adult males and females are expected to be reflected in agonistic and grooming networks. However, it is not known if friendships are also typified by higher rates of affiliative behaviours other than grooming.

5.1.2.4 Factors shaping social structure

As outlined above, several ecological and social factors have been identified as affecting individual behavioural strategies, and consequently, social relationships. Despite this growing evidence for the influence of both social and ecological strategies on individual interactions, it has been difficult to understand how complex decisions at the level of the individual shape patterns of social relationships at the level of the troop.

Furthermore, to date it is not clear how a species' social structure is related to its social organisation. The social organisation and social structure of primate groups may be linked through causation, evolution, or correlation (Kappeler and van Schaik 2002). Social organisation and social structure are linked in a causal sense if the form of one limits the form of the other (Kappeler and van Schaik 2002). For example, if the social organisation includes a high degree of fission-fusion dynamics, not all individuals in a social group may be available for social interactions, thus limiting the social structures that can occur. In the between-troop comparisons in this chapter, associations will be controlled for, as what is of interest is the difference in social relationships over and above the availability of troop members. The social relationships in turn may limit associations, for example, individuals that have strong grunting or grooming relationships may also have stronger associations.

The link between social organisation and social structure is evolutionary if the adaptive outcomes in one have led to certain adaptive outcomes in the other (Kappeler and van Schaik 2002). This may happen, for example, when alliances between males in small foraging parties or between one-male-units are selected for, leading to larger aggregations or 'bands' such as those seen in hamadryas baboons (Kummer 1968; Barton *et al.* 1996), selecting for a particular social organisation.

A correlational link exists between social organisation and social structure when the two components do not strongly affect each other, but are both affected by a third factor (Kappeler and van Schaik 2002). For example, female philopatry affects both the social organisation, such as the size and demography of a group, and the social structure, as females may form stronger bonds with kin. The causal, evolutionary, and correlational relationships between social organisation and social structure are not mutually exclusive.

However, it has also been suggested that the social organisation and social structure are not related, and that these vary independently from each other (Kappeler and van Schaik 2002), because of the wide range of social structures observed across the primate order. Thus, it is not clear if social relationships are in fact influenced by the social organisation of a group.

In this chapter, the difference in the structure of social relationships of two troops, shown to differ in ecology (chapter 3) and association patterns (chapter 4), is investigated, to test whether troops also differ in the nature of their social relationships. Furthermore, the influence of social factors on the structure of social relationships is examined.

5.1.3 Aims of this chapter

In this chapter, a social network approach is used to test whether the structures of social relationships vary when different social interactions are considered, and whether these different dimensions of social relationships influence each other. The structure of networks and the positions of individuals within networks based on affiliative, agonistic, grooming and grunting behaviours of two troops of olive baboons are investigated. Network comparisons are also made between troops to test if differences in local ecology and association patterns are linked with differences in the structure of social relationships. Additionally, the influence of social strategies on the structure of these networks is examined. The specific research questions of this chapter are as follows:

1. Do network structures differ across behaviours?
2. How are relationships based on different behaviours related?
3. Do individuals have the same roles across behavioural networks?
4. Do the behavioural networks of the Gamgam and Kwano troop differ?
5. Are behavioural networks regulated by social factors?
    a. Are behavioural networks assorted by age or sex?
    b. Are the social relationships of females affected by the presence of dependent offspring or reproductive state?
    c. Are the social relationships of females affected by dominance relationships?
    d. Are the social relationships of females and males affected by lactation or cycling?

5.2 Methods

A summary of the questions addressed in this chapter, along with the analyses and the data used, is given in Table 5.5.

5.2.1 Behavioural networks

For both troops, five behavioural networks were constructed based on affiliative, agonistic, and grooming interactions, and unidirectional grunts and grunt exchanges that were calculated from behavioural data collected during focal observations. The affiliative, agonistic, and unidirectional grunt networks were based on the average rate each dyad engaged in these interactions per minute. The affiliative behaviours are: lip smack, present for grooming, present rear, embrace, touch genitals, touch muzzles, offer or hold hands, touch, present genitals, approach, give a 'friendly face', grasp of rear, tongue protrusion, mount, and give and receive grooming (see chapter 2 for definitions of behaviours). Aggressive behaviours are: attack, chase, bite, hit, head bob, ground slap, lunge, tooth grind, eyebrow raise, ears back, stare, contact aggression, non-contact aggression. For the unidirectional grunt network, all grunts were included apart from when three or more grunts were exchanged between individuals in a dyad (*i.e.* 'grunt exchange'). Grooming networks were based on the proportion of overall grooming time an individual spent grooming another individual. Total grooming time was calculated including only those grooming bouts for the individuals that were included in the network. Thus, time spent grooming juveniles, or adults that were not present for the entire study period was not included in this. The grunt exchange network was based on the average rate of grunt exchanges (*i.e.* exchange of three or more grunts each between two baboons) per minute calculated for each dyad. The affiliative, agonistic, unidirectional grunt and grooming networks are all directed networks (see below), whereas the grunt exchange networks are undirected.

It was not possible to construct behavioural networks for each season (see section 2.2.1), as too few data were available for each three-month period to construct social networks. Especially in the larger Kwano troop, not all troop members were observed in a focal follow in each three-month period. Therefore, the data were pooled over the entire study period.

5.2.1.1 Filtering of behavioural networks

Behavioural networks were compared to 50 Erdös-Rényi random graphs to determine the appropriate level of filtration (see section 2.5.1 for a full description of this method). For the Gamgam troop the grooming and unidirectional grunt networks and for the Kwano troop the grunt exchange network were significantly different from random before filtering (Table 5.1). Only three networks differed from random, and there was no consistency across troops in the networks that deviated from random networks. Therefore, all networks were filtered to the same ratio of filtering level to mean network value as was used for association networks (see section 4.2.1), allowing for comparison across behavioural networks and with association networks within troops. The filtration levels used for each of the networks are given in Table 5.2.

Table 5.1: Results for the comparison of the behavioural networks to 50 Erdös-Rényi random graphs. For each behavioural network the mean clustering coefficient and mean shortest path length is given. Metrics marked * are significantly different from mean of the metrics for the random networks. Bold values indicate networks that were different from random, *i.e.* where both metrics were significantly different from random.

		Mean clustering coefficient			Mean shortest path length		
Troop	Network	Observed	Random	SD random	Observed	Random	SD random
GAMGAM	Affiliative	0.829*	0.804	0.009	1.196	1.196	0.000
	Agonistic	0.319	0.351	0.070	1.698	1.836	0.172
	Grooming	**0.735***	**0.497**	**0.045**	**1.449***	**1.565**	**0.047**
	Grunt exchange	0.904*	0.793	0.047	1.214	1.214	0.000
	Single grunt	**0.832***	**0.697**	**0.017**	**1.204***	**1.306**	**0.007**
KWANO	Affiliative	0.700*	0.624	0.005	1.375	1.375	0.001
	Agonistic	0.078	0.115	0.048	1.667*	2.707	0.422
	Grooming	0.376*	0.291	0.028	1.893	1.901	0.045
	Grunt exchange	**0.605***	**0.334**	**0.073**	**1.513***	**1.760**	**0.032**
	Single grunt	0.495*	0.361	0.019	1.769	1.732	0.029

Table 5.2: Table showing the levels of filtering for each of the behavioural networks in the Gamgam and Kwano troop. Ties that were weaker than these values were not included in the networks to help focus on those ties that are more likely to represent meaningful relationships. The filtration levels have the same ratio to the mean network value as the filtering level to the mean network value in the association networks.

	Filtration level	
Network	GAMGAM	KWANO
Affiliative	0.0030	0.0060
Agonistic	0.0004	0.0002
Grooming	0.0800	0.0400
Grunt exchange	0.0150	0.0040
Single grunt	0.0190	0.0080

5.2.1.2 Metrics in directed networks

In directed networks, the direction of a tie is also considered, with each relationship having an actor and a recipient (see section 2.5 for example data and network). In the calculations for network metrics in directed networks, both the ties *leaving* a node and the ties *coming in* to a node have to be considered. The *in-degree*, for example, considers the ties coming in to a node, whereas the *out-degree* is the number or weights of ties that leave a node. The grooming, affiliative, agonistic, and unidirectional grunt networks are directed, whereas the grunt exchange network is undirected.

The in- and outdegree are considered in network centralisation measures, individual centrality measures (see below), and the influence of social factors on the patterning of relationships. For the comparison of the degree values across behavioural networks and between troops, a mean degree value is taken over the whole network; therefore, the in- and out-degree are equal. Therefore, only one degree value is given in those analyses.

5.2.2 Individual centrality measures

One of the principal uses of social network analysis is the identification of the importance of individuals within their social networks (Wasserman and Faust 1994). Social network analysis allows us to quantify the 'involvement' of individuals in social relationships within their network through a range of centrality measures (Wasserman and Faust 1994). Centrality measures used in this thesis are given in Table 5.3.

Table 5.3: Definitions of individual centrality measures (adapted from: Wasserman and Faust 1994; Newman 2007).

Centrality measures	
Degree centrality	The degree centrality is a measure of the number of social partners an individual has, and is denoted as: $$C_D(n_i) = \sum_j x_{ji}$$ Where x_{ji} is the relationship between node j and i. In directed networks both the ties coming into a node (indegree) and leaving a node (outdegree) are considered. In weighted networks, the degree centrality measures the frequency of an individual's social relationships, taking into consideration the strength rather than the number of connections.
Eigenvector centrality	The eigenvector centrality is a measure of the prominence of an individual in their network taking into account both the number of social partners and the centrality of those partners. The eigenvector centrality indicates the number of connections as a proportion of their eigenvector centrality score, and is calculated as follows: $$x_i = \frac{1}{\lambda} \sum_{j=1}^{n} x_{ij} a_j$$ where λ is the largest eigenvector value in the network, and a_j is the eigenvector centrality of node i. This measure can be directed, but does not take into account the weights of the relationships.
Closeness centrality	Closeness centrality is a measure of the distance between an individual and all other nodes in their network and is denoted as: $$C_D(n_i) = \left[\sum_{j=1}^{g} d(n_i, n_j) \right]^{-1}$$ Where $d(n_i, n_j)$ is the path length between node j and i. This measure can be directed and weighted.
Betweenness centrality	Betweenness centrality measures the influence an individual has over the relationships of others, and is indicated by the fraction of shortest paths that run via a particular individual: $$C_b(n_i) = \sum_{j<k} \frac{g_{jk}(n_i)}{g_{jk}}$$ where g_{jk} is the number of shortest paths that link the two actors, and $g_{jk}(n_i)$ is the number of shortest paths linking the two actors, that contain actor i. This measure ranges between zero and the number of pairs there are in the network, not including the individual itself. This measure can be directed and weighted.

Several of these measures, such as the *degree* and *strength* of nodes, are equal to traditional dyadic measures used in primatology (Brent *et al.* 2011). The measure of *degree centrality* indicates the number of social partners an individual has. Thus, individuals with a *high degree centrality* are connected to a high number of individuals in their group, and are therefore central to their network, whereas individuals with a low *degree centrality* are more peripheral (Wasserman and Faust 1994). The weighted version of this measure, the *node strength*, considers the strength of the relationships of a node, and thus corresponds to the traditional measure of the frequency of social interactions (Brent *et al.* 2011).

Besides these direct measures of an individual's relationships, the social network approach also provides further measures of an individual's importance that take the entire network into account (Sueur *et al.* 2011a). These indirect measures of centrality are based on the idea that individuals are not only prominent in a network because of their own relationships, but also through indirect connections in which they are intermediaries. Thus, an individual may have few ties, but if through those ties two distinct subgroups are connected, that individual is central to the overall network. For example, young adult males act as brokers between the male and female subgroups in spider monkey groups (Ramos-Fernández *et al.* 2009), and are therefore central to their networks. Indirect centrality measures can help to identify the importance of certain individuals for the overall structure of their social networks and to quantify social relationships beyond dyadic interactions (Brent *et al.* 2011). This is particularly important for the study of sociality in primates, as primates may recognize the social relationships between other troop members

(Tomasello 1998; Cheney and Seyfarth 1999; Silk *et al.* 1999; Silk 2007) and these third party relationships may influence their own dyadic interactions. In this chapter, three such indirect centrality measures are used in addition to the degree centrality measure to determine the role of individuals in their social networks.

The *eigenvector centrality* is a refinement of the degree centrality. This measure takes into account that not all relationships are of equal importance to an individual's prominence in their network; having a relationship with an influential individual may increase an individual's own influence, whereas a relationship with a peripheral individual would have much less impact (Newman 2007). The eigenvector centrality of an individual is thus proportional to the eigenvector centralities of its neighbours; in other words, it depends both on the number of social partners and the quality of those partners (Newman 2007) with high quality being indicated by a high eigenvector centrality. Thus, an individual with a small number of high quality partners may have a higher eigenvector centrality than an individual with a large number of peripheral partners (Newman 2007).

The *closeness centrality* and *betweenness centrality* measures are both based on the distances between individuals in the network. *Closeness centrality* considers how close an individual is to all others in their network, and thus how quickly they would be able to reach others. This measure is calculated as the inverse sum of all the shortest path lengths between a node and all other individuals in a network. Thus, the most central nodes have the highest closeness (Wasserman and Faust 1994).

The *betweenness centrality* measure also uses the concept of shortest paths between individuals, but it considers the fraction of these shortest paths that run via an individual; it measures the probability of an individual lying on the shortest path, or being 'between', two other individuals (Wasserman and Faust 1994; Opsahl *et al.* 2010). The minimum value for this measure is 0, where the node does not fall on any shortest paths in the network, and the maximum value is the number of pairs there are in the network, not including the actor itself, indicating that all shortest paths go via that individual. A high *betweenness* centrality score thus indicates that an individual plays an important role in connecting different parts of their network. This measure is important as indirect relationships may be influenced by a third party, especially by individuals who are intermediaries in that indirect relationship (Wasserman and Faust 1994).

The centrality measures outlined here indicate how direct and valuable an individual's connections are, the level of control they have over the relationships of others, and their overall involvement in the network. These complementary measures indicate different aspects of the importance of individuals in their social networks, thus giving a good indication of an individual's social role.

5.2.2.1 Weighted centrality measures

In weighted networks, the strength of the ties (*i.e. node strength*) is frequently used instead of the number of ties considered in binary networks. However, considering only the strength of ties is a crude measure of a node's involvement in their network, as individuals can have an overall similar frequency of interactions, but the number of individuals they interact with can be very different. Opsahl *et al*. (2010) proposed a generalisation to weighted networks that combines the binary *degree* and the *node strength* through a tuning parameter α that sets the relative importance of the tie weights compared to the number of ties. With this α the *degree centralisation* then becomes:

$$C_D^{\omega\alpha}(n_i) = x_i{}^{(1-\propto)}\, s_i^{\propto}$$

Where x_i is the number of partners of node *i* and s_i is the strength of the relationships of node *i* (Opsahl *et al.* 2010). An example of the effect of this tuning parameter on the *degree centralisation* score of individuals in the network given in Figure 5.1 is given in Table 5.4.

This generalisation was used to calculate the *weighted degree centrality*, to identify the shortest paths between individuals in the *betweenness centralisation* calculations, and to determine the length of the paths between individuals (Opsahl 2009) in the *closeness centralisation* calculations.

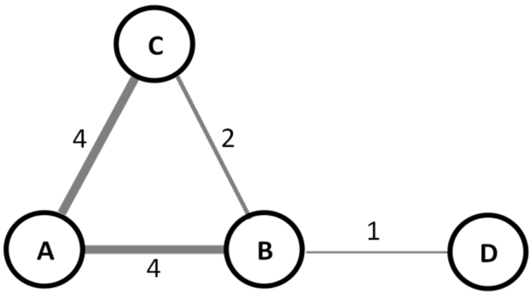


Figure 5.1: Example of a weighted network (adapted from Opsahl *et al.* 2010). The strength of relationships is indicated by the thickness of ties and the value next to the tie. The *degree centrality* scores for this network are given in Table 5.4.

Table 5.4: The *degree centrality* scores for nodes in the network given in Figure 5.1 (adapted from Opsahl *et al.* 2010). The binary and weighted *degree centrality* scores are given in the second and third columns. In the latter three columns the *degree centrality* scores are given in which the number and the weight of the ties are both considered. The tuning parameter α determines the relative importance of the number of ties or the weight of the ties, with α = 0 only the number of partners are considered, and α = 1 only the weight of ties is considered.

			Combined degree centrality with α		
Node	Binary degree centrality	Weighted degree centrality	0	0.5	1
A	2	8	2	4	8
B	3	7	3	4.6	7
C	2	6	2	3.5	6
D	1	1	1	1	1

5.2.3 Data analysis

The analyses used to answer each research question are outlined below. Research questions, analyses and variables are summarised at the end of this section in Table 5.5.

5.2.3.1 Do network structures differ across behaviours?

Behavioural networks were visualised using Netdraw visualisation software (Borgatti 2002). Graphs were laid out using spring embedding (Croft *et al.* 2008), with line thickness indicating the strength of ties. To quantify and compare the structure of the networks, ten network metrics were calculated: the *largest strong component*; *density*; *weighted diameter*; *weighted mean geodesic*; *compactness*; *mean degree*; *mean node strength*; *average tie weight*; *weighted mean clustering coefficient*; *weighted network centralisation* (see section 2.5.2 for a full discussion of these metrics). For the directed networks both the in- and out-degree, and the network centralisation for the in- and outdegree were calculated. Networks were tested for significant differences in density using permutations tests in UCINET (Borgatti *et al.* 2002). All other comparisons of network metrics were made qualitatively.

5.2.3.2 How are relationships based on different behaviours related?

To test if social relationships based on different behaviours were related to each other the behavioural networks were correlated using QAP correlation in UCINET, with 5000 permutations.

5.2.3.3 Do individuals have the same roles across behavioural networks?

To determine if olive baboons occupy the same network positions across behavioural networks, three weighted centrality measures (*degree centrality, closeness centrality and betweenness centrality*) and one binary centrality measure (*eigenvector centrality*) were calculated for each individual in each behavioural network.

For the weighted centrality measures, the tuning parameter was set to 0.5, thus weighting the number and the strength of ties equally, and these were calculated in *tnet* (Opsahl 2009). The eigenvector centrality was calculated in the igraph (Csardi and Nepusz 2006) package for R (R Development Core Team 2010). Individual scores for each of the four centrality measures, or five in the case of directed networks, were correlated across behavioural networks to determine if network positions were similar. For this analysis a Kendall's tau-b correlation was run, as samples were small.

5.2.3.4 Do the behavioural networks of the Gamgam and Kwano troop differ?

When comparing behavioural networks between two troops with differential spatial associations the availability of partners has a potentially confounding effect (Sailer and Gaulin 1984), *e.g.* individuals may not be able to have grooming relationships with troop members who are not frequently in close proximity. In the comparison of the behavioural networks between troops, spatial associations were controlled for by weighting the behavioural network by the inverted value of the twice weight index (TWI) (Sailer and Gaulin 1984). These networks were then filtered to the same ratio of filtering level to mean value as the association network. Networks were visualised and metrics were calculated as outlined in section 5.2.3.1.

Furthermore, as network metrics may be influenced by the number of nodes, (Anderson *et al.* 1999) troop size should be controlled for. In order to test for a difference in network density between the two troops, controlling for the sizes of the networks, a conditional uniform graph test procedure was performed on the behavioural networks.

For the directed networks, in addition to the density, the networks were also tested for difference in reciprocity and transitivity. Reciprocity measures the extent to which ties in a network are reciprocated, and is defined as the proportion of dyads in a network that are symmetric (Butts 2010). Relationships are considered transitive when:

$$a \rightarrow b \rightarrow c \Rightarrow a \rightarrow c$$

(Wasserman and Faust 1994). The transitivity measure indicates the fraction of potentially intransitive triads, thus the triads in which a relationship between *a* and *b*, and between *b* and *c* exist, in which a relationship between *a* and *c* also exists, *i.e.* when relationships are transitive (Butts 2010). The transitivity of a network thus indicates the extent to which relationships are influenced by third party relationships; it indicates how likely it is that if *a* has a relationship with *b*, and *b* has a relationships with *c*, *a* also has a relationships with *c*. These types of relationships for example may occur in a dominance hierarchy, where if *a* is dominant to *b*, and *b* is dominant to *c*, *a* is also likely to be dominant to *c*.

Currently, it is not possible to use conditional uniform graph tests for network metrics other than density, reciprocity and transitivity.

5.2.3.5 Are behavioural networks assorted by age or sex?

To test if social interactions were assorted by age or sex, for undirected networks a joint count analysis was used, comparing the densities of ties within and between each category. For this type of analysis, matrices need to be symmetrical; consequently for the directed networks it was not possible to perform this. Instead, for these networks a relational contingency analysis was used, which compares the observed frequencies of ties within and between categories to expected frequencies of ties. The number of individuals in each age and sex class is given in Chapter 4, Table 4.2.

5.2.3.6 Are the social relationships of females affected by the presence of dependent offspring or reproductive state?

To determine if the presence of young infants influenced social interactions, a node-level t-test was performed (Borgatti *et al.* 2002) comparing the total node strength of females with dependent offspring to that of females without dependent offspring. Dependent offspring were defined as infants up to eight months old. The number of females in each category is given in Chapter 4, Table 4.3. As the affiliative, agonistic, grooming and unidirectional grunt networks are directed, comparisons were made both between the indegree and the outdegree. For the grunt exchange network one value of node strength was calculated.

To test if female interactions were influenced by their reproductive state, node-level ANOVA's were run (Borgatti *et al.* 2002), in which the average node strength of females was compared across three categories; cycling females, lactating females, and pregnant females. Females that had anovulatory cycles (*i.e.* not pregnant, lactating, and no sexual swellings) were grouped with cycling females. Females were classified according to the reproductive state that they were in for the majority of the study period. The number of females in each category is given in Chapter 4, Table 4.4. For directed networks, both the node strength of behaviour received and given were calculated.

5.2.3.7 Are the social relationships of females affected by dominance relationships?

Relational contingency table analysis was performed in UCINET (Borgatti *et al.* 2002) to determine if behavioural networks were assorted by dominance rank. The observed frequencies of ties within and between rank classes were compared to expected frequencies of ties. As it was not possible to determine a dominance hierarchy for the males in either troop, only females were included in the analyses of the effect of dominance rank. The number of females in each rank category is given in Chapter 4, Table 4.5.

5.2.3.8 Are the social relationships of females and males affected by lactation or cycling?

Two-sample permutation tests (10000 permutations) were performed for each of the behavioural networks to test if lactation or cycling influenced the behavioural interactions between males and females. The strength of relationships of males and lactating females were compared to those of males and non-lactating females (*i.e.* cycling and pregnant females). The numbers of females in each reproductive category are given in Chapter 4, Table 4.4.

Similarly, the bonds of males and cycling females were compared to those between males and non-cycling females. Non-cycling females were defined as females that were lactating, pregnant, giving birth, and ‘non-cycling’ (*i.e.* females that were not lactating or pregnant, but also showed no sexual swellings); cycling females were defined as both cycling and nulliparous cycling females. Females were assigned the state they were in for the majority of days in the study period. For the majority of females this was relatively clear-cut; in Gamgam three out of five females and in Kwano half of females were in the same state (cycling or non-cycling) for the entire study period. A fifth of Gamgam females and two-fifth of Kwano females were in the same state for over two-thirds of days in the study period. One female in the Gamgam troop was cycling on 59% and non-cycling on 41% of days in the study period. Similarly, in the Kwano troop one female was cycling and non-cycling for an equal amount of days in the study period. The numbers of cycling and non-cycling females are given in Chapter 4, Table 4.6. For the directed networks, differences were calculated both for receiving and giving the behaviours.

Table 5.5: Questions addressed in this chapter, the type of analyses and the data used.

Question	**Analyses**	**Data used**
1. Do network structures differ across behaviours?	Comparison of social network metrics	• Behavioural networks
	Compare densities permutation test	• Behavioural networks
2. How are relationships based on different behaviours related?	QAP correlation	• Behavioural networks
3. Do individuals have the same roles across behavioural networks?	Kendall's tau-b correlation	For each individual across behavioural network: • Degree centrality • Eigenvector centrality • Betweenness centrality • Closeness centrality

Question (*continued*)	**Analyses**	**Data used**
4. Do the behavioural networks of the Gamgam and Kwano troop differ?	Comparison of social network metrics	• Behavioural networks controlling for associations
	Conditional uniform graph test for difference in density, reciprocity, and transitivity	• Behavioural networks controlling for associations
5a. Are behavioural networks assorted by age or sex?	Joint count analysis	• Undirected behavioural networks • Age • Sex
	Relational contingency table analysis	• Directed behavioural networks • Age • Sex
5b. Are the social relationships of females affected by the presence of dependent offspring or reproductive state?	Node-level t-test	• Node strength of females with dependent offspring for behavioural networks • Node strength of females without dependent offspring for behavioural networks
	Node-level ANOVA	• Female node strength in behavioural networks • Female reproductive state
5c. Are social relationships of females affected by dominance relationships?	Relational contingency table analysis	• Behavioural networks including only females • Female rank class membership
5d. Are the social relationships of females and males affected by lactation or cycling?	Two-sample permutation test	• Strength of ties of males and lactating females in behavioural networks • Strength of ties of males and non-lactating females in behavioural networks • Strength of ties of males and cycling females in the behavioural networks • Strength of ties of males and non-cycling females in the behavioural networks

5.3 Results

5.3.1 Do network structures differ across behaviours?

The behavioural networks for Gamgam are shown in Figure 5.2a-e, and the network metrics are given in Table 5.6. Kwano behavioural networks are given in Figure 5.3 and the corresponding network metrics in Table 5.7.

In the Gamgam troop the affiliative, agonistic, and unidirectional grunt networks were all fully connected, whereas the grooming and grunt exchange networks had one isolate, DRW (Figure 5.2 a & e). For the directed networks, the majority of individuals had reciprocal ties to all troop members in the grooming and unidirectional grunt networks as indicated by the *largest strong component*. This was lower for the affiliative and agonistic networks.

The Kwano grooming, affiliative, and unidirectional grunt networks were fully connected (Figure 5.3 a, b, d). The Kwano agonistic network had one isolate, DRN, who did not give or receive agonistic behaviours frequently enough to be included in the network (Figure 5.3 c). The Kwano grunt exchange network had three isolates; DRN, SAM, and SDA (Figure 5.3 e), three adult males who did not exchange grunts frequently enough with troop members to be included in the network. For the directed networks, ties were reciprocal between the majority (13-15) of troop members for the grooming, affiliative, and unidirectional grunt networks (*largest strong component*). None of the Kwano baboons had reciprocal aggressive ties (*largest strong component* of 1, *normalised largest strong component* of 6%). Consequently, it was not possible to calculate distance-based measures, *i.e.* the *weighted diameter* and *weighted mean geodesic* for the Kwano aggression network. These metrics are calculated on the *largest strong component* so that all pairs are reachable in order to avoid infinities and in the Kwano agonistic network there was only one node to be considered.

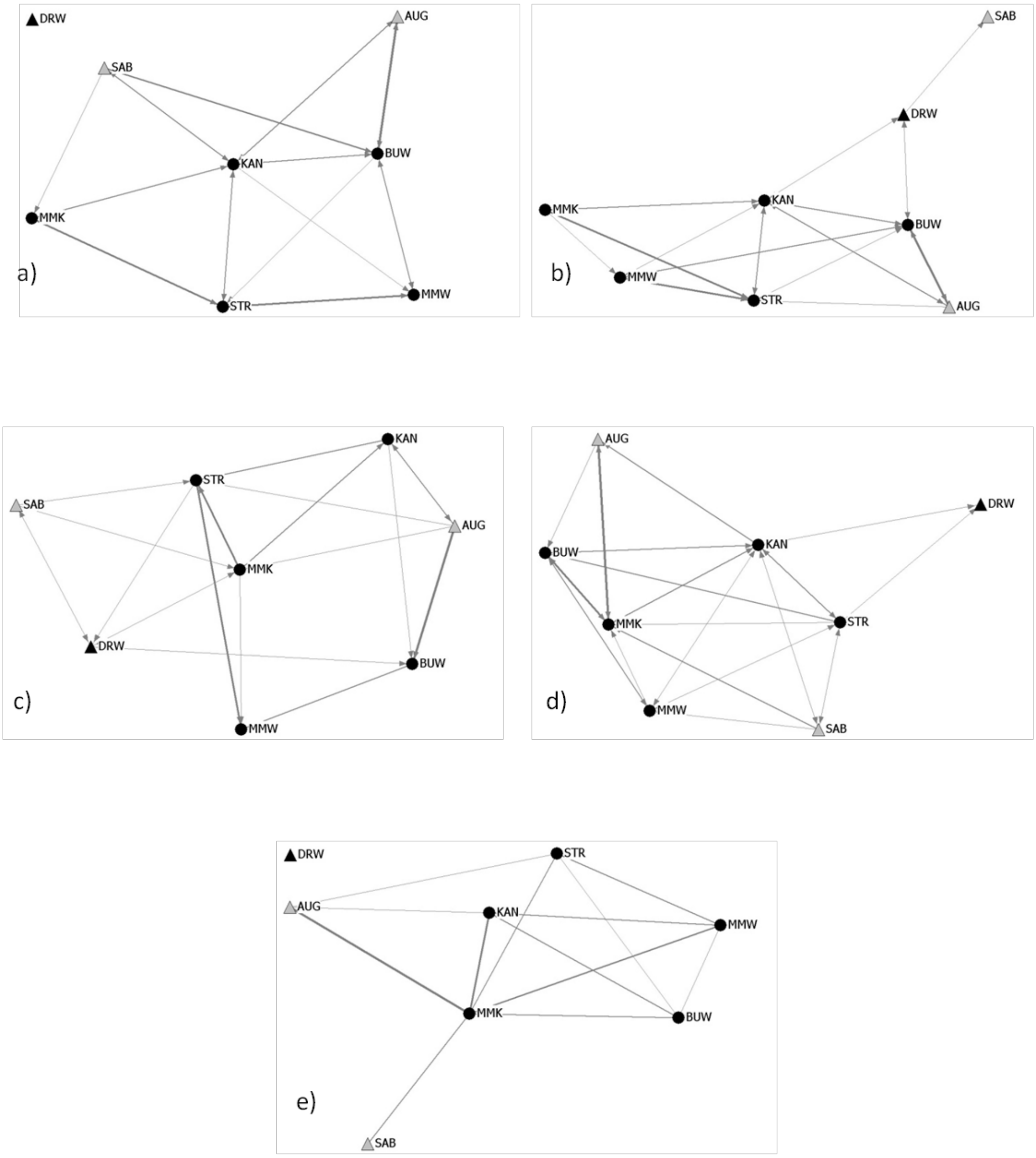


Figure 5.2: Gamgam networks for a) grooming, b) affiliative behaviour, c) agonistic behaviour, d) unidirectional grunt, e) grunt exchange networks. Networks are laid-out using spring embedding. Line thickness indicates the strength of the tie. Arrows indicate the direction of the relationship. Grunt exchange networks are undirected and therefore have no arrows. Females are represented by circles, males by triangles. Black nodes are adult, grey nodes subadults.

Table 5.6: Structural network properties of Gamgam behavioural networks. The grooming, affiliative, agonistic and unidirectional grunt networks are directed and consequently have an in- and out- degree. The grunt exchange network is undirected and thus has a single weighted network centralisation value.

Network metric	Grooming	Affiliative	Agonistic	Unidirectional grunt	Grunt exchange
Largest strong component	7	6	6	7	7
Normalised largest strong component (%)	88	75	75	88	88
Density	0.375	0.446	0.357	0.518	0.464
Weighted diameter	4.589	3.494	6.622	3.675	1.966
Weighted mean geodesic	1.936	1.653	2.505	1.691	1.289
Compactness	0.554	0.595	0.543	0.688	0.607
Mean degree (in & out)	2.625	3.125	2.500	3.625	3.250
Mean node strength	0.846	0.027	0.005	0.188	0.096
Average tie weight	0.322	0.009	0.002	0.052	0.030
Weighted mean clustering coefficient	0.469	0.664	0.416	0.703	0.658
Weighted network centralisation (in-degree)	0.216	0.039	0.014	0.125	0.123
Weighted network centralisation (out-degree)	0.126	0.036	0.015	0.113	

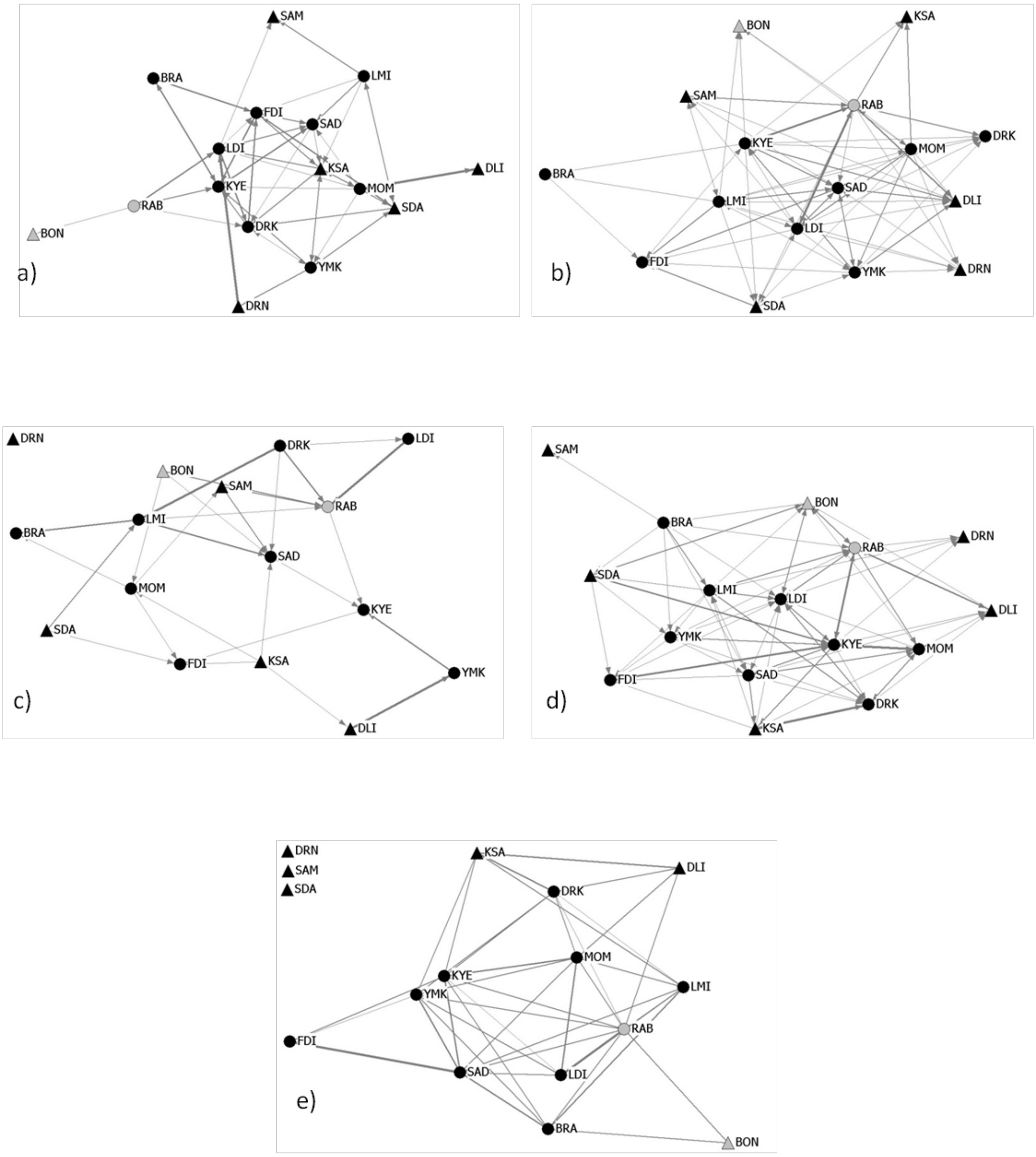


Figure 5.3: Kwano networks for a) grooming, b) affiliative behaviour, c) agonistic behaviour, d) unidirectional grunt, e) grunt exchange networks. Networks are laid-out using spring embedding. Line thickness indicates the strength of the tie. Arrows indicate the direction of the relationship. Grunt exchange networks are undirected and therefore have no arrows. Females are represented by circles, males by triangles. Black nodes are adult, grey nodes subadults.

Table 5.7: Network metrics of Kwano behavioural networks. The grooming, affiliative, agonistic and unidirectional grunt networks are directed and consequently have an in- and out- degree. The grunt exchange network is undirected and thus has a single weighted network centralisation value. The weighted diameter and weighted mean geodesic could not be calculated for the agonistic network as this network had a largest strong component of one.

Network metric	Grooming	Affiliative	Agonistic	Unidirectional grunt	Grunt exchange
Largest strong component	13	14	1	15	13
Normalised largest strong component (%)	81	88	6	94	81
Density	0.217	0.329	0.113	0.354	0.342
Weighted diameter	6.158	10.816	-	7.567	3.677
Weighted mean geodesic	2.250	3.148	-	2.073	1.543
Compactness	0.443	0.569	0.169	0.624	0.492
Mean degree (in & out)	3.250	4.938	1.688	5.313	5.125
Mean node strength	0.853	0.120	0.004	0.174	0.063
Average tie weight	0.262	0.024	0.002	0.033	0.012
Weighted mean clustering coefficient	0.320	0.581	0.152	0.508	0.570
Weighted network centralisation (in-degree)	0.164	0.049	0.013	0.082	0.039
Weighted network centralisation (out-degree)	0.073	0.123	0.010	0.068	

Results for comparisons of network densities are given in Table 5.8 and Table 5.9. In both troops, the grooming and agonistic networks were the sparsest; the densities of the agonistic and grooming networks were lowest and these were not significantly different from each other. While in Gamgam the number of observed relationships was not significantly different across networks, in Kwano both the grooming and agonistic networks were significantly sparser than the densest network of unidirectional grunts. The density of the agonistic network was also significantly lower than the densities of the affiliative and grunt exchange networks. None of the other networks differed significantly in density.

Both troops also had less cohesive grooming and agonistic networks, compared to the affiliative, unidirectional grunt and grunt exchange networks. Both the grooming and the agonistic networks were least clustered, least compact, and individuals had fewer interaction partners for these relationships (*weighted mean clustering coefficient, compactness, mean degree*), indicating that these behaviours were more spread across the troop rather than occurring between clumps of interconnected individuals, and that a relatively small proportion of troop members had direct aggressive and grooming interactions. Additionally, agonistic interactions were most rare as the *average tie weight* was lowest in the agonistic networks. The score for the *average tie weight* in the grooming network is not comparable to that of the other networks, as the grooming network was based on a proportion of grooming time, rather than a rate per minute. For the Kwano but not the Gamgam troop, the agonistic and grooming networks themselves also differed, with the grooming network being better connected than the agonistic network (*compactness, mean degree, clustering* *coefficient*), indicating that overall individuals had more direct grooming relationships than agonistic relationships, and that they were more selective in their partners for aggressive interactions than for grooming.

Table 5.8: Results for the t-test on the differences in densities (row-column) of Gamgam behavioural networks (UCINET compare densities t-test). The t-statistics are given along with their *p*-values in brackets. A positive *t*-value shows that the network in the row had a higher density, a negative *t*-value shows that the network in the column had a higher density.

	Agonistic	Grooming	Grunt exchange	Unidirectional grunt
Affiliative	0.741 (0.445)	0.830 (0.387)	-0.139 (0.892)	-0.575 (0.569)
Agonistic	-	-0.144 (0.887)	-0.849 (0.384)	1.286 (0.194)
Grooming		-	-0.758 (0.448)	-0.418 (0.155)
Grunt exchange			-	-0.578 (0.552)

Table 5.9: Results for the t-test on the differences in densities (row-column) of Kwano behavioural networks (UCINET compare densities t-test). The t-statistics are given along with their p-value in brackets. A positive *t*-value shows that the network in the row had a higher density, a negative *t*-value shows that the network in the column had a higher density. Significant differences are given in bold.

	Agonistic	Grooming	Grunt exchange	Unidirectional grunt
Affiliative	**3.376** **(0.0008)**	1.950 (0.052)	-0.173 (0.860)	-0.416 (0.669)
Agonistic	-	-1.863 (0.065)	**-3.661** **(0.0006)**	**-0.221** **(0.0008)**
Grooming		-	-1.800 (0.073)	**-2.210** **(0.027)**
Grunt exchange			-	-0.214 (0.826)

Overall, these metrics indicate that grooming and agonistic behaviours were rare, that the networks were sparse, and individuals were most selective in their interaction partners for these behaviours.

The grooming and the agonistic networks were distinct from the affiliative, unidirectional grunt and grunt exchange networks in both troops. The affiliative, unidirectional grunt and grunt exchange networks were much better and stronger connected, all these networks had high levels of clustering (*weighted mean clustering coefficient*) indicating that the majority of these behaviours occurred between individuals that were interconnected. Furthermore, individuals interacted with a larger proportion of their troop through affiliative behaviours, grunt exchanges and grunts (*mean degree*), and networks were denser (*density*). The high *density* of the affiliative network may in part be due to the greater number of behaviours that were entered into this network, compared to the other networks. The affiliative network includes grooming, however, it differs from the grooming network in that the frequency of grooming bouts are used, rather than the duration of grooming bout, as is the case in the grooming networks.

Relationships were most cohesive and strongest through unidirectional grunts; *compactness* was highest in the unidirectional grunt network, indicating that 69% of Gamgam troop members and 62% of Kwano troop members were adjacent to each other. Additionally, the unidirectional grunt network had the highest *average tie weight*, indicating that individuals most frequently interacted through unidirectional grunts. In Gamgam, grunt exchanges occurred at similar high frequencies (*average tie weight*) as unidirectional grunts.

Furthermore, the lowest *diameter* and *weighted mean geodesic* were found in the grunt exchange network and these are very similar for the affiliative network, indicating that individuals had the closest relationships through grunt exchanges and affiliative behaviours.

In the Kwano troop on the other hand, the frequency of affiliative behaviours was more similar to that of the unidirectional grunt network than of the grunt exchange network (*average tie weight*). The troop had closest relationships through grunt exchanges (*diameter*, *weighted mean geodesic*). The highest distance measures were found in the affiliative network (*weighted diameter, weighted mean geodesic*), and these measures were lower for both the grooming and unidirectional grunt networks (*weighted diameter, weighted mean geodesic*).

In both troops, network centralisation was relatively low across networks (*i.e.* between 0.010 – 0.164), where a value of one indicates one individual completely dominates all interactions. Thus, the number of partners and the rates at which individuals initiated behaviours were similar across troop members. The aggression networks were least centralised (*weighted network centralisation in- and out-degree* Table 5.6) in both troops, indicating that troop members were aggressive and received aggression at similar rates to each other, and had aggressive interactions with a similar number of troop members. The Gamgam troop was most differentiated in the receipt and giving of grooming, which indicates that some individuals received more grooming from a greater number of individuals than others, and individuals also differed in their tendency to groom others (*weighted network centralisation in- and out-*

degree). The Kwano troop was most differentiated in the receipt of grooming (*weighted network centralisation in-degree*), indicating some individuals are groomed for longer and by a wider range of troop members.

In brief, in both troops the grooming and agonistic networks had a similar structure to each other. In these networks the lowest proportion of possible ties was observed, networks were least clustered, and the mean degree was lowest. In other words, baboons were most selective in their choice of partners for grooming and aggression interactions and their interaction partners were spread over the network, rather than occurring in clusters. The affiliative, unidirectional grunt, and grunt exchange networks were denser, more clustered, and baboons had ties with a larger proportion of their network, indicating that these behaviours were more widespread, that baboons more frequently interacted with a larger proportion of their troop through affiliative behaviours, unidirectional grunts and grunt exchanges.

5.3.2 How are relationships based on different behaviours related?

Correlations were run between behavioural networks to investigate how these are related. Results are given in Table 5.10. In both troops a positive correlation was found between the grooming and affiliative networks, and the unidirectional grunt and grunt exchange networks, indicating that individuals had similar relationships through grooming and affiliative behaviours, and through unidirectional grunt and grunt exchanges. In Kwano, both the grooming network and the affiliative network also correlated with the unidirectional grunt and grunt exchange networks. Additionally, in Kwano the grunt exchange network was found to correlate positively with the agonistic and unidirectional grunt networks. In Gamgam none of the other behavioural networks were found to correlate.

Table 5.10: QAP Pearson correlation coefficients for the correlations between a) Gamgam behavioural networks (N = 56); b) Kwano behavioural networks (N = 240). Bold r values indicate a significant correlation between the networks, * = $p < 0.05$; ** = $p < 0.01$.

a)

	Agonistic	Grooming	Grunt exchange	Unidirectional grunt
Affiliative	0.151	**0.388***	0.035	-0.030
Agonistic	-	0.019	0.022	-0.004
Grooming		-	0.108	0.021
Grunt exchange			-	**0.592****

b)

	Agonistic	Grooming	Grunt exchange	Unidirectional grunt
Affiliative	0.080	**0.264****	**0.287****	**0.304****
Agonistic	-	0.031	**0.125***	0.075
Grooming		-	**0.154***	**0.195***
Grunt exchange			-	**0.339****

The correlation between the affiliative and the grooming network could be due to the inclusion of data on grooming bouts in both networks; in the affiliative networks the frequency of grooming bouts was included, whereas in the grooming networks this was the duration of grooming bouts. Therefore, a correlation was run between the grooming network and affiliative behaviour networks in which the frequency of grooming bouts was excluded. In both troops the correlation between the grooming and affiliative networks remained (QAP correlation: grooming – affiliative without grooming: Gamgam: r = 0.427, p = 0.007; Kwano: r = 0.241, p = 0.002), indicating that individuals have similar relationships through grooming as they do through other affiliative behaviours.

Correlations between behavioural networks may be a result of the time dyads spent in association. When individuals spend more time associated, they are more often available as a partner for interactions, and consequently behavioural networks may correlate. In order to test for the confounding effect of association time, behavioural networks were correlated with the association network. In both troops a positive correlation was found between the association network and the grooming network (Table 5.11). In Kwano the affiliative, grunt exchange and unidirectional grunt networks were also positively correlated with the association network. Therefore, QAP multiple regressions (Borgatti *et al.* 2002) were run using 2000 permutations, to see if these result still held when associations were controlled for. Results are given in Table 5.12. In the Kwano troop, the correlation between the grunt exchange and both the agonistic and grooming networks disappeared when associations were controlled for.

A regression was also run with data on affiliative behaviour other than grooming; the significant association between the affiliative and grooming networks remained when grooming bout frequency was excluded from the affiliative network, and association were controlled for (QAP multiple regression GROOMING - AFFILIATIVE without grooming: Gamgam n = 56, b = 5.482, p = 0.037; Kwano: n = 240, b = 5.789, p = 0.010).

Table 5.11: QAP Pearson correlation coefficients for the correlations between association networks and behaviour networks of the Gamgam (N = 56) and Kwano (N = 240) troops. Bold r values indicate a significant correlation between the networks, * = p < 0.05; ** = p < 0.01.

	Affiliative	Affiliative without grooming	Agonistic	Grooming	Grunt exchange	Unidirectional grunt
GAMGAM	0.189	**0.386***	-0.090	**0.492****	0.423	0.245
KWANO	**0.247****	**0.314****	0.132	**0.211****	**0.376****	**0.236****

Table 5.12: Un-standardised QAP regression coefficient of a) Gamgam behavioural networks (N = 56); b) Kwano behavioural networks (N = 240) controlling for TWI. Bold values indicate a significant relationship between the networks when the TWI is controlled for, * = p < 0.05; ** = p < 0.01. Lightly shaded values indicate relationships that were no longer significant when associations were controlled for.

a)

	Agonistic	Grooming	Grunt exchange	Unidirectional grunt
Affiliative	0.000	**10.709***	-0.019	-0.012
Agonistic	-	-0.001	0.007	0.001
Grooming		-	-1.049	-0.446
Grunt exchange			-	**0.224***

b)

	Agonistic	Grooming	Grunt exchange	Unidirectional grunt
Affiliative	0.000	**1.881****	**0.590****	**0.181****
Agonistic	-	0.001	0.011	0.002
Grooming		-	1.883	**0.894***
Grunt exchange			-	**0.071****

Overall, in both troops individuals that had strong grooming relationships also had strong affiliative relationships. Likewise, individuals related to troop members similarly through grunts and grunt exchanges. In Kwano, individuals with strong affiliative relationships also had strong grunt exchange and unidirectional grunt relationships, and grooming relationships also correlated positively with relationships through unidirectional grunts.

5.3.3 Do individuals have the same roles across behavioural networks?

Centrality measures were calculated for each troop member, and correlated across behavioural networks to investigate if individuals played similar roles in networks based on different behaviours. Results are given in Table 5.13 & Table 5.14.

The low number of correlations of centrality measures across behavioural networks indicates that there was little correspondence between an individual's network position across networks. In both troops the *in-and outdegree* scores showed the greatest association, indicating that there may be individual differences in sociality which influence the number of interaction partners across behaviours, yet even here centrality measures across few networks were correlated; in Gamgam this was three out of a possible 30 correlations; in Kwano this was eleven out of 30. In the Gamgam troop the only other significant correlation was between the *eigenvector* scores in the unidirectional grunt and grunt exchange networks. This indicates that in Gamgam individuals had different social roles depending on the type of behaviour considered.

Table 5.13: Results for the correlations between centrality measures across Gamgam behavioural networks. For the *in- and outdegree centrality* the coefficients in the upper triangle are those for the *in-degree*; in the lower triangle those for the *out-degree*. For each correlation $N = 8$. Bold Kendall's τ coefficients indicate a significant correlation, * $p < 0.05$. It was not possible to correlate *betweenness* values of the association network, as all troop members had a score of zero as a result of their direct connections with all other troop members.

IN & OUTDEGREE

	Affiliative	Agonistic	Grooming	Unidirectional grunt	Association	Grunt exchange
Affiliative	-	0.000	**0.571***	0.000	0.357	0.286
Agonistic	0.000	-	0.000	0.000	0.357	0.143
Grooming	-0.036	-0.182	-	0.429	0.357	0.286
Unidirectional grunt	-0.036	-0.071	0.182	-	0.071	**0.714***
Association	0.071	-0.357	-0.255	**0.571***	-	0.357
Grunt exchange	0.143	-0.143	0.255	0.500	0.357	-

EIGENVECTOR

	Affiliative	Agonistic	Grooming	Unidirectional grunt	Association	Grunt exchange
Affiliative	-	-0.286	0.357	0.000	0.429	0.286
Agonistic		-	-0.500	-0.286	-0.429	-0.286
Grooming			-	0.214	0.500	0.071
Unidirectional grunt				-	0.143	**0.571***
Association					-	0.429
Grunt exchange						-

CLOSENESS

	Affiliative	Agonistic	Grooming	Unidirectional grunt	Association	Grunt exchange
Affiliative	-	0.143	-0.214	0.071	-0.071	-0.071
Agonistic		-	0.071	0.071	-0.357	-0.071
Grooming			-	0.429	-0.143	0.286
Unidirectional grunt				-	0.429	0.286
Association					-	0.429
Grunt exchange						-

BETWEENNESS

	Affiliative	Agonistic	Grooming	Unidirectional grunt	Association	Grunt exchange
Affiliative	-	0.267	0.257	0.309	-	-0.330
Agonistic		-	-0.320	0.144	-	0.463
Grooming			-	0.416	-	-0.148
Unidirectional grunt				-	-	0.445
Association					-	-
Grunt exchange						-

Table 5.14: Results for the correlations between centrality measures across Kwano behavioural networks. For the *in- and outdegree centrality* the coefficients in the upper triangle are those for the *in-degree*; in the lower triangle those for the *out-degree*. For each correlation N = 16. Bold Kendall's τ coefficients indicate a significant correlation, * p < 0.05, ** p < 0.01.

IN & OUTDEGREE

	Affiliative	Agonistic	Grooming	Unidirectional grunt	Association	Grunt exchange
Affiliative	-	0.035	**0.367***	0.283	**0.367***	0.008
Agonistic	-0.026	-	0.035	0.193	0.281	**0.569****
Grooming	**0.390***	0.103	-	0.217	0.100	0.025
Unidirectional grunt	**0.504****	-0.017	**0.420***	-	0.283	0.363
Association	0.067	-0.051	0.353	0.300	-	**0.397***
Grunt exchange	**0.553****	-0.060	**0.502****	**0.684****	**0.397***	-

EIGENVECTOR

	Affiliative	Agonistic	Grooming	Unidirectional grunt	Association	Grunt exchange
Affiliative	-	0.183	0.083	**0.450***	**0.483****	**0.498****
Agonistic		-	0.000	0.133	0.033	0.312
Grooming			-	0.333	0.100	0.177
Unidirectional grunt				-	**0.367***	**0.582****
Association					-	**0.430***
Grunt exchange						-

CLOSENESS

	Affiliative	Agonistic	Grooming	Unidirectional grunt	Association	Grunt exchange
Affiliative	-	-0.102	0.151	**0.460***	0.109	0.339
Agonistic		-	0.254	-0.076	0.059	-0.154
Grooming			-	0.176	0.259	0.186
Unidirectional grunt				-	0.183	**0.650****
Association					-	**0.380***
Grunt exchange						-

BETWEENNESS

	Affiliative	Agonistic	Grooming	Unidirectional grunt	Association	Grunt exchange
Affiliative	-	**0.517***	0.047	0.159	0.148	0.249
Agonistic		-	-0.141	0.090	0.101	**0.578****
Grooming			-	-0.045	-0.144	-0.194
Unidirectional grunt				-	0.275	0.232
Association					-	0.056
Grunt exchange						-

In Kwano, *eigenvector* scores were correlated across four networks; the affiliative, unidirectional grunt, association and grunt exchange networks all showed a significant correlation with each other. This indicates that individuals that had connections with prominent individuals in one of these networks were also likely to have important connections in the other networks. None of the *eigenvector* scores in the remaining networks were correlated. Roles of Kwano individuals were most similar in the association and grunt exchange networks, the affiliative and unidirectional grunt networks, and the grunt exchange and unidirectional grunt networks, because correlations were found for these networks in both the *eigenvector* and *closeness centrality* scores. Kwano individuals had distinct network positions in the agonistic and grooming networks, as indicated by the lack of correlations for these networks in *eigenvector* and *closeness* centrality, and the few correlations in the *betweeness centrality* scores.

Overall, individual network positions varied across behaviours, particularly in the Gamgam troop. Furthermore, less correspondence was found between centrality measures that take the wider network structure into account. These results therefore highlight the importance of considering multiple behavioural interactions in the study of primate sociality and the utility of the social network approach in finding patterns of relationships that move beyond dyadic interactions.

5.3.4 Do the behavioural networks of the Gamgam and Kwano troop differ?

Network metrics were calculated for behavioural networks in which associations were controlled for and compared between troops to examine if troops differed in the structure of behavioural networks, over and above the between-troop differences in associations. Results are given in Table 5.15. In addition, the density, reciprocity, and transitivity of relationships based on behavioural interactions were compared whilst controlling for troop size. Results are given in Figure 5.4 and Table 5.16. A clear difference was found between the structures of the grooming, agonistic and affiliative networks of the two troops, whilst the difference between the unidirectional grunt and grunt exchange networks was less pronounced.

Table 5.15: Structural network properties of the grooming, affiliative, agonistic, unidirectional grunt and grunt exchange networks of the Gamgam and Kwano troops, controlling for spatial association. The weighted mean geodesic is divided by its maximum value (diameter) to allow for comparison between troops. The weighted diameter and weighted mean geodesic could not be calculated for the Kwano agonistic network as this network had a largest strong component of one.

	Grooming		Affiliative		Agonistic		Single grunt		Grunt exchange	
Network metric	Gamgam	Kwano	Gamgam	Kwano	Gamgam	Kwano	Gamgam	Kwano	Gamgam	Kwano
Largest strong component	7	12	5	13	6	1	7	15	8	13
Normalised largest strong component (%)	88	75	63	81	75	6	88	94	100	81
Density	0.375	0.217	0.286	0.321	0.321	0.108	0.446	0.321	0.500	0.333
Weighted diameter	4.561	4.882	4.051	8.806	7.066	-	4.572	6.240	2.545	3.102
Weighted mean geodesic	1.949	2.381	2.053	2.545	2.705	-	2.206	2.350	1.450	1.534
Weighted mean geodesic / diameter	0.427	0.488	0.507	0.289	0.383	-	0.483	0.377	0.570	0.495
Compactness	0.610	0.430	0.408	0.534	0.522	0.161	0.637	0.604	0.738	0.488
Mean degree (in & out)	2.625	3.250	2.000	4.813	2.250	1.625	3.125	4.813	3.500	5.000
Mean node strength	2.882	7.160	0.131	0.957	0.022	0.029	0.717	1.314	0.382	0.450
Average tie weight	1.098	2.203	0.066	0.199	0.010	0.018	0.229	0.273	0.109	0.090
Weighted mean clustering coefficient	0.409	0.335	0.397	0.565	0.268	0.199	0.600	0.425	0.473	0.560
Weighted network centralisation (in-degree)	0.493	0.521	0.099	0.123	0.019	0.035	0.222	0.222	0.227	0.093
Weighted network centralisation (out-degree)	0.293	0.245	0.098	0.304	0.051	0.029	0.243	0.196		

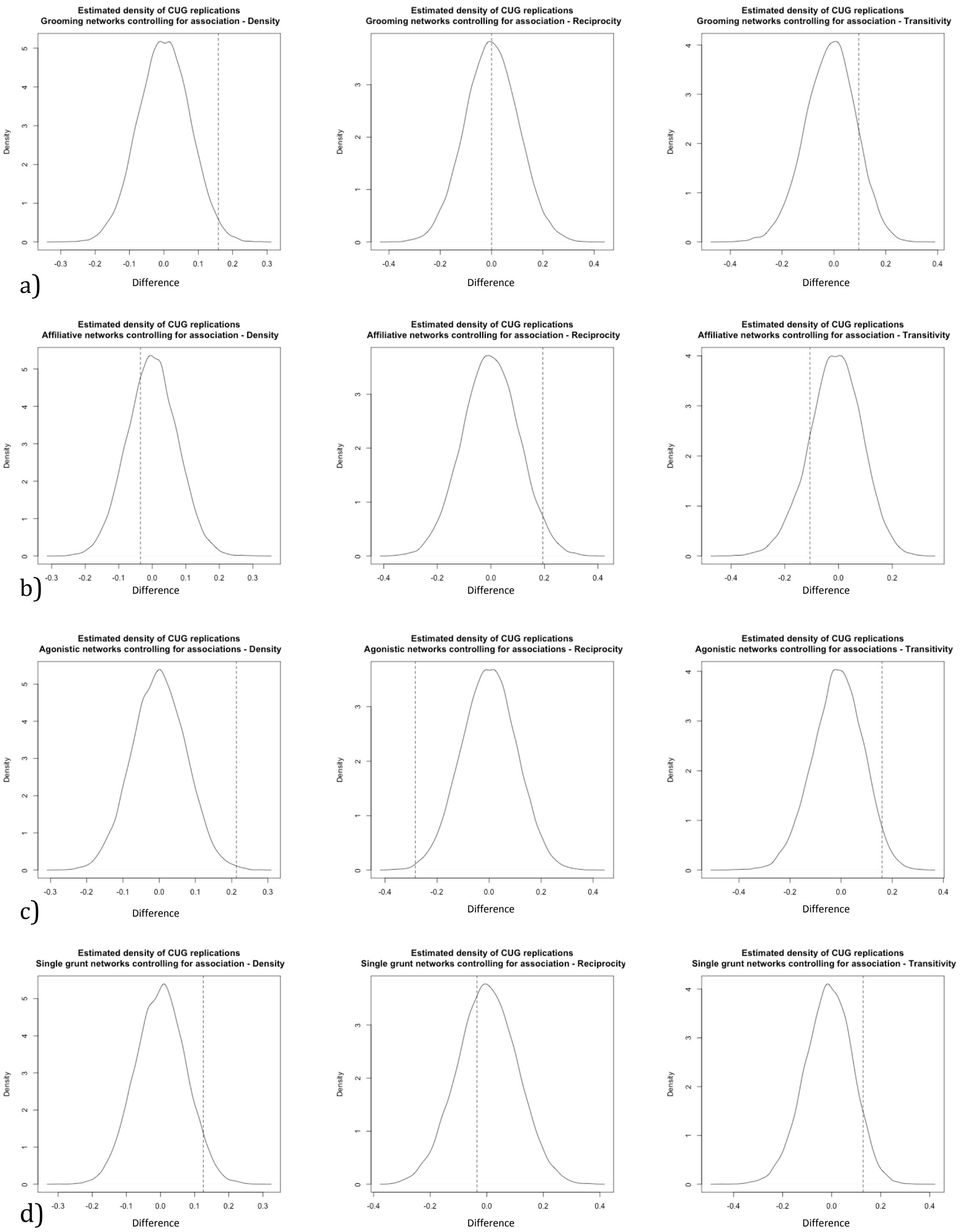
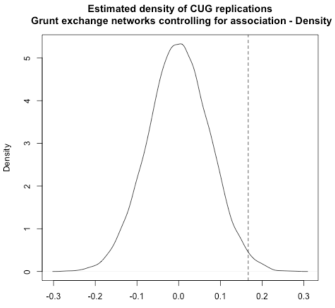


Figure 5.4 a-e: Graphs showing the difference in *density*, *reciprocity*, and *transitivity* between the Gamgam and Kwano behavioural networks for: a) grooming; b) affiliative; c) agonistic; d) unidirectional grunt. The observed between-troop difference in the network metric (*i.e.* the test statistic) is indicated by the dotted line, while the curve shows the distribution of 20000 differences in *density*, *reciprocity*, and *transitivity* between random networks of the same size as the Gamgam and Kwano networks. Positive values indicate that the score in the test statistic was higher for the Gamgam troop; negative values indicate the Kwano troop had a higher score for the test statistic.

(*continued*)



e)

Figure 5.4 a-e: (*continued*) Graphs showing the difference in *density* between the Gamgam and Kwano behavioural networks for: e) grunt exchange. Differences are indicated by dotted lines, the curve is the distribution of 20000 differences in *density*, between random networks of the same size as the Gamgam and Kwano networks. The observed between-troop difference in the network metric is indicated by the dotted line, while the curve shows the distribution of 20000 differences in *density*, *reciprocity*, and *transitivity* between random networks of the same size as the Gamgam and Kwano networks. Differences in *reciprocity* and *transitivity* scores are not given for the grunt exchange networks, because these networks are undirected. Positive values indicate that the score in the test statistic was higher for the Gamgam troop; negative values indicate the Kwano troop had a higher score for the test statistic.

Table 5.16: Results for the conditional uniform graph tests showing the difference in *density*, *reciprocity*, and *transitivity* between the Gamgam and Kwano behavioural networks. Positive values indicate the metric was higher in Gamgam, negative values indicate the metric was higher in Kwano. Bold values indicate a significant difference.

	Density		Reciprocity		Transitivity	
Network	Difference	*p*	Difference	*p*	Difference	*p*
Grooming	**0.158**	**0.016**	0.000	0.505	0.096	0.129
Affiliative	**-0.035**	**0.034**	**0.194**	**0.033**	-0.107	0.164
Agonistic	**0.213**	**0.002**	**-0.283**	**0.003**	**0.160**	**0.034**
Single grunt	**0.126**	**0.046**	-0.035	0.366	0.128	0.070
Grunt exchange	**0.167**	**0.013**	0.000	0.505	-0.021	0.458

Grooming networks

The Gamgam troop had a better-connected, more cohesive grooming network than did the Kwano troop; the Gamgam network was more inclusive (*normalised largest strong component*), more compact (*compactness*), had a greater number of possible ties (*density*), a greater proportion of the tie weights was between interconnected individuals (*weighted mean clustering coefficient*), and the Gamgam baboons had more direct grooming relationships indicated by the lower values for the *weighted mean geodesic/weighted diameter*. Furthermore, the difference in *density* was significantly larger than expected for networks of this size, indicating that the Gamgam troop had a greater proportion of grooming relationships than the Kwano troop, over and above the difference in the number of relationships that are due to troop size differences. However, in absolute terms, Kwano baboons had grooming relationships with a greater number of individuals (*mean degree*) and grooming relationships on average were stronger than in the Gamgam troop (*average tie weight*).

Troops had similar levels of *reciprocity* and *transitivity* of grooming relationships, indicating that the fundamental nature of grooming interactions did not differ between troops. Grooming relationships were equally likely to be reciprocated and to be influenced by third parties in the Gamgam and Kwano troop.

Affiliative networks

Compared to Gamgam baboons, Kwano baboons invested more ‘effort’ into affiliative relationships and maintained closer affiliative relationships, and a more cohesive affiliative network; the affiliative network of the Kwano troop was more inclusive (*normalised largest strong component*), denser (*density*), and more compact (*compactness*) than the Gamgam network. On average, Kwano baboons had closer relationships (lower *weighted mean geodesic/weighted diameter*), with a greater proportion of stronger ties between clusters of interconnected individuals (*weighted mean clustering coefficient*). Kwano baboons had a higher number of affiliative partners (*mean degree)*, had a greater total strength of affiliative relationships (*mean node strength*), affiliative ties were stronger (*average tie weight*), and Kwano individuals were connected to a greater proportion of their troop through affiliative relationships (*density*) compared to Gamgam baboons. However, the results of the conditional uniform graph test indicate that the difference in *density* did not deviate significantly from the difference between random networks. It therefore cannot be ruled out that the difference in the proportion of possible affiliative relationships is a secondary effect of the difference in troop size. Similarly, the difference in *transitivity* of affiliative relationships is likely to be due to troop size differences. However, affiliative ties were more reciprocal in the Gamgam troop compared to Kwano.

Agonistic networks

The agonistic networks of the troops differed markedly and significantly in *density*; the Gamgam network was denser, whilst the Kwano network was so sparse that it was not possible to calculate distance-based measures for this network. Overall, the Gamgam troop had a much more cohesive agonistic network; in addition to being more dense, the Gamgam network was more clustered (*weighted mean clustering coefficient*) and compact (*compactness*). Gamgam baboons had agonistic interactions with a greater number (*mean degree*) of troop members. However, agonistic relationships were slightly stronger in the Kwano troop (*average tie weight*), indicating that when Kwano baboons had an agonistic relationship, agonistic interactions occurred more frequently.

The conditional uniform graph tests further indicate that there was a fundamental difference in the way agonistic relationships were patterned, over and above what may be expected due to differences in troop size. Aggression was more reciprocal in the Kwano troop, and more transitive in the Gamgam troop.

Unidirectional grunt and grunt exchange networks

The differences in the unidirectional grunt and grunt exchange networks between the two troops were less pronounced than for other behaviours described above. A larger proportion of possible ties was observed (*density*) and the troop differences in densities were significantly different from random indicating that Gamgam baboons had unidirectional grunt and grunt exchange relationships with a greater proportion of their troop. However, Kwano baboons had unidirectional grunt and grunt exchange relationships with a greater number of troop members (*mean degree*), and these relationships were more direct (lower value in *weighted mean geodesic/weighted diameter*). The Gamgam troop had more compact (*compactness*) unidirectional grunt and grunt exchange relationships. Unidirectional grunt relationships were more clustered (*weighted mean clustering coefficient*) in the Gamgam troop, whilst the *average tie weight* was higher in the Kwano unidirectional grunt network. Conversely, the *average tie weight* was higher for the Gamgam troop in the grunt exchange network, whereas Kwano grunt exchanges were more clustered. Troops did not differ significantly in the reciprocity and transitivity scores of the single grunt network.

In summary, over and above the between-troop differences in associations, the grooming, agonistic, and affiliative networks were found to differ between the Gamgam and Kwano troop. Gamgam baboons had a more cohesive, better-connected grooming network, whereas Kwano baboons seemed to have a more focused grooming network. Despite this difference in grooming network structures, the *reciprocity* and *transitivity* of grooming relationships did not differ between troops. Aggressive relationships were more widespread and common in the Gamgam troop compared to the Kwano troop, although the average strength of each aggressive relationship was slightly higher in the Kwano troop. Aggression was more likely to be reciprocated in the Kwano troop, and to be transitive in the Gamgam troop. Over and above their weaker associations, baboons in the Kwano troop maintained a stronger and more cohesive affiliation network, although the difference in the number of relationships may be due to a difference in troop size. Affiliative relationships in the Gamgam troop were more reciprocal. No clear difference was found between the unidirectional grunt and grunt exchange networks of the two troops.

5.3.5 Are behavioural networks regulated by social factors?

5.3.5.1 Are behavioural networks assorted by age or sex?

Relational contingency analyses were run for directed networks, and joint count analyses for undirected networks, to determine if individuals interacted more frequently with troop members that were similar in age. Results are given in Table 5.17 & Table 5.18.

Age was found to have little influence on the behavioural networks of either troop. In neither troop were the densities of the affiliative, unidirectional grunt, or grunt exchange relationships between and within age groups different than expected. In Gamgam, adults were less aggressive towards subadults than expected, whereas subadults were more aggressive to adults than expected, and subadults were not seen to behave aggressively towards each other (Figure 5.5). Agonistic relationships were not assorted by age in the Kwano troop. Conversely, in the Gamgam troop grooming relationships were not assorted by age, whereas in Kwano grooming relationships among adults and among subadults were significantly higher than expected. Subadults groomed adults less than expected, and adults were not seen to groom subadults (Figure 5.6).

Table 5.17: Results for joint count analysis of the Gamgam and Kwano grunt exchange networks by age comparing the densities of ties within and between adults and subadults.

	GAMGAM (*N* = 13)		KWANO (*N* = 41)	
	Difference expected - observed	*p*	Difference expected - observed	*p*
Adult - adult	2.04	0.245	-1.09	0.447
Adult - subadult	-1.57	0.245	0.43	0.546
Subadult - subadult	-0.46	0.528	0.66	0.340

Table 5.18: Pearson chi-square statistic for the relational contingency table analysis to test for the assortativity of behavioural networks by age. The ratio of observed / expected frequencies of ties between and within age classes are given, along with the χ2 and p-value. For actors read across rows, for recipient read down columns. Significant values are given in bold.

	GAMGAM				KWANO			
NETWORK	*N*		Adults	Subadults	*N*		Adults	Subadults
Affiliative	25	Adults	1.42	0.56	79	Adults	1.02	0.76
		Subadults	0.56	0.00		Subadults	1.08	1.52
			χ2 = 5.315, p = 0.105				χ2 = 0.797, p = 0.762	
Agonistic	20	Adults	1.03	0.47	27	Adults	0.93	1.27
		Subadults	1.63	0.00		Subadults	0.95	4.44
			χ2 = 3.660, p = 0.038				χ2 = 3.012, p = 0.255	
Grooming	21	Adults	1.07	0.89	52	Adults	1.22	0.00
		Subadults	1.11	0.00		Subadults	0.49	2.31
			χ2 = 0.911, p = 0.716				**χ2 = 10.219, p = 0.0001**	
Unidirectional grunt	29	Adults	1.22	0.64	85	Adults	0.98	1.11
		Subadults	0.97	0.00		Subadults	0.91	2.82
			χ2 = 2.605, p = 0.333				χ2 = 2.591, p = 0.307	

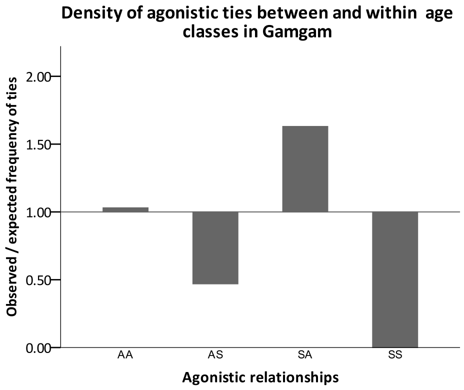


Figure 5.5: The ratio of the observed / the expected number of agonistic ties between and within age classes in Gamgam (*N* = 20). AA = adult-adult relationship; AS = adult-subadult; SA = subadult-adult; SS = subadult-subadult. Values above one indicate a greater number of ties were found than expected, values below one indicate fewer ties than expected were found.

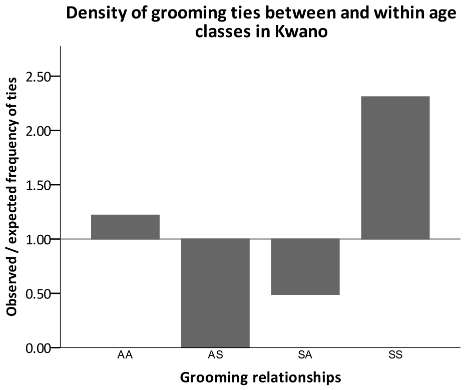


Figure 5.6: The ratio of the observed / the expected number of grooming ties between and within age classes in Kwano (*N* = 52). AA = adult-adult relationship; AS = adult-subadult; SA = subadult-adult; SS = subadult-subadult. Values above one indicate a greater number of ties were found than expected, values below one indicate fewer ties than expected were found.

Relational contingency and joint count analyses were also run to determine if individuals interacted more frequently with troop members of the same sex. Results for the assortativity by sex are given in Table 5.19 & Table 5.20.

Sex was found to have a greater influence on behavioural interactions than age. In both troops, sex influenced unidirectional grunt and grunt exchange relationships. In both troops, females had more unidirectional grunt and grunt exchange relationships with each other than expected and fewer than expected with males (Figure 5.7 & Figure 5.8). Males had fewer than expected unidirectional grunt relationships with females, and fewer than expected (Kwano), or absent completely (Gamgam) between adult males. Grunt exchanges between males were rare, although the density of these ties was not different from expected in either troop.

Table 5.19: Pearson chi-square statistic for the relational contingency table analysis to test for the assortativity of behavioural networks by sex. The ratio of observed / expected frequencies of ties between and within the sexes are given, along with the χ2 and *p*-value. For actors read across rows, for recipient read down columns. Significant values are given in bold.

	GAMGAM				KWANO			
NETWORK	*N*		Females	Males	*N*		Females	Males
Affiliative	25	Females	1.68	0.60	79	Females	1.45	1.37
		Males	0.75	0.37		Males	0.35	0.20
			χ2 = 6.696, p = 0.068				**χ2 = 23.211, p = 0.012**	
Agonistic	20	Females	0.98	0.56	27	Females	1.38	0.15
		Males	1.49	0.93		Males	1.63	0.30
			χ2 = 2.353, p = 0.178				**χ2 = 10.728, p = 0.003**	
Grooming	21	Females	1.60	0.71	52	Females	1.45	1.09
		Males	0.89	0.00		Males	0.74	0.00
			χ2 = 5.489, p = 0.159				**χ2 = 15.295, p = 0.007**	
Unidirectional grunt	29	Females	1.64	0.77	85	Females	1.54	0.85
		Males	0.77	0.00		Males	0.75	0.19
			χ2 = 8.172, p = 0.0001				**χ2 = 17.996, p = 0.002**	

Table 5.20: Results for joint count analysis of the Gamgam and Kwano grunt exchange networks by sex, comparing the densities of ties within and between the sexes. Bold values indicate a significantly different density of ties.

	GAMGAM (*N* = 13)		KWANO (*N* = 41)	
	Difference expected - observed	*p*	Difference expected - observed	*p*
Female - female	**4.36**	**0.016**	**15.63**	**0.001**
Female - male	**-2.96**	**0.016**	**-11.50**	**0.001**
Male - male	-1.39	0.190	-4.13	0.054

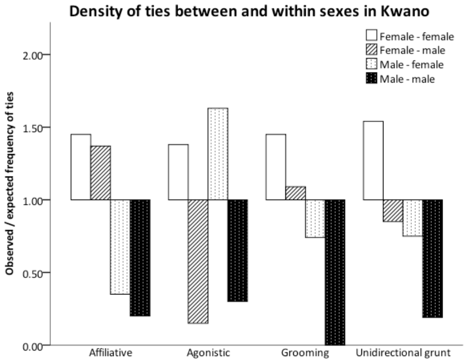


Figure 5.7: The ratio of the observed / the expected number of ties between and within sexes for the affiliative (*N* = 79), agonistic (*N* = 27), grooming (*N* = 52) and unidirectional grunt (*N* = 85) networks in Kwano. Values above one indicate a greater number of ties were found than expected, values below one indicate fewer ties than expected were found.

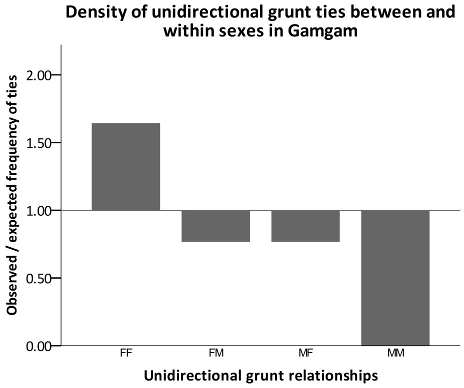


Figure 5.8: The ratio of the observed / the expected number of ties between and within sexes for the unidirectional grunt networks in Gamgam. Values above one indicate a greater number of ties were found than expected, values below one indicate fewer ties than expected were found.

In the Gamgam troop, the affiliative, agonistic and grooming networks were not significantly assorted by sex, although for the affiliative network this was close to significance. In the Kwano troop on the other hand sex was an assortative force in these networks. Kwano females had more affiliative relationships with other females than expected, whereas males had fewer affiliative relationships than expected, both with females, and with other males. Kwano females also had more affiliative ties than expected with males. In the Kwano troop, both males and females had more agonistic relationships than expected with females, and fewer than expected with males, and females groomed each other and males more than expected. Males groomed females less than expected, and were not seen to groom other males.

Overall, sex was found to play a more important role in the patterning of social behaviour than age, particularly in the Kwano troop. Here, more interactions were seen between females, and males avoided interacting with each other. Furthermore, females largely directed socio-positive behaviours at males, whereas males directed aggression at females. Sex was a less important factor in the Gamgam troop, where only in the vocalisation networks some assortativity by sex was found. Here, few inter-sexual vocalisation ties were observed, while females had more vocalisation relationships with other females than expected. Age had little influence on the interaction patterns of either troop. Only in the agonistic network of the Gamgam troop and the grooming network of the Kwano troop were relationships assorted by age.

5.3.5.2 Are the social relationships of females affected by the presence of dependent offspring or reproductive state?

Node-level t-tests and ANOVAs were run to explore if females' social relationships were influenced by the presence of dependent offspring (Table 5.21) or by female reproductive state (Table 5.22).

Table 5.21: Results of node-level t-tests for the behavioural networks for Gamgam & Kwano. Table shows the difference in the total strength of relationships of females without dependent offspring (Gamgam: n = 3; Kwano: n = 7) and females with dependent offspring (Gamgam: n = 2; Kwano: n = 3) for both giving (out) and receiving (in) the behaviour, along with *p*-values. Bold values indicate a significant difference. Dependent offspring were defined as infants up to eight months.

		GAMGAM (*N* = 5)		KWANO (*N* = 10)	
		t	*p*	*t*	*p*
Affiliative	in	-0.014	0.492	**-0.147**	**0.018**
	out	-0.003	0.491	0.075	0.326
Agonistic	in	-0.002	0.399	0.000	0.944
	out	0.000	1.000	0.002	0.595
Grooming	in	-0.768	0.194	**-1.207**	**0.014**
	out	0.184	0.403	-0.030	0.943
Unidirectional grunt	in	0.059	0.497	**-0.213**	**0.005**
	out	-0.065	0.201	0.009	0.851
Grunt exchange		0.027	0.409	0.007	0.714

Table 5.22: *F*-statistics for node-level ANOVAs on the difference in female node strength as a function of reproductive state for behavioural networks for both giving (out) and receiving (in) the behaviour (Gamgam: cycling n = 3, lactating n = 2, pregnant n= 0; Kwano: cycling n = 3, lactating n = 7, pregnant n= 0). Bold values indicate a significant effect of reproductive state.

		GAMGAM		KWANO	
		F (1, 3)	*p*	*F* (2, 7)	*p*
Affiliative	in	0.404	0.601	3.115	0.091
	out	1.291	0.400	2.320	0.170
Agonistic	in	0.135	0.700	0.905	0.385
	out	0.025	0.799	**5.697**	**0.038**
Grooming	in	0.279	0.706	2.582	0.160
	out	0.470	0.595	0.826	0.481
Unidirectional grunt	in	0.865	0.393	0.181	0.834
	out	0.113	1.000	1.883	0.220
Grunt exchange		0.001	1.000	1.221	0.365

In neither troop did the presence of young offspring influence how frequently a female interacted (*i.e.* 'out'). There was also no significant difference between females with and without dependent offspring in the frequency at which they received aggression, or in the strength of grunt exchange relationships. In Gamgam, there was no significant difference in the rate at which females with and without dependent offspring received affiliative behaviours, grooming, and unidirectional grunts. In Kwano on the other hand, females with dependent offspring received significantly more affiliative behaviours, more grooming, and more unidirectional grunts.

Female reproductive state did not influence the frequency of behavioural interactions females gave or received in either troop; node-level ANOVA's yielded no significant differences between cycling, lactating and pregnant females in regard to their node strength of giving and receiving affiliative, grooming, and unidirectional grunts, or grunt exchange relationships. While reproductive state did not influence the strength of the agonistic behaviour a female received, it did influence the strength of the agonistic behaviour females gave. However, *post hoc* Mann-Whitney tests showed that while pregnant females had a higher agonistic outdegree than cycling and lactating females, none of these differences were significant (Mann-Whitney tests: cycling – lactating: U = 6.00, p = 0.512; cycling – pregnant: U = 0.00, p = 0.500; lactating – pregnant: U = 0.00, p = 0.143 - Figure 5.9). Furthermore, the 'pregnant' category contained a single female, DRK, which was in fact the highest-ranking female in the troop. Therefore, this high outdegree in agonistic behaviours is likely to be due to individual tendency for aggression rather than to female reproductive state.

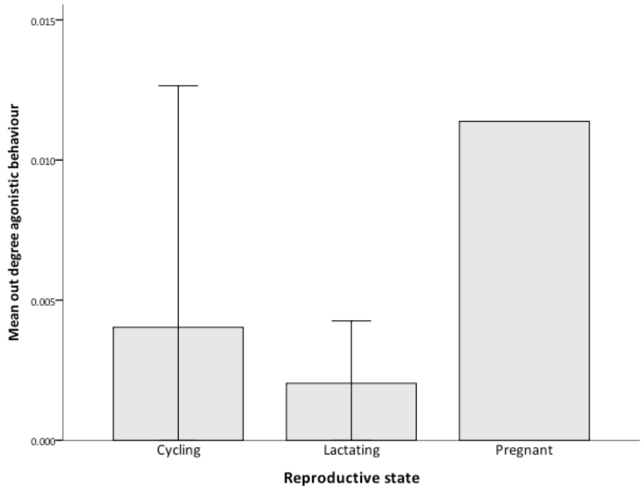


Figure 5.9: Comparison between the mean out degree for agonistic behaviours for Kwano females that were cycling (*n* = 3), lactating (*n* = 6), and pregnant (*n* = 1).

5.3.5.3 Are the social relationships of females affected by dominance relationships?

Relational contingency tests were run to test if dominance rank influenced the relationships between females. Results are given in Table 5.23.

Dominance rank did not influence social relationships in either troop; in neither troop was the frequency of ties within and between rank classes significantly different from random for the affiliative, grooming, grunt exchange and unidirectional grunt networks. The significant result for the patterning of agonistic relationships by dominance rank seen in both troops is because the agonistic interactions that were used to build the networks were also used to estimate the dominance rank of individuals.

Table 5.23: Pearson chi-square statistics for the relational contingency table analyses to test for assortativity by female dominance (high, middle, low rank) in Gamgam and Kwano behaviour networks. Bold values indicate networks in which the frequency of ties within and between rank classes differed significantly from expected frequencies.

	GAMGAM			KWANO		
Network	*N*	χ2	*p*	*N*	χ2	*p*
Affiliative	15	1.667	0.399	43	4.674	0.300
Agonistic	**7**	**5.143**	**0.032**	**14**	**9.750**	**0.042**
Grooming	15	2.167	0.530	38	5.393	0.352
Grunt exchange	17	1.955	0.803	62	3.447	0.926
Unidirectional grunt	18	1.235	0.101	49	1.612	0.844

5.3.5.4 Are the social relationships of females and males affected by lactation or cycling?

The average strength of relationships between males and females were compared for lactating and non-lactating females, and cycling and non-cycling females. Results are given in Table 5.24 & Table 5.25.

In the Gamgam troop, non-lactating females received slightly more aggression from males than did lactating females, as would be expected if patterns of friendship influenced behavioural networks. Similarly, in the Gamgam troop, cycling females received slightly more aggression from males than non-cycling females. Contrary to expectation, non-lactating females in Kwano had somewhat higher rates of affiliative behaviours and grunt exchanges with males than did lactating females. In the Kwano troop, cycling females directed more affiliative behaviours to males than non-cycling females did. There was no significant difference in male-female interaction between lactating and non-lactating females, or between cycling and non-cycling females for any of the other behaviours in either troop.

Table 5.24: Results for the permutation t-tests comparing the strength of relationships with males for lactating and non-lactating females. Bold values indicate a significant difference.

		GAMGAM (*N* = 20)		KWANO (*N* = 60)	
		t	*p*	*t*	*p*
Affiliative	in	0.002	0.628	0.001	0.746
	out	0.004	0.263	**-0.010**	**0.014**
Agonistic	in	**-0.001**	**0.046**	0.000	1.000
	out	0.000	1.000	0.000	0.398
Grooming	in	-0.120	0.478	-0.027	0.617
	out	0.046	0.384	-0.009	0.760
Unidirectional grunt	in	-0.023	0.493	-0.006	0.465
	out	-0.008	0.933	0.000	0.943
Grunt exchange		-0.009	0.202	**-0.002**	**0.004**

Table 5.25: Results for the permutation t-tests comparing the strength of relationships with males for cycling and non-cycling females. Bold values indicate a significant difference.

		GAMGAM (*N* = 15)		KWANO (*N* = 60)	
		t	*p*	*t*	*p*
Affiliative	in	-0.002	0.632	0.000	0.997
	out	-0.004	0.268	**0.017**	**< 0.001**
Agonistic	in	**0.001**	**0.043**	0.000	0.495
	out	0.000	1.000	0.000	0.305
Grooming	in	0.120	0.477	0.032	0.643
	out	-0.046	0.402	0.034	0.278
Unidirectional grunt	in	0.023	0.488	-0.002	0.811
	out	0.008	0.928	0.002	0.631
Grunt exchange		0.009	0.196	0.001	0.249

As the definitions of cycling females and non-lactating females largely overlap, they only differ by the inclusion or exclusion of pregnant females, the higher rates of affiliative behaviours of non-lactating females may in fact be an effect of increased affiliative behaviours between males and cycling females or vice versa. However, due to small sample size it was not possible to distinguish between these alternatives.

These results indicate that overall, female reproductive state had little influence on the social relationships of males and females, with the exception that Gamgam males targeted cycling, non-lactating females aggressively, while Kwano females that were cycling or not lactating increased rates of affiliative behaviour towards males, and non-lactating females had more grunt exchanges with males.

A summary of all the results described in this chapter is given in Table 5.26.

Table 5.26: Summary of the questions addressed in this chapter and the result of the analyses.

Question	Result
1. Do network structures differ across behaviours?	Grooming and agonistic networks were sparsest and least clustered, indicating that baboons were more selective in partner choice for these behaviours and partners were spread out over the networks. Affiliative, unidirectional grunt, and grunt exchange networks were denser, more clustered, and individuals had more partners, indicating that baboons had stronger relationships with a larger proportion of the troop through these behaviours.
2. How are relationships based on different behaviours related?	Controlling for the time spent in association, networks based on grooming and non-grooming affiliative behaviour were found to correlate positively, indicating that individuals had similar relationships through these behaviours. Additionally, individuals had similar relationships through unidirectional grunt and grunt exchanges. In Kwano, the affiliative network correlated positively with the unidirectional grunt and grunt exchange networks while grooming networks correlated with the unidirectional grunt network. These results reflect the use of grunts to facilitate positive interactions.
3. Do individuals have the same roles across behavioural networks?	Few correlations were found between network positions across behavioural networks, particularly for measures that take the wider network structure into account, indicating that individual have different social roles in networks based on different behaviours
4. Do the behavioural networks of the Gamgam and Kwano troop differ?	Over and above between-troop differences in association rates, clear between-troop differences were found in grooming, agonistic, and affiliative networks. The Gamgam grooming network was cohesive and well-connected, while the Kwano grooming network was more focused. Aggression was more common and widespread in Gamgam than in Kwano. The Kwano affiliation network was stronger and more cohesive than that of the Gamgam affiliation network. Grooming relationships were fundamentally similar in troops, whereas affiliative relationships were more reciprocal in Gamgam. Aggression was reciprocal in Kwano, and transitive in Gamgam. Unidirectional grunt and grunt exchange networks were similar in Gamgam and Kwano.

Question (*continued*)	**Result**
5a. Are behavioural networks assorted by age or sex?	Age had little influence on behavioural networks; with the exception of aggression (Gamgam) and grooming (Kwano). Sex had a stronger influence on behavioural networks, particularly in Kwano. In Kwano, in all networks females had more ties with other females, while males avoided interactions with other males. Apart from aggression, males had fewer than expected ties with females. Females had more affiliative and grooming relationships with males, and fewer agonistic, unidirectional grunt, and grunt exchange ties. Similar results were found in the Gamgam unidirectional grunt and grunt exchange networks.
5b. Are the social relationships of females affected by the presence of dependent offspring or reproductive state?	The presence of dependent offspring and female reproductive state did not affect the strength of females' social relationships. Reproductive state also did not affect the behavioural interactions a female received. In Kwano, females with dependent offspring received more affiliative behaviours, grooming and grunts. This was not found in the Gamgam troop.
5c. Are social relationships between females affected by dominance relationships?	Dominance rank did not affect social relationships of females in either troop.
5d. Are the social relationships of females and males affected by lactation or cycling?	Overall reproductive state had little influence on the social relationships of females and males. In Gamgam, males directed more aggression towards cycling, non-lactating females. In Kwano females that were not lactating and not cycling directed more affiliative behaviours towards males, and non-lactating females exchanged grunts with males more frequently than lactating females.

5.4 Discussion

Results presented in this chapter demonstrate the various dimensions of olive baboon social relationships; the structures of networks based on different behaviours were shown to differ across some, but not all, behaviours, individuals had different social roles depending on the behaviours considered, and these distinct relationships did not necessarily influence each other.

These results show the importance of considering a variety of behavioural interactions in the study of primate social relationships. Between-troop differences in ecology (chapter 3) and association patterns (chapter 4) were shown to be associated with differences in grooming, affiliative, and agonistic relationships, while grunting and grunt exchanges were similar across troops. Sex was found to be the most important social factor regulating social relationships.

5.4.1 Variation in networks across behaviours

Network structures and the social roles of individuals were compared across behaviours to determine if the structure of social relationships varies depending on the type of interaction. Networks were correlated to determine how these various dimensions of social relationships relate to each other. Results presented in this chapter show that grooming and agonistic relationships were clearly distinct types of relationships, whereas affiliative, unidirectional grunt and grunt exchange relationships showed marked similarities with each other. In both troops, network metrics showed a clear resemblance in the structure and density of the affiliative, unidirectional grunt and grunt exchange relationships. The highest concordance was found between the unidirectional grunt and grunt exchange networks in both troops, perhaps not surprising as these networks reflect very similar behaviours. For the Kwano troop, there was further correspondence between the two types of grunting networks and the affiliative networks, and individual's position within these networks, most probably because grunts are used to initiate and facilitate affiliative contact (Cheney *et al.* 1995). Grooming and agonistic networks were much sparser, indicating that these behaviours were less common, and for both troops mean degree was also lower, indicating that baboons were more selective in their partners for these behaviours. Furthermore, the roles of individuals in their grooming and agonistic networks did not correspond with their roles in the unidirectional grunt, grunt exchange or affiliative networks. However, the grooming and agonistic networks also differed from each other; there was no correspondence in individual network positions or correlation between the two networks. This suggests that grooming and aggressive interactions did not influence each other. Interestingly, none of the other networks correlated with the agonistic network in either troop, suggesting that aggression has little influence on other social relationships.

Similar results were found in a previous study on behavioural network of the Kwano troop where it was shown that grooming and agonistic networks were similar in structure, and that these were less dense and less clustered than the mounting, displacement and presenting networks (Lehmann and Ross 2011). Additionally, individual network positions were most distinct in the grooming and agonistic networks; there was little correlation between individual positions in the agonistic and grooming networks, or between positions in these networks and all others (Lehmann and Ross 2011).

The differences in network structures and the roles of individuals across behavioural networks seem to be due to a combination of the cost of the behaviours involved and whether the behaviour is socio-positive or socio-negative. Individuals may be more selective in the choice of partners for interactions when the behaviours they engage in are costly; grooming behaviour requires an investment of time from both the groomer and the groomee (Dunbar 1988) and therefore individuals may be limited and more selective in their grooming relationships compared to other socio-positive relationships. Similarly, aggression can be costly in terms of energy expended (Key and Ross 1999) and the risk of injury (Drews 1996). In male baboons, it has been shown that the high cost of escalated aggression has selected for an avoidance of escalation of conflicts (Drews 1996). Furthermore, aggression is costly if it is directed at the wrong individual. Because individuals are highly selective in choosing their grooming partners and targets of their aggression, both these networks were sparser and less clustered. However, because these behaviours have opposite outcomes on social relationships, *i.e.* grooming being socio-positive and aggression being socio-negative, these two networks did not correlate and individuals did not occupy the same network positions.

The structure of the grooming networks differed from the other socio-positive behaviour networks in that individuals were less selective for affiliative, unidirectional grunt and grunt exchange interactions. Baboons are less limited in the use of affiliative behaviours, grunts and grunt exchange because these behaviours are less costly in terms of time, and therefore these behaviours can be more widespread. For this reason it has been suggested that vocalisations are an efficient way of expressing joint commitment to a relationship, and that vocalisations add to social bonding that is achieved through grooming interactions (Aiello and Dunbar 1993). Some association was found between the grooming networks, and the networks based on other socio-positive behaviours, indicating that broadly speaking these positive behaviours are directed at the same individuals. Furthermore, individuals had similar network positions in the low cost socio-positive networks and the association network, suggesting there were individual differences in sociality; troop members that associated frequently with a large part of their troop also had more and stronger affiliative, unidirectional grunt, and grunt exchange relationships.

Nevertheless, the structure of behavioural networks may not solely be determined by the costs and the effect of the behaviours, and instead there seem to be troop-specific differences in behavioural networks. Currently, very few other studies in primatology have directly compared structures of networks derived from data on different behaviours. One exception is a study in which agonistic and grooming networks of three groups of white-faced capuchins were compared (Crofoot *et al.* 2011). For these capuchin groups, the aggression and grooming networks were also found to have distinct structures; however, here the structures were different because the grooming network was more inclusive and egalitarian than the agonistic network (Crofoot *et al.* 2011). While in Kwano the grooming network was more dense than the agonistic network, these networks were similar in the Gamgam troop, suggesting that the network structure is not only due to the type of behaviour, but that some of the network structure may be characteristic of a troop or population, such as the size or composition of troops, or local ecological conditions.

In sum, these results indicate that there are differences in the network structures and individual social roles across behaviours, and that these differences are partly due to the type of behaviour considered. It was suggested here that networks can be broadly categorised into three groups; low cost socio-positive behaviours, high cost socio-positive interactions, and socio-negative interactions. Nevertheless, network structures were not solely due to the type of behaviour considered, as some differences may also be due to particular troop characteristics. Therefore, between-troop differences in the nature of social relationships are discussed next, in reference to between-troop differences in fission-fusion dynamics.

5.4.2 Fission-fusion dynamics and the nature of social relationships

The behavioural networks of the Gamgam and Kwano troops were compared to determine if the network structures differ between troops. As patterns of association differed between the two troops, associations were controlled for in these analyses. Comparison of network metrics showed a clear distinction in the agonistic and grooming networks of the two troops, a less marked difference between the affiliative networks, and least difference between the unidirectional grunt and grunt exchange networks. In the previous chapters, it was shown that differences in food availability and predation risk were associated with differences in the associations of the troops; it was suggested that within-group competition was lower for the Gamgam troop and consequently there was less need to adjust association patterns to reduce this competition, leading to a more cohesive association network with little sub-grouping. Lower food abundance and larger troop size increased within-group resource competition in Kwano, leading to a more fragmented association network with fewer and weaker ties and more sub-grouping. Results presented in this chapter further indicate that these between-troop differences in social organisation are associated with differences in social structure. However, it is not clear in all cases if the patterns of associations limit the social relationships of individuals, or if social relationships determine the patterns of associations.

The structure of agonistic relationships seems to result from the social structure of troops. A clear difference was found between the agonistic networks of the two troops, with aggressive relationships in the Gamgam troop being stronger and more widespread. For the Kwano troop the agonistic network was so sparse that it was not possible to calculate all network metrics. Importantly, the difference in the number of aggressive relationships was not due solely to troop size.

A fundamental difference was also found in the nature of aggressive relationships of the two troops. Aggression was more reciprocal in the Kwano troop, whereas the Gamgam troop had more transitive agonistic relationships. Thus in Gamgam, when an individual was aggressive to a troop member, and that troop member was aggressive to a third, that original individual was more likely to also be aggressive towards the third individual. In Kwano on the other hand, an individual was more likely to receive aggression back when they were aggressive towards a troop member. This suggests that the dominance hierarchy was clearer in the Gamgam troop with individuals being aggressive to all troop members in lower dominance positions, and this aggression is not reciprocated. Whereas in the Kwano troop the hierarchy may be less defined, or more often challenged as aggression was more frequently reciprocated. This is further supported by Landau's h' index of linearity, which was 1.00 in Gamgam, indicating a strongly linear hierarchy, but lower in Kwano at 0.65.

The difference in the density and structure of agonistic relationships may be due to a difference in social organisation and resulting levels of within-group contest competition. The Kwano troop may have avoided high levels of within-group contest competition by splitting into subgroups more frequently; when tension arises troops that are able to be relatively flexible in their spatial cohesion due to lower predation risk, can avoid aggression by splitting up into smaller subgroups. This idea relating to avoidance of within-group contest competition is further supported by the less strict dominance hierarchy in Kwano suggested by more reciprocal agonistic relationships; the socioecological model predicts that the dominance hierarchy is relaxed when within-group competition is low (Sterck *et al.* 1997). The more frequent and widespread aggression in the Gamgam troop may therefore be a result of an inability to avoid within-group competition. When cohesive associations are crucial, for example when predation risk is high, individuals may be forced to feed within the same food patch, increasing the risk of aggression over food (Pruetz and Isbell 2000; Koenig 2002; Majolo *et al.* 2009), leading to a more despotic, stricter hierarchy (Sterck *et al.* 1997). However, aggression may occur over issues other than food, as in troops that are spatially cohesive, the escalation of tension into aggression may be inevitable (Aureli *et al.* 2008a).

Similarly, social organisation seemed to affect affiliative relationships; Kwano baboons invested more effort into their affiliative relationships, and they were able to maintain closer affiliative relationships and a more cohesive affiliative network, over and above their weaker associations. However, the between-troop difference in the number of affiliative relationships is, at least in part, due to the different sizes of the Kwano and Gamgam troops. As the density of ties has a large influence on other network metrics (Anderson *et al.* 1999), it is likely that the difference in network structure seen here is due to a troop size difference. Similarly, troops did not differ in the *transitivity* of their affiliative relationships. However, the troops did differ in the extent to which affiliative relationships were reciprocal, with reciprocity being higher in Gamgam affiliative relationships compared to Kwano. Thus, there are some differences between the troops in the way affiliative behaviours are distributed even after taking into account differences in troop size. Furthermore, only the number and not the weight of relationships were considered in the conditional uniform graph test. Thus, whilst the number of affiliative partners was largely influenced by the size of the troop, the strength of the relationships need not be.

Affiliative behaviours, such as touching or embracing, help to repair and maintain social bonds (Silk *et al.* 1996; Cheney and Seyfarth 2007) and may help individuals to update social information after a period without contact (Okamoto *et al.* 2001). When part of a troop has been out of sight for a period of time, the fusion of the subgroups can be tense and create conflict. For example, during the fusion of spider monkeys subgroups, individuals of different subgroups behave aggressively towards each other (Aureli and Schaffner 2007). In the period after fusion however, rates of affiliative behaviours increase, as these behaviours signal benign intent and thus help to reduce post-fusion aggression (Schaffner and Aureli 2005; Aureli and Schaffner 2007). It has been suggested that the behaviours that facilitate social interaction and reduce tension, are likely to vary quantitatively with levels of fission-fusion dynamics (Aureli *et al.* 2008b). Thus, in troops with higher levels of fission-fusion dynamics, *i.e.* those with more fluid grouping patterns, higher rates of affiliative behaviours are expected. Hence, Kwano baboons may invest more in affiliative relationships due to their more fragmented spatial associations. In Kwano after a period of separation, affiliative behaviours may be used to signal benign intent, re-establish social bonds, and provide information about changes in social bonds that occurred during the period of absence. As associations were more cohesive in Gamgam troop, each affiliative relationship may be less intense, and these were more likely to be reciprocal.

The way the social organisation and grooming networks are linked is less clear. Grooming is the most common behaviour for social bonding in primates (Sueur *et al.* 2011b), as it helps to establish and strengthen relationships (Dunbar 1988; Aureli *et al.* 1999) and helps repair relationships after conflict (Silk *et al.* 1996; Aureli *et al.* 1999). When considering grooming as a mechanism for social bonding, the association between the degrees of cohesion in the association networks and the grooming network may be due to a constraint on grooming. Constraints on grooming may affect group cohesion in two, non-mutually exclusive ways. In larger groups, the number of available partners, and thus the number of relationships that need to be maintained, increases (Dunbar 1992; Dunbar 1993) and consequently individuals may need to spend more time grooming. A positive correlation between group size and time spent grooming has been observed across primate taxa (Dunbar 1993; Lehmann *et al.* 2007b). This increase in grooming time is possible as long as individuals have enough time allocated to other essential activities, such as feeding or travelling. When groups become too large, it becomes impossible to groom all troop members in the time available, which could lead to unstable social relationships and less cohesive groups (Lehmann *et al.* 2007b). This direct constraint on grooming time has been shown to explain the distribution of troop sizes in populations in chacma baboons in Drakensberg and Amboseli (Henzi *et al.* 1997a). As troop size increases female chacma baboons firstly decrease the length of their grooming bouts, whilst maintaining grooming relationships with all females in their troop (Henzi *et al.* 1997b). With further increases in troop size females limit the number of grooming partners, but increase the grooming bout length, weakening the overall network of social relationships (Henzi *et al.* 1997b).

A second, indirect pressure may further limit the time a group has available for grooming, and consequently the cohesion of the group. An increase in group size could lead to an increase in the time spent on other activities, to such an extent that it limits time available for grooming, leading to less stable groups (Sueur *et al.* 2011b). For example, as larger groups deplete resources more quickly, day journey length and food competition may increase, and consequently raise the amount of time spent foraging (Henzi *et al.* 1997a; Sueur *et al.* 2011b).

It is possible to distinguish between this direct or indirect constraint on grooming time by comparing the time budgets of the troops, particularly the proportion of time spent on grooming and foraging. In the case of a direct constraint, larger groups are expected to spend more time grooming, whereas for the indirect constraint larger groups are expected to spend a smaller proportion of their time grooming. Comparison of activity budgets (See Appendix C, Table C.1) shows that the Kwano troop spent a smaller proportion of their time on social activities, which includes grooming as well as other social interactions, than did the Gamgam troop, however this difference was not significant. Either way, it may be that the ability to maintain grooming relationships with troop members constrains grouping patterns.

Conversely, social organisation may constrain grooming relationships, as was suggested to be the case for agonistic relationships. For primates, grooming serves also as one of the principle ways to reduce stress (Aureli *et al.* 1999; Shutt *et al.* 2007; Wittig *et al.* 2008). The Gamgam troop may have a more cohesive grooming network to reduce tension and repair relationships due to their more cohesive spatial associations and resulting higher levels of tension and aggression. In Kwano splitting into subgroups may help individuals avoid tension, which reduces aggression and the need to repair relationships and alleviate stress.

Relatively little difference was found between the unidirectional grunt and grunt exchange relationships of the troops. When associations were not controlled for in these networks (*i.e.* in section 5.3.1), Gamgam baboons had stronger unidirectional grunt and grunt exchange relationships, but these were similar in both troops once associations were controlled for. This suggests that olive baboons may not preferentially grunt to particular individuals in order to maintain proximity to them, but that instead they simply grunt to those individuals that they are in close proximity to, most probably to facilitate friendly interactions (Silk *et al.* 1996; Cheney and Seyfarth 1997; Rendall *et al.* 1999; Silk 2002a). Both grunts and grunt exchanges thus seem to 'oil the wheels' of baboon association, by facilitating friendly interactions. In this case, social organisation may influence social relationships as it determines which troop members are available for social relationships.

In these between-troop comparisons of behavioural networks, associations were controlled for, as the availability of individuals for interactions may limit the relationships of individuals in these networks. Such an approach thus assumes that a social interaction between individuals that rarely associate is more important (*i.e.* stronger relationships) than a social interaction between individuals that associate frequently. In these analyses, individuals may thus have strong relationships because they did not associate frequently, but did interact at some point. Alternatively, not controlling for associations would allow for a direct comparison of the strength of the relationships of individuals, but in these analyses individuals may have stronger relationships simply because they had a greater opportunity for interaction. Comparing the troops' network metrics for the networks not weighted by the DAI (see Table 5.6 & Table 5.7), some of the comparisons remain the same; the grooming and agonistic networks of the Gamgam troop remain more dense, more compact, and more cohesive tan the Kwano networks. The comparison between the affiliative networks is however somewhat affected by which networks are compared, with the Gamgam troop having a denser network, with more direct relationships, although *compactness* is similar in the affiliative networks of the troops. As unidirectional grunt and grunt exchanges were similar between troops when association were controlled for, the comparison between these networks was most affected by whether associations were controlled for in networks.

Overall, between-troop differences in social organisation seem to have some effect on the nature of social relationships, particular with regards to agonistic and affiliative behaviours. Grouping patterns affected relationships based on grunts and grunt exchange only to the extent the availability of troop members for interactions. Grooming may be used more in cohesive groups to reduce stress, and to help repair social bonds. However, grooming relationships may also constrain the social organisation. Another reason for between-troop differences in behavioural networks could be differences in troop demography.

5.4.2.1 Influence of demography on troop differences in behavioural networks

One limitation of the between troop comparison is that it was not possible to control for demographic effects other than troop size. This may be especially important given the findings on the sex-specific differences in sociability and aggression. However, the ratio of females to males was the same in the troops; 5:3 in the Gamgam troop and 10:6 in the Kwano troop. Therefore, sex ratio is unlikely to have influenced troop differences in the behavioural network structures. The ratio of adults to subadults did however, differ between troops, this was 6:2 in Gamgam and 16:3 in Kwano. If adults and subadults differed in the frequency at which they engage in certain behaviours, the observed troop differences in behavioural networks may thus be due to the different age composition of troops; however, age was found to have little effect on the behavioural networks. Individuals that were not included in the network, such as juveniles, infants and black infants, may also have influenced the behaviour of individuals that were included in the network. Again, the proportions of immature troop members were similar across troops; this was 52% in Gamgam and 53% in Kwano (see Chapter 2, Table 2.3). Thus, the age composition of the rest of the troop is not likely to have influenced the difference in the behavioural network structures of the troops.

The number of cycling females may also have affected patterns of behavioural interactions, and this number differed between the troops; taken over the entire study period, in Gamgam 40% of females were cycling for the majority of days, whereas in Kwano this was 80%. This difference in the proportion of cycling females may have influenced the results for the affiliative network, where cycling females were found to direct more affiliative behaviour towards males than non-cycling females. Thus, the higher density of affiliative ties in the Kwano troop may be a side effect of the greater proportion of cycling females. For the agonistic networks, in Gamgam cycling females received more aggression from males than did non-cycling females. In this case, the difference between the rates of aggression of the two troops may be underestimated, as Gamgam had a denser agonistic network, but fewer cycling females.

5.4.3 Social preferences

While age had little effect on patterns of behavioural interactions, sex was found to be the most important factor influencing the affiliative, unidirectional grunt and grunt exchange relationships in both troops, and agonistic and grooming relations in the Kwano troop. Given that the sex ratio was similar in both troops, it is somewhat surprising that sex had an influence on all behavioural networks in Kwano, but not in Gamgam. This may be due to a combination of the smaller troop size, and the low density of the grooming and aggression networks (grooming: 0.375; agonistic: 0.57). As a result, the numbers of ties that were observed in these networks was low (grooming ties $N = 21$; agonistic ties: $N = 20$), making the sample size for these analyses small. Given this small sample size, the statistical power of the test for the assortativity of grooming and agonistic networks by sex may have been low, particularly as some of the ratios between the observed and expected frequencies of ties between and within the sexes were relatively high (see Table 5.19). Thus, the reason that sex was not found to have an influence on the structure of the agonistic and grooming network in Gamgam, may be due to small sample size. The assortativity of the other behavioural networks (*i.e.* affiliative, unidirectional grunt, grunt exchange) by sex may be due to sex-biased dispersal and the maintenance of bonds amongst the philopatric sex, or due to sex-specific differences in behaviour.

In species with sex-biased dispersal, behavioural interactions that are used to maintain social bonds may be strongly influenced by sex, as these behaviours may be used more frequently between members of the philopatric sex (Fedigan and Baxter 1984). In this study, females had more unidirectional grunt relationships with other females than expected by chance, and fewer than expected with males, whereas males had fewer than expected grunting relationships with both males and females. Additionally, grunt exchange relationships occurred more frequently between females, than between males and females. These results are in line with findings from another female-bonded primate species; rhesus macaque females also directed their vocalisations significantly more to other females than to males (Greeno and Semple 2009). Thus, these results show that it is mainly females who use grunting vocalisations, suggesting that vocalisations may play an important role in maintaining social relationships between females in their natal troops.

Sex-specific differences in behaviour have been observed across primate taxa (Fedigan and Baxter 1984; Fedigan 1993; Cooper and Bernstein 2000; Lehmann and Boesch 2008), including baboons (Seyfarth 1976; Smuts 1985; Dunbar 1988; Lehmann and Ross 2011). In this study, the organisation of three behavioural networks was due to these sex-specific behaviours; firstly, in the Kwano troop, females had more than expected grooming and affiliative relationships with both females and males, whereas males' grooming and affiliative relationships occurred less than expected for both males and females, with grooming relationships between males being completely absent. These results indicate that females were more sociable, in terms of grooming and other affiliative behaviours than males were, which is in line with previous findings on sex-differences in grooming and other affiliative relationships in baboons (Smuts 1985). Furthermore, these results confirm the sex-specific partner preferences in grooming relationships found in a previous study on the Kwano troop (Lehmann and Ross 2011), and extend these to other affiliative behaviours as well.

Secondly, in the Kwano troop agonistic relationships were also assorted by sex, with both males and females directing their aggressive behaviours at females more than expected, and at males less than expected, confirming findings of an earlier study (Lehmann and Ross 2011). Male baboons are known to be more aggressive than females (Seyfarth 1976), which in this case has led to a sex-assorted aggression network.

The relationships of females did not appear to be affected by their reproductive state, but were apparently affected by presence of dependent offspring. In the Kwano troop, the presence of dependent offspring was found to influence grooming, affiliative and unidirectional grunt relationships. Females with dependent offspring received more affiliative behaviours, grooming, and unidirectional grunts than females without dependent offspring. These results are in line with previous studies that have shown that baboon mothers with young infants are groomed preferentially (Frank and Silk 2009) and at high rates (Seyfarth 1977; Henzi and Barrett 2002; Silk *et al.* 2003b), as this grooming is traded for access to their infants (Henzi and Barrett 2002; Frank and Silk 2009). The results presented here show that these findings can be generalised to other affiliative behaviours. Additionally, mothers with young offspring are approached more frequently (Seyfarth 1977; Henzi and Barrett 2002; Silk *et al.* 2003b). During friendly approaches, baboons often grunt to signal benign intent to the individual being approached (Cheney *et al.* 1995), which may be the reason for the higher frequency of grunts being directed at females with dependent offspring.

Because the trade of grooming for infant handling can be subject to laws of supply and demand (Henzi and Barrett 2002), the influence of dependent offspring on grooming relationships may fluctuate. The lack of influence of dependent offspring on grooming, grunting or affiliative relationships amongst Gamgam females may be due to different levels of supply and demand for infant handling, compared to the Kwano troop. In other words, if there were more black infants available per female in the Gamgam troop, females may have needed to groom mothers for a shorter period in order to gain access to their infants. In chacma baboons for example it has been shown that when fewer infants were available, infant handlers groomed the infants' mother for longer (Henzi and Barrett 2002). Consequently, the distribution of grooming relationships would be less influenced by the presence of dependent offspring. However, compared to the Gamgam troop, in Kwano a greater number of black infants was available per female without dependent offspring (Gamgam 0.354; Kwano 0.409), and per total number of females (Gamgam 0.250; Kwano 0.286) over the entire study period. Thus, black infants were scarcer in the Gamgam troop, suggesting that Gamgam mothers could demand more grooming for access to their infants than Kwano mothers, and the presence of offspring should therefore have a greater impact on grooming patterns in Gamgam. The small sample size of females in the Gamgam troop may be the reason no influence of dependent offspring on grooming relationships was found here.

There was some evidence that relationships between males and females were influenced by whether the female was lactating or cycling. Contrary to expectation, the proportion of total grooming time and the frequency of affiliative behaviours females received from males did not differ as a function of lactation in either troop, nor did the grooming that females directed at males. Some influence was found on the patterns of agonistic relationships; in the Gamgam troop, lactating females received less aggression from males than non-lactating females. This result was not found in the Kwano troop. Contrary to expectation, in Kwano, non- lactating females were more frequently involved in grunt exchanges with males and also directed higher rates of affiliative behaviours at males than did lactating females. This latter result corresponds with the result for the differences between cycling and non-cycling females in rates of affiliative behaviours directed at males; cycling females were more affiliative towards males than non-cycling females were.

Little evidence was found for the influence of age on the networks' structure, dominance on relationships between females, or of female reproductive state on the relationships of females. The lack of influence found may be due to the broad categories used; as the exact ages were not known for the majority of baboons in these troops, broad categories of 'adult' and 'subadult' were used. If exact ages were known, differences in patterns of interaction between age groups may have been clearer, especially if age is used as a context-dependant proxy for paternal kinship (Alberts 1999; Widdig *et al.* 2001; Silk 2002b; Boyd and Silk 2006; Silk *et al.* 2006). Similarly, female reproductive state was assigned as the state a female was in for the majority of the study period. Whilst this may be appropriate for longer-term states, such as pregnancy or lactation, it may not be for shorter-term states such as cycling. In fact, female baboons are known to change their pattern of grooming over the course of their cycle (Rowell 1968), thus behavioural interactions may change over a shorter time frame than the periods that were analysed here.

Additionally, as the study troops are relatively small for olive baboons (*e.g.* troops on average contain 20-100 individuals - Ransom 1981), comparing the relationships over two or three categories may have reduced the sample size in each category to such an extent that the power of the statistical tests was too low, especially when only female relationships were considered. Thus, some caution is needed with the interpretation of these results, as the influence of age on the behavioural networks may not have been noted because of small sample sizes.

Furthermore, it is likely that multiple social factors act simultaneously on preferences for social interactions. For example, because in baboon troops maternal kin often occupy adjacent ranks within the dominance hierarchy, matriline should be controlled for in analyses of the influence of rank on behavioural interactions, as assortativity by rank could in fact be due to a preference for interacting with maternal kin. However, due to the small troop sizes in this study, it has not been possible to control for these multiple social influences.

In sum, sex was found to be the most important factor that influenced patterns of behaviour in olive baboon troops at GGNP. Sex-specific differences in sociability and aggression explain patterns of assortativity by sex in the affiliative, grooming and agonistic networks. Furthermore, grunting and grunt exchanges primarily occur between females. As vocalisations play an important role in social bonding (Aiello and Dunbar 1993; McComb and Semple 2005) grunts and grunt exchanges are used by females to maintain their social relationships in these female-bonded troops. Other social factors, such as the presence of dependent offspring, lactation, or cycling, were found to have some influence on individual preferences, but had a less consistent effect on the networks across troops.

5.5 Summary of chapter

- Broadly, networks were found to differ across behaviours; the networks differed in structure, individuals had different social roles across networks, and the majority of behavioural networks were not correlated, indicating that baboons relate to troop members differently through different behaviours.
- Based on the comparison of network metrics, the correlation of networks and individual network positions, the behavioural networks were divided into three categories of distinct social relationships; low cost socio-positive relationships that include unidirectional grunt, grunt exchange and affiliative relationships; high cost socio-positive relationships based on grooming interactions, and high cost socio-negative relationships based on agonistic interactions.
- Clear between-troop differences were found between both the agonistic networks of the Gamgam and Kwano troop, and between the grooming networks of the two troops, while a smaller between-troop difference was found in the affiliative networks. More cohesive association patterns in the Gamgam troop were associated with stronger and more widespread aggression, and it was suggested that this was due to individuals being unable to avoid tension. Additionally, the Gamgam

troop had a more cohesive, stronger grooming network, either because grooming helps with social bonding and to maintain group cohesion, or to reduce stress levels and repair bonds. It was suggested that more fragmented associations of the Kwano troop allowed the Kwano troop to avoid aggression, but that they used affiliative behaviours more frequently to re-establish social relationships.

- Unidirectional grunt and grunt exchange network structures did not clearly differ between the two troops indicating that both troops used these vocalisations in a similar way. Baboons directed their grunts to individuals that were in proximity, thus reiterating that grunts help to facilitate social interactions and ease associations in baboons.
- Sex was found to be the most important factor influencing patterns of interactions in olive baboons. Unidirectional grunt and grunt exchange relationships occurred primarily between females, the philopatric sex, and these behaviours are important for maintaining social relationships. Sex-specific differences in sociability and aggression further influenced patterns of affiliative, grooming and agonistic behaviours, with females being more social, and males more aggressive.
- In Kwano, but not in Gamgam, females with dependent offspring received more affiliative behaviours, grooming and unidirectional grunts than females without young offspring, suggesting that mothers were approached more frequently and grooming was traded for infant handling. Age and female reproductive state had little influence on any behaviour. Other social factors seemed to have some influence on

individual preferences, but had a less consistent effect on the networks across troops.

Chapter 6

Fission-fusion dynamics

6.1 Introduction

Over the past four years the modal classification of primate societies has come under scrutiny, and instead it has been suggested that primate societies should be characterised by their relative degree of fission-fusion dynamics (Aureli *et al.* 2008a), which refers to the amount of variation in individual group membership and spatial cohesion (Figure 6.1). The concept of fission-fusion dynamics has become generally accepted over the past few years; researchers have examined, for example, the way social relationships may affect grouping patterns in species with an intermediate level of fission-fusion dynamics (Sueur *et al.* 2010), how fission-fusion dynamics impact on levels of scramble and contest competition (Asensio *et al.* 2008), and how fission-fusion dynamics affect communication and collective decisions (Sueur *et al.* 2011b). Moreover,

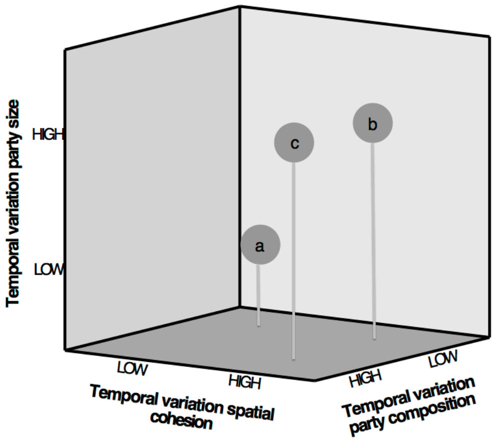


Figure 6.1: Graph representing the three-dimensional framework for the degree of fission-fusion dynamics. The degree of fission-fusion dynamics is measured by the temporal variation in spatial cohesion (x-axis), party composition (y-axis) and party size (z-axis). Examples are given for a) groups with low variation in all three dimensions (*i.e.* traditional 'cohesive' groups); b) groups with high variation in spatial cohesion and party size, but low variation in party composition (*i.e.* multi-level societies); c) groups with high variation in all three dimensions (*i.e.* traditional 'fission-fusion' societies). Graph was adapted from Aureli *et al.* (2008a).

several studies have examined how differences in the degree of fission-fusion dynamics may influence tactical deception (Amici *et al.* 2009) and behavioural flexibility in primates (Amici *et al.* 2008a) as well as how these differences may result from differences in cognitive abilities (Amici *et al.* 2010). Recently, a paper was published reporting on the fission-fusion dynamics of southern muriquis (*Brachyteles arachnoides*), in which estimates were made of the three dimensions of fission-fusion dynamics, which were compared across seasons (Coles *et al.* 2012). However, crucially, the temporal variation of each of these dimensions was not measured, an aspect central to the concept of fission-fusion dynamics. Thus, despite a general acceptance of the fission-fusion dynamics concept, its central framework has not been implemented; none of the above studies have quantified the degree of fission-fusion dynamics by measuring variation along the three axes in the fission-fusion dynamics framework (see Figure 6.1). Instead, the degree of fission-fusion dynamics is used anecdotally, with study groups being described as having either a low or a high degree of fission-fusion dynamics. Quantification of fission-fusion dynamics is crucial for making comparisons across populations and species, for investigations into the continuum of variation in primate social systems, for understanding the impact of fission-fusion dynamics on social relationships, and the cognitive demands it makes on primates.

In this chapter, the extent of the flexibility of olive baboon grouping patterns and how this flexibility relates to adjustments of behaviour is investigated. Furthermore, a method for the quantification of fission-fusion dynamics is suggested and applied to the GGNP baboons.

6.1.1 Flexibility of primate grouping patterns

Over the last few decades, evidence from an increasing number of field studies indicated that primates may be flexible in their grouping patterns, both within species (Kinzey and Cunningham 1994; Pusey *et al.* 1997; Schulke and Ostner 2005; Itoh and Nishida 2007; Lehmann and Boesch 2009), and within populations (Dias and Strier 2003; Sussman and Garber 2007), giving rise to the concept of fission-fusion dynamics. While this is of crucial importance to our understanding of primate behaviour, to date little is known about such intra-specific variation (Strier 2003b), particularly in terms of the temporal variation in party composition, and in spatial cohesion.

One dimension of fission-fusion dynamics, party size, has been relatively well studied in primates. Under the ecological constraints model (Chapman and Chapman 2000), primate social groups have been suggested to be largely determined by food distribution and availability. The size of food patches, and the density, distribution or abundance of food were found to be the main determinants of party size in spider monkeys and chimpanzees (Symington 1988; Chapman *et al.* 1995; Newton-Fisher *et al.* 2000; Hashimoto *et al.* 2003; Basabose 2004; Asensio *et al.* 2009), although other studies also highlight the importance of demography and activity of the party (Matsumoto-Oda *et al.* 1998; Hashimoto *et al.* 2001; Lehmann and Boesch 2004).

The flexibility in the spatial cohesion of groups has been studied less extensively in primates. However, several studies suggest that primates may also adjust the spatial cohesion of their groups seasonally to the availability and distribution of food. For example, a group of Japanese macaques was found to split into smaller subgroups during the summer, when individuals fed on sparse and scattered foods, whereas they remained cohesive during the winter and autumn when foods were more abundant and more clumped respectively (Sugiura *et al.* 2011).

Other studies of primate spatial cohesion have focused on the cohesion within a *party* (*i.e.* the individuals that can be seen at the same time) by recording nearest-neighbour distances, rather than cohesion of the *troop* or *community*. Foraging requirements are key in the spatial position of individuals within their party (Robinson 1981). For example, in diademed sifakas (*Propithecus diadema*), individuals were closely spaced when food patches were large, as food competition was low, while the distance between individuals was greater during times when food patches were small and dispersed (Irwin 2007). While spatial position within a party influences an individual's vulnerability to predation (Robinson 1981), predation risk may have little influence on the cohesion of a party, as was, for example, found in chacma baboons (Cowlishaw 1999). Furthermore, feeding competition only affected party cohesion during foraging, while at other times male reproductive strategies were more important determinants of spacing between individuals (Cowlishaw 1999).

Very little is known about whether primates adjust the composition of their parties. In most studies, the age-sex composition of subgroups is considered, and very few studies have looked at the composition of parties at the level of specific individuals, or how quickly party composition changes (e.g. Suarez 2001). For example, mating strategies and food distribution largely determine the age-sex membership of parties in capuchins (*Cebus apella nigritus*) (Alfaro 2007). Similarly in chimpanzees, party composition depends mainly on the presence of receptive females, food availability and the activity of the party (Anderson *et al.* 2002).

While there is some evidence that primates adjust the size or composition of parties, the spread of the group, or the spread of the party, it is not known how each of these aspects are adjusted within a single primate group. Because these adjustments to grouping patterns are likely to be an interrelated set of responses, it is important that all of these strategies are considered in a single study. Furthermore, it is not clear what the extent of this flexibility in grouping patterns is; is this limited to differences between troops within a population, or do troops also adjust grouping patterns seasonally, or even to different habitat types?

In this chapter, the flexibility of olive baboon grouping patterns is investigated by examining if troops adjust party size, party composition, and spatial cohesion to habitats, by season, and to local ecology. In previous chapters it was shown that food availability differed between troops and between seasons, and that predation risk differed by habitat types (chapter 3). These ecological variations were associated with seasonal and between-troop differences in patterns of associations (chapter 4). Given these results, grouping patterns are also expected to differ between habitats, seasons, and troops.

6.1.2 Flexibility of grouping patterns and social behaviours

In previous chapters it was shown that differences in association patterns (chapter 4) were associated with differences in the structure of social relationships (chapter 5) based on several behaviours. However, as social networks are generated from data over some time, in this case over the entire study period, it is not clear if this is evidence of flexibility in olive baboon social behaviour in association with adjustments in grouping patterns, or simply a between-troop difference in social relationships. In other words, while this evidence shows a between-troop difference, it does not indicate *how* flexible olive baboons are. For example, it is not clear if, when grouping patterns are adjusted, the social behaviours that are used are also adjusted.

It is important to understand better the flexibility of primate social behaviours in the context of the variations in grouping patterns, as it has been suggested that the degree of fission-fusion dynamics affects the mode and the function of social interactions that are used in a primate group (Maestripieri 1999; Milton 2000; Aureli *et al.* 2008a) and ultimately the social structure (Whitehead 1997). To date, it is not known if this includes qualitative differences in the evolved repertoires of social behaviours between species, and/or if this includes quantitative differences in the use of certain social behaviours between troops or populations within species.

In this chapter, the existence of quantitative, small-scaled differences in the social behaviours of two troops, which are associated with adjustments in grouping patterns, is explored to test the relationships between grouping patterns and social behaviour.

6.1.3 Estimating fission-fusion dynamics and defining parties

A standardised measure of fission-fusion dynamics is a crucial first step to test if fission-fusion dynamics differ in a scalar manner across groups, populations, or species. While some general suggestions have been made (Aureli *et al.* 2008a), no such measure has yet been proposed. Furthermore, while three dimensions of fission-fusion dynamics have been identified, it is not clear how party size, party composition, and spatial cohesion relate to each other. It is therefore not known if these three dimensions can vary independently, and therefore measure different aspects of grouping patterns, or if these dimensions co-vary and thus measure the same underlying phenomena.

Moreover, the way a 'party' is defined is central to two out of the three fission-fusion dimensions (*i.e.* party size and party composition). However, due to their temporary nature, parties are difficult to define (Chapman *et al.* 1993; Reynolds 2005) and various definitions, such as visual and spatial ones, have been used across studies (Itoh and Nishida 2007; Coles *et al.* 2012). The visual definition of a party is most commonly used, and here a party consists of all individuals that can be seen during a scan (Chapman and Lefebvre 1990; Itoh and Nishida 2007) and are therefore assumed to be in visual contact (Lehmann and Boesch 2004). These are the 'face-to-face' parties described by Itoh & Nishida (2007). At times, auditory contact between individuals is included in the definition of a party, mainly by lengthening the time period in which individuals are considered to be in the same party. For example, a 'nomadic party' (Itoh and Nishida 2007; Coles *et al.* 2012) includes all the individuals seen in a day; Chapman, Chapman and Wrangham (1995) define an 'acoustic group' as all individuals seen in the previous hour; Matsumoto-Oda *et al*. (1998) include all individuals that *interacted* during a given day. In a spatial definition of a party, individuals are considered to be in the same party if they are found within a certain radius (Sakura 1994; Newton-Fisher *et al.* 2000) or using a chain rule (Ramos-Fernández 2005; Aureli and Schaffner 2007; Asensio *et al.* 2009), under which an individual belongs to a party if it is not further away than the cut-off distance from at least one individual in that party. The cut-off distance or radius that is used may however be arbitrary.

In this chapter, the relationship between the three dimensions of fission-fusion dynamics is tested. Throughout this study, a party was defined as the individuals that were seen together during a scan. Because researchers spent five minutes before each scan walking around the area to locate baboons, parties here were thus beyond a strict visual definition of a party. However, given the difficulties in knowing what level of grouping is most important to the study animal and the effect habitat visibility may have on a visual definition of a party, an objective, statistical definition of the cut-off distance at which individuals are no longer considered to be in the same party is also determined in this chapter. In this method, the cut-off value for the chain rule is determined statistically, through analysis of inter-individual distances (for full explanation of methodology see section 6.2.3.9), allowing for a comparison of how each of these definitions of a party reflects patterns of subgrouping.

6.1.4 Aims of this chapter

The aims of this chapter are to investigate the flexibility of the grouping patterns of olive baboons, by making comparisons across habitats, seasons, and between troops, and to test if this flexibility is associated with adjustments in non-vocal social behaviour and vocalisations. Furthermore, methods for quantifying fission-fusion dynamics are developed and applied to the two study troops. The specific research questions of this chapter are as follows:

1. Spatial cohesion
    a. Does spatial cohesion differ by season and by troop?
2. Party size
    a. Does party size differ by habitat, by season, and by troop?
    b. What is the proximate mechanism for the formation of parties?
3. Party composition
    a. Does the rate of party composition change differ by season and by troop?

4. How do spatial cohesion, party size, and party composition change relate to each other?
5. Are variations in social interactions related to variations in spatial cohesion, party size, and party composition change?
6. Does the degree of fission-fusion dynamics differ by season and troop?
7. Does party spread differ by habitat, by season, and by troop?
8. At what distance can individuals be considered to be in different parties?

6.2 Methods

A summary of the questions addressed in this chapter, along with the type of analyses and the data used, is given in Table 6.7.

6.2.1 Quantifying the dimensions of fission-fusion dynamics

6.2.1.1 Spatial cohesion

Spatial cohesion was estimated through the inter-individual distances of focal animals. GPS locations were recorded every 15 minutes for two focal animals, and the distance between two simultaneously recorded GPS locations was measured using MapSource (Garmin 2011). Rather than measuring the distance between individuals in the same party (*i.e.* party spread), this measure gives an indication of the spacing between individuals in a troop irrespective of whether they are in the same party, and therefore indicates the spatial cohesion of a troop. When a troop is less spatially cohesive, the average distance between focal animals should be greater.

The temporal variation of spatial cohesion was measured through the coefficient of variation (CV) of daily mean of inter-individual distances (see section 6.2.3.7).

6.2.1.2 Party size

A party was defined as all troop members that were visible during a scan (Chapman 1990). Habitat visibility may influence the number of individuals that are visible, and consequently the party size measure (Chapman *et al.* 1993). This effect was minimised by spending several minutes prior to each scan walking through the area in the vicinity of the focal animal locating animals. Party size is simply the number of individuals seen during a scan, including all adults, subadults, juveniles and infants. Party size is also given as a proportion of troop size to account for differences in troop size.

The temporal variation of party size was estimated through the CV of daily mean proportion of the troops that was found together in a party (see section 6.2.3.7).

6.2.1.3 Party composition

The variation in party composition measures the number of individuals that leave and join, and was estimated from hourly scan data. Only scans in which all adults, subadults, and juveniles could be identified were included in the analyses. Infants were included in these analyses, but rather than individual identities, the number of infants present was compared between scans, as infants rarely move independently from their mothers. For each scan record, the exact time from the previous scan record was determined, as was the number of changes in party composition. A change in party composition occurred when one or more individuals left or joined the party and these changes were summed (see Figure 6.2). These data were used to calculate a rate of change per minute, which was averaged over each day. Furthermore, troop size fluctuated in both troops due to several disappearances and emigrations. Therefore, as troop size fundamentally influences the number of changes that are possible in any given party, the temporal variation in party composition was also expressed as a proportion of the maximum possible number of changes for each day. This maximum value is the troop size for a given day, minus the focal animal, as the focal animal was present in every scan, and thus could not be classified as joining or leaving a party.

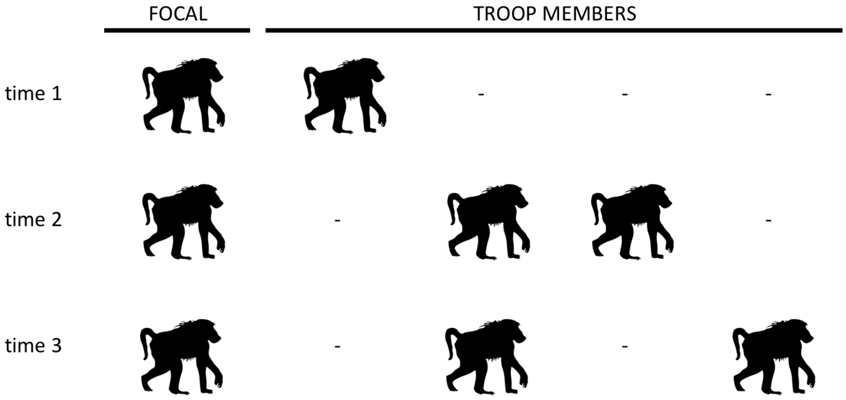


Figure 6.2: Diagram outlining the rate of party composition change calculations for a troop of five over three time periods. For each individual in the troop it was noted whether they remained present or absent in the party (no change) or whether they joined or left the party (change). Thus, between time period 1 and 2, one individual remained (focal), one individual left the party, 2 joined the party, and one remained absent, making for a total of three changes. Between time period 2 and 3 there were 2 changes. Party composition changes were also expressed as a proportion of the total possible number of changes, which is the number of troop members minus one (focal). Thus, between time period 1 and 2 the relative party composition changes were 3/4 = 0.75, whereas between time periods 2 and 3 this was 2/4 = 0.50.

Temporal variation of party composition change was measured through the CV of daily mean proportion of changes in party composition (see section 6.2.3.7).

6.2.2 Quantifying party spread

The spread of the party was estimated using two measures. Firstly, party spread was measured by the 3-dimensional space over which the party was spread. This measure was calculated from the distance between the two furthest individuals in the party, the distance between the two furthest individuals perpendicular to the furthest distance measurement, and the average distance these four individuals were from the ground (see red arrows in Figure 6.3).

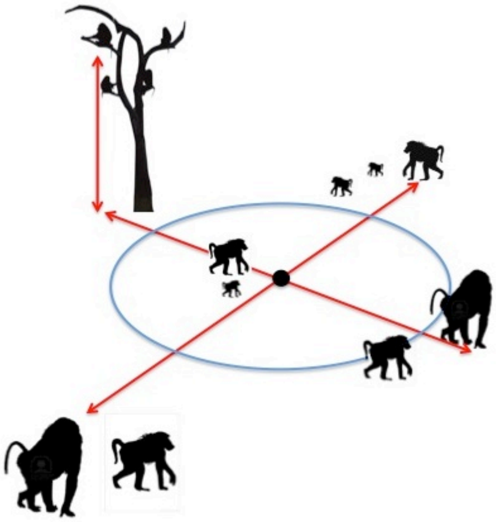


Figure 6.3: Diagram outlining the two measures of party spread. The black circle indicates the estimated centre of the party. Spatial party cohesion was firstly measured by the 3-dimensional space over which the troop was spread. This was calculated with the distance between the two furthest individuals in the party, the distance perpendicular to that between the two furthest individuals and the average height at which those four individuals were found. The red arrows indicate these measurements. The blue circle indicates the second measure of spatial cohesion; for this measure the centre of the party was determined and all individuals that were within a 10m radius from that centre were recorded.

These values were multiplied to get the 3-dimensional space over which a party was spread. Secondly, party spread was measured by the number of individuals that were found in the central area of a party. For this measurement, the centre of the party was first estimated, and individuals that were within a 10m radius of that centre were recorded (see blue circle in Figure 6.3). These measurements were taken hourly. To avoid non-independence of data, measurements were averaged per day.

6.2.3 Data analysis

Party size and party spread measurements were taken from hourly scan data, and averaged per day. Sample sizes for these measurements per habitat, per season, and per troop are given in Table 6.1 and Table 6.2. The habitat types that occur in the home ranges of both troops should be the same across home ranges; for example, gallery forest in the Kwano home range should not differ fundamentally from gallery forest in the Gamgam home range. Therefore, for the between habitat comparisons, data from the troops were pooled. Because of low sample sizes, measurements taken in the agricultural land, elephant grass, and mango forest were excluded from the between-habitat analyses. Sample sizes are smaller for party composition changes, as these were measured between two scans; sample sizes for party composition changes measurements are given in Table 6.3. Sample sizes for the number of inter-individual distances are given in Table 6.4. The analyses used to answer each research question are outlined below. Research questions, analyses and variables are summarised at the end of this section in Table 6.7.

Table 6.1: Sample sizes for the daily mean party size and party spread estimates per habitat type.

Habitat	Number of daily mean estimates
Gallery forest	107
Lowland forest	51
Guinea savannah	97
Burned Guinea savanı	36
Agricultural land	8
Elephant grass	2
Mango forest	6
Palm forest	33

Table 6.2: Number of daily mean party size and party spread estimates per season per troop.

Season	Gamgam (*N*)	Kwano (*N*)
BEG WET	51	72
END WET	16	37
BEG DRY	36	49
END DRY	36	43
TOTAL	139	201

Table 6.3: Number of daily mean party composition change estimates per season per troop.

Season	Gamgam (*N*)	Kwano (*N*)
BEG WET	60	126
END WET	-	7
BEG DRY	131	198
END DRY	72	124
TOTAL	263	455

Table 6.4: Number of inter-individual distances per season per troop. No or few inter-individual distances were collected during the end of the wet season, as for the majority of this season there was only a single researcher observing the troops.

SEASON	**Gamgam (*N*)**	**Kwano (*N*)**
BEG WET	60	126
END WET	-	7
BEG DRY	131	198
END DRY	72	124
TOTAL	263	455

6.2.3.1 Does spatial cohesion differ by season and troop?

To examine if season affected spatial cohesion, comparisons were made between daily mean inter-individual distances across seasons separately for each troop. As data were not normally distributed, seasonal values were compared with Kruskal-Wallis tests and *post hoc* Mann-Whitney tests. Comparisons were made between the daily mean inter-individual distances to test if the troops differed in their spatial cohesion, using Mann-Whitney tests. As individuals within the troop may be in several different habitat types at once, it was not possible to measure spatial cohesion by habitat type.

6.2.3.2 Does party size differ by habitat, by season, and by troop?

The effect of habitat type on party size was tested by comparing the daily mean party size and the daily mean proportion of the troop found in a party across habitat types using Kruskal-Wallis tests and *post hoc* Mann-Whitney tests. As habitat types should be fundamentally similar in both home ranges, for these analyses the data were pooled across troops. Conversely, the effect of season on party size was examined by comparing daily mean party size across seasons within troops. Comparisons were made both between absolute values and values relative to troop size.

The data for the Kwano troop, and the Gamgam relative party size data were not normally distributed, so seasonal values were compared with Kruskal-Wallis tests and *post hoc* Mann-Whitney tests. Gamgam absolute seasonal party size differences were compared using an ANOVA with *post hoc* Tukey tests, as they were normally distributed.

Independent t-tests were run to determine if the Gamgam and Kwano troops differed in the daily mean size of parties. Comparisons were both between absolute party sizes and between party sizes relative to troop size.

6.2.3.3 What is the proximate mechanism for the formation of parties?

The frequency distribution of observed party sizes is a direct result of the rules that individuals use for joining and leaving parties (Cohen 1972; Beauchamp 2011). As a result it is possible to discriminate between competing hypotheses for the formation and disbanding of parties by testing which distribution best fits the observed data. This method has been used to identify the mechanism for the formation and maintenance of groups of primates (e.g. Cohen 1972; Cohen 1975; Patzelt *et al.* 2011), flocks of birds (e.g. Caraco 1980; Beauchamp 2011), and shoals of fish (e.g. Niwa 2003; O'Neill and Faddy 2003). Models used in previous studies include Poisson, negative binomial, and exponential distributions. The probability density function for each of these distributions is given in Table 6.5, and the predictions for the proximate mechanism for party formation and cohesion for each model are outlined below.

If individuals have a general attraction to larger groups, or to particular individuals within a party (Beauchamp 2011; Patzelt *et al.* 2011), the number of individuals that join a party increases linearly with party size. If the number of individuals that leave a party also increases linearly with party size, for example due to increased levels of competition in larger parties (Beauchamp 2011), the party size distribution follows a negative binomial. In such a distribution large parties occur more frequently, producing a left skew to the distribution, and the sizes of parties is variable. A negative binomial group size distribution has been observed in some species of fish (O'Neill and Faddy 2003) and in several primate species, including howler monkeys (*Alouatta* spp.), gibbons (*Hylobates* spp.), black and white colobus (*Colobus* spp.), Hanuman langurs (*Semnopithecus entellus*), chacma baboons (*Papio ursinus*), yellow baboons (*Papio hamadryas cynocephalus*) (Cohen 1969), and Guinea baboons (*Papio hamadryas papio*) (Patzelt *et al.* 2011).

Table 6.5: Discrete frequency distributions that were fitted to the party size data along with the parameters and probability density function (PDF), which indicates the probability of finding a party of size *j*. Distributions were zero-truncated as party sizes of zero were not recorded (adapted from Beauchamp 2011).

Distribution	**Parameters**	**PDF**
Zero-truncated negative binomial	α, λ	$\Pr(Y_{i=j} \mid Y_i > 0) = \left\{ \frac{\Gamma\left(j + \frac{1}{\alpha}\right)}{\Gamma(j+1)\Gamma\left(\frac{1}{\alpha}\right)} \right\} (\alpha\lambda)^j (1 + \alpha\lambda)^{-(j+\frac{1}{\alpha})} \, [1 - F(0)]^{-1}$
Zero-truncated Poisson	λ	$\Pr(Y_{i=j} \mid Y_i > 0) = \frac{\lambda^j}{[\exp(\lambda) - 1]} \, j!$
Zero-truncated exponential	λ	$\Pr(Y_{i=j} \mid Y_i > 0) = \exp(-\lambda j) \, [\exp(\lambda) - 1]$

When the size or the members of a party do not influence the decision to join a party (Cohen 1972; Patzelt *et al.* 2011), but rather a party is formed by random aggregation at certain attractive sites, such as feeding patches or waterholes, the party size frequency distribution follows a Poisson distribution. In this case, mean party size should be small relative to the size of the troop due to a low rate of fusion relative to fission (Couzin and Laidre 2009). As was the case with the negative binomial distribution, under the Poisson model the rate at which individuals leave a party increases with party size, but the rate of individuals joining does not (Beauchamp 2011). The Poisson distribution has, for example, been observed in the group sizes of yellow-eyed juncos (Caraco 1980), orang-utans (Cohen 1975), and humans (Coleman and James 1961).

The party size distribution would follow an exponential distribution if mean party size is relatively small compared to troop size, and thus the rate of fusion is low relative to the rate of fission, and individual decisions to join or leave a party for reasons other than the size of the party (Beauchamp 2011), for example when a group decision is not beneficial for the individual. The shoal size of some species of fish has been shown to follow an exponential distribution (Niwa 2003).

By fitting the observed party size frequency distribution for both troops with each of these models, and comparing how well these models describe the data, it is possible to determine which mechanism of the formation and cohesion of parties receives most support. Models were fitted via maximum-likelihood estimation and compared using AICs. Fitted models were zero-truncated so that the probability of observing a party size of zero was zero. *G*-tests for the goodness-of-fit (Sokal and Rohlf 1995) were used to determine if the best-fit model provided a good description of the observed distribution. The *G*-test compares the observed frequencies of party sizes to the predicted frequencies obtained from the best-fit model.

6.2.3.4 Does the rate of party composition change differ by season and by troop?

To examine if season affected the rate at which party composition changed, comparisons were made across seasons between the daily mean rates of party composition changes (rate per minute), and the daily mean rate of party composition changes as a proportion of the maximum possible number of changes. Kruskal-Wallis tests and *post hoc* Mann-Whitney tests were used, as data were not normally distributed.

The daily mean rate of party composition change was compared between the two troops using independent t-tests. Furthermore, to control for troop size, comparisons were also made between the numbers of observed party composition changes as a proportion of possible changes using independent t-tests. It was not possible to test the effect of habitat type on the rate of party composition change, as this was measured as the number of changes between two scans, and over this period the party may have ranged in several habitat types.

6.2.3.5 How do spatial cohesion, party size and party composition change relate to each other?

Correlations and partial correlations were run on party size, the changes in party composition, and spatial cohesion to determine if and how each of the three fission-fusion dynamics components influence each other. Party size, and party composition changes were recorded hourly whilst spatial cohesion measures were recorded every 15 minutes, and all of these were averaged over each day. In these analyses, party size is defined as the proportion of the troop that was seen in a single party. The rate of change in party composition was defined as the number of observed changes in the party as a proportion of the maximum possible number of changes. Spatial cohesion was defined as the daily mean of inter-individual distances. Non-parametric correlations were used, as data were not normally distributed.

6.2.3.6 Are variations in social interactions related to variations in spatial cohesion, party size, and party composition change?

To determine how social behaviours are associated with grouping patterns, correlations were run between the daily means of spatial cohesion, party size, and party composition change, and rates of social behaviours and vocalisations. In these analyses, party size was expressed as the proportion of the troop that was seen together in a scan, spatial troop cohesion as the daily mean of inter-individual distances and party composition change as the number of changes per minute as a proportion of the maximum possible number of changes. Correlations were run for each troop, with five types of social interactions: affiliative and agonistic behaviours, and friendly, agonistic and contact vocalisations. The affiliative behaviours are: lip smack, present for grooming, present rear, embrace, touch genitals, touch muzzles, offer or hold hands, touch, present genitals, approach, give a ‘friendly face’, grasp of rear, tongue protrusion, mount, and give and receive grooming (see chapter 2 for definitions of behaviours). Aggressive behaviours are: attack, chase, bite, hit, head bob, ground slap, lunge, tooth grind, eyebrow raise, ears back, stare, contact aggression, non-contact aggression. Friendly vocalisations are grunts and grunt exchanges; aggressive vocalisations are the roar grunt, pant, scream, wahoo bark, and alarm bark; contact barks were considered as a separate category. As data were not normally distributed, non-parametric correlations were used.

6.2.3.7 Does the degree of fission-fusion dynamics differ by season and troop?

As fission-fusion dynamics refer to the *temporal variation* in party size, party composition, and spatial cohesion, the coefficient of variation (CV) was calculated for each of the fission-fusion dynamics components by dividing the standard deviation of the fission-fusion measure by the mean. The CV thus indicates the amount of variation found in the three dimensions of fission-fusion dynamics in a troop over the entire study period. In these analyses, party size was expressed as the daily mean proportion of the troop that was seen together in a scan, spatial cohesion as the daily mean of inter-individual distances, and party composition change is expressed as the daily mean number of changes per minute as a proportion of the maximum possible number of changes.

A fission-fusion dynamics index (FFDI) is suggested here, which combines the coefficient of variation for each of the three fission-fusion dynamics components as follows:

$$FFDI = \frac{1}{3}\,CV_{party\ size} + \frac{1}{3}\,CV_{party\ composition} + \frac{1}{3}CV_{spatial\ cohesion}$$

To determine if fission-fusion dynamics differ by season, for each troop the FFDI was also calculated and compared qualitatively across seasons.

6.2.3.8 Does party spread differ by habitat, by season, and by troop?

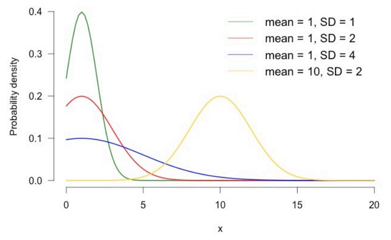
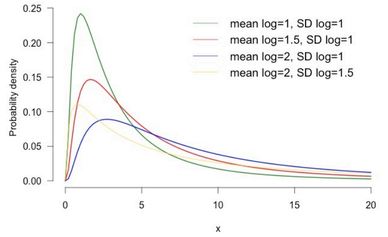
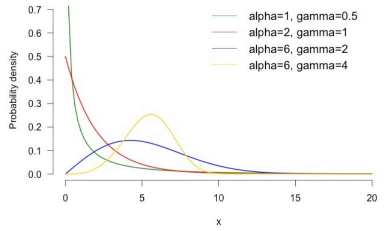
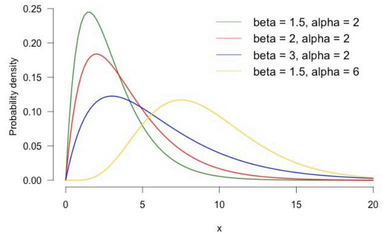
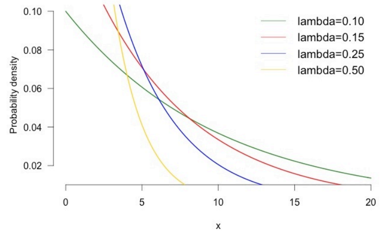
To examine the effect of habitat type on the spatial cohesion of parties, party spread as measured by daily mean volume and by daily mean number of individuals in the centre of the party were compared across habitat types using Kruskal-Wallis tests and *post hoc* Mann-Whitney tests. Comparisons were made between absolute measures of party cohesion and between measures of party cohesion per individual in the party. To examine if season affected the spatial cohesion of parties, comparisons were made between the mean daily party spread, as measured by the 3-dimensional space and the number of individuals in the centre of the party. Comparisons were made both between absolute values and values relative to party size. To determine if the troops differed in the spatial cohesion of parties, comparisons were made between the daily averages of party spread as measured by the 3-dimensional space over which parties were spread, and as measured by the number of individuals that were found within a 10m radius of the party centre. In order to take possible differences in party size into account, comparisons were also made between individual 3-dimensional space of party members and the proportion of the party that were found within a 10m radius. Comparisons were made via independent t-tests.

6.2.3.9 At what distance can individuals be considered to be in different parties?

The distance at which individuals could be considered to be in different parties was determined by fitting two-process models to the frequency distribution of inter-individual distances based on the method outlined by Sugiura *et al.* (2011). This methodology was originally developed to split behaviour into bouts (Slater and Lester 1982; Langton *et al.* 1995), but has more recently been used to determine the distance at which subgrouping occurred in troops of Japanese macaques (*Macaca fuscata*) (Sugiura *et al.* 2011). The location of two focal animals was recorded every 15 minutes with a handheld GPS. Focal individuals were chosen in a way to ensure a similar number of inter-individual distance measurements were taken for each age/sex class combination (*e.g.* adult male – adult female; adult male – adult male). Spatial cohesion measured here is therefore a description of the cohesion of adult and subadult males and females, but excludes juveniles and infants. These GPS locations were transferred into MapSource (Garmin 2011) and the distance between two simultaneously recorded GPS locations was measured. Data were analysed separately for each season, in order to see if there was temporal variation in the inter-individual distances. Too few inter-individual distances were available for the end of the wet season (see Figure 6.4), and therefore this season was omitted from these analyses.

Five standard continuous distributions, *i.e.* a normal, log-normal, Weibull, gamma, and exponential distribution (see Table 6.6 for probability density functions and examples of these distributions) were fitted to the frequency distribution of inter-individual distances in each season, and Akaike's information criterion (AIC) (Johnson and Omland 2004) was calculated and compared to select the model of best fit.

Table 6.6: The standard continuous distributions that were fitted, along with their parameters, probability density function (PDF), and examples of the probability density under different values for the parameters. Probability density functions were taken from Joyce (2006) and NIST/SEMATECH (2012).

Distribution	Parameters	PDF	Examples
Normal	μ, σ^2	$f(x) = \frac{1}{\sigma\sqrt{2\pi}}\exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right)$	
Log-normal	μ, σ	$f(x) = \frac{e^{-\left(\frac{\left(\ln\left(\frac{x}{m}\right)\right)^2}{2\sigma^2}\right)}}{x\sigma\sqrt{2\pi}}$	
Weibull	γ, α	$f(x) = \frac{\gamma}{\alpha}\left(\frac{x}{\alpha}\right)^{(\gamma-1)}\exp\left(-\left(\frac{x}{\alpha}\right)^{\gamma}\right.$	
Gamma	α, β	$f(x) = \frac{x^{\alpha-1}e^{-x/\beta}}{\beta^{\alpha}\Gamma(\alpha)}$	
Exponential	λ	$f(x) = \lambda e^{-\lambda x}$	

A model with a mixture of two component distributions was then fitted to the data and AICs were compared to test if the goodness-of-fit improved with the two-process model compared to the single process model. If a single distribution best describes the data, a single process of maintaining troop cohesion underlies the observed distribution of inter-individual distances. In other words, subgrouping does not occur. If the observed frequency distribution was the result of two processes, a mixture distribution of two of the same or two different distributions will be a better fit to the data. In this case there are two sources of variation; variation in distances between individuals in the same party, and variation in the distances between individuals that are in different parties. When troops are known to split up temporarily into smaller parties, it is expected that there are many short inter-individual distances when individuals are found within the same party, and that there is a second peak in longer inter-individual distances when individuals are found within different parties. Such a frequency distribution of inter-individual distances can be described by a finite mixture distribution, which is a distribution that consists of two overlapping component probability distributions (red curves in Figure 6.4) (Macdonald and Green 1988; Macdonald and Du 2011). The probability density function of this mixture distribution is a convex combination, *i.e.* this is the sum of the component probability density functions that have each been given a non-negative weight that sums to one, and together these probability distributions add to one (green curve in Figure 6.4) (Macdonald and Green 1988). The probability density function of a mixture distribution is thus described by:

$$g(x|x,\mu,\sigma) = \pi_1 f(x|\mu_{1,}\sigma_1) + \cdots + \pi_k f(x|\mu_{k,}\sigma_k)$$

Where k is the number of components, and π is the mixture weight for each component (Macdonald and Green 1988). If the observed frequency distribution was better described by a mixed distribution than by a single distribution, the inter-individual distance at which individuals could be considered to be in different parties is the distance at which the probability density is the same for both component distributions, *i.e.* the distance at the intersection of the curves of the two component distributions.

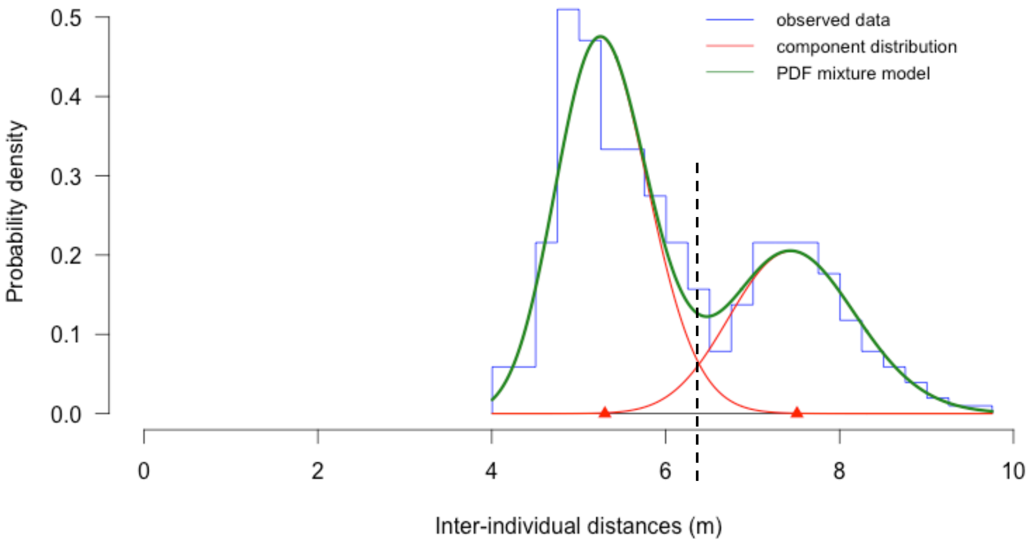


Figure 6.4: Example of a gamma mixture distribution. The red curves indicate two overlapping component gamma distributions, with each of their means indicated by a triangle. The green curve indicates the probability density function of the mixture distribution, which is the sum of the weighted component distributions. The total area under the probability density function equals one. The dashed line indicates the distance at which individuals can be considered to be in different parties.

Table 6.7: Questions addressed in this chapter, the type of analyses and the data used.

Question	**Analyses**	**Data used**
1a. Does spatial cohesion differ by season and by troop?	Kruskal-Wallis tests *Post hoc* Mann-Whitney tests	• Daily mean distance between two focal animals measured from GPS locations taken every 15 minutes per season
	Independent t-test / Mann-Whitney test	• Daily mean distance between two focal animals measured from GPS locations taken every 15 minutes per troop
2a. Does party size differ by habitat, by season, and by troop?	Kruskal-Wallis tests *Post hoc* Mann-Whitney tests	• Daily mean party size in each habitat type (absolute and relative to troop size)
	Kruskal-Wallis tests *Post hoc* Mann-Whitney tests / ANOVA *post hoc* Tukey tests	• Daily mean party size in each habitat type (absolute and relative to troop size) per season
	Independent t-test	• Daily mean party size in each habitat type (absolute and relative to troop size) per troop
2b. What is the proximate mechanism for the formation of parties?	Fitting of discrete models	• Frequency distribution of observed party size, recorded hourly
3a. Does the rate of party composition change differ by season and by troop?	Kruskal-Wallis tests *Post hoc* Mann-Whitney tests	• Daily mean rate of party composition change (absolute and relative to the maximum number of party size changes) per season
	Independent t-test	• Daily mean rate of party composition change (absolute and relative to the maximum number of party size changes) per troop
4. How do spatial cohesion, party size, and party composition change relate to each other?	Kendall's tau-b correlation	• Daily mean proportion of the troop seen together as a party • Daily mean number of party composition changes as a proportion of the maximum number of party composition changes • Daily mean distances between two focal animals

Question (continued)	Analyses	Data used
5. Are variations in social interactions related to variations in spatial cohesion, party size, and party composition change?	Pearson's correlation	• Three components of fission-fusion dynamics: • Seasonal mean party size as proportion of troop size • Seasonal mean rate of party composition changes as a proportion of the maximum possible number of changes • Seasonal mean distances between two focal animals • Daily mean rate per minute: • Affiliative behaviour • Agonistic behaviour • Affiliative vocalisation • Agonistic vocalisation • Contact vocalisation
6. Does the degree of fission-fusion dynamics differ by season and troop?	Comparison of Fission-Fusion Dynamics Index (FFDI)	• FFDI for Gamgam and Kwano troop calculated from: • CV of spatial troop cohesion • CV of party size • CV of party composition changes
7. Does party spread differ by habitat, by season, and by troop?	Kruskal-Wallis tests *Post hoc* Mann-Whitney tests	• Daily mean volume of party per habitat type (absolute and relative to party size) • Daily mean number of individuals within a 10m radius of the centre of the party, per habitat type (absolute and relative to party size)
	Kruskal-Wallis tests *Post hoc* Mann-Whitney tests	• Daily mean volume of party (absolute and relative to party size) by season • Daily mean number of individuals within a 10m radius of the centre of the party (absolute and relative to party size) by season
	Independent t-test – Mann-Whitney test	• Daily mean volume of party per habitat type (absolute and relative to party size) • Daily mean number of individuals within a 10m radius of the centre of the party, per habitat type (absolute and relative to party size)
8. At what distance can individuals be considered to be in different parties?	Fitting of single and mixture models	• Distances between two focal animals by season measured from GPS locations taken every 15 minutes

6.3 Results

6.3.1 Does spatial cohesion differ by season and by troop?

Daily mean inter-individual distances were compared across seasons and troops. Season did not significantly affect the spatial cohesion in either troop (Gamgam: χ^2 (2)= 2.08, p = 0.376 - Figure 6.5; Kwano: $\chi^2(2)$ = 1.67, p = 0.445 – Figure 6.6). However, Figure 6.6 shows that the daily mean distances were more variable in the Kwano troop during the beginning of the dry season compared to the beginning of the wet and the end of the dry season. Daily mean distance between focal animals was significantly shorter in the Gamgam troop (median = 39.5m, IQR = 34.5-52.7m) compared to the Kwano troop (median 106.0m=, IQR = 62.6-150.6m) (Mann-Whitney U = 87.00, p < 0.001 - Figure 6.7). These results indicate that Gamgam troop was more spatially cohesive than the Kwano troop throughout the study period.

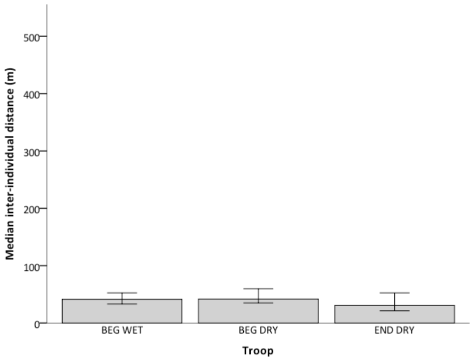


Figure 6.5: Comparison of Gamgam seasonal spatial troop cohesion as measured by the daily mean inter-individual distances of two focal animals. Here, the seasonal medians of the daily average distances are shown.

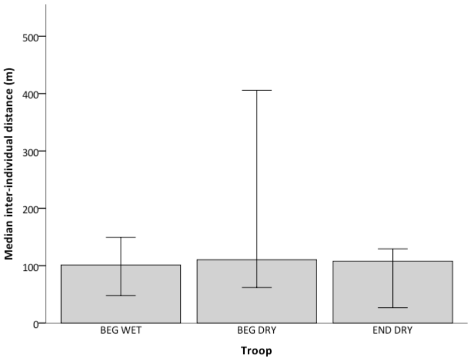


Figure 6.6: Comparison of Kwano seasonal spatial troop cohesion as measured by the daily mean inter-individual distances of two focal animals. Here, the seasonal medians of the daily average distances are shown.

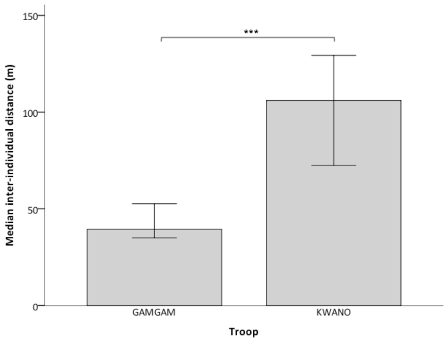


Figure 6.7: Between-troop comparison of spatial troop cohesion as measured by the daily mean inter-individual distances between focal animals. Here, the seasonal medians of the daily average distances are shown. *** indicates $p < 0.001$.

6.3.2 Does party size differ by habitat, by season, and by troop?

Gamgam parties on average consisted of 8.0 individuals (± 3.14) whereas Kwano parties consisted on average of 6.4 individuals (± 3.36). The effect of habitat type, season, and troop on the size of parties is discussed below.

Habitat

Both the size of parties and the proportion of the troop found in a single party were found to differ significantly by habitat type (party size: χ^2 (4) = 17.56, p = 0.002; proportion of troop: χ^2 (4) = 36.94, $p < 0.001$). Results for *post hoc* Mann-Whitney tests are given in Appendix D, Table D.1 & Table D.2. The largest parties were found in the gallery forest and burned Guinea savannah, where parties on average (*i.e.* over the two troops) consisted of 7.33 (*IQR:* 5.25-10.00) and 7.75 (*IQR*: 6.17-9.00) individuals respectively (Figure 6.8). The smallest parties were found in the lowland (*median*: 5.00; *IQR*: 3.33-8.00) and palm forest (*median*: 5.00; *IQR*: 3.00-8.75). When relative party size was considered (Figure 6.9), results were similar, although here no significant difference was found between the party size in the burned Guinea savannah and either the gallery forest or the Guinea savannah.

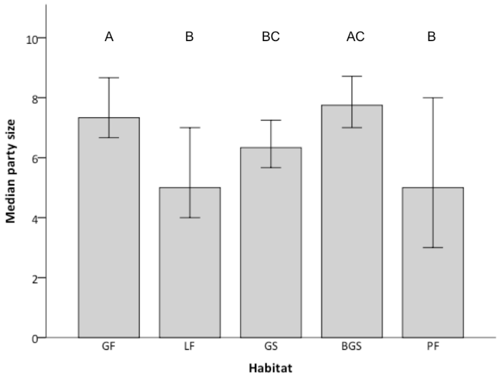


Figure 6.8: Comparisons of habitat-specific party size. Party sizes were not significantly different between habitat types with the same letter. GF = gallery forest, LF = lowland forest, GS = Guinea savannah, BGS = burned Guinea savannah, PF = palm forest.

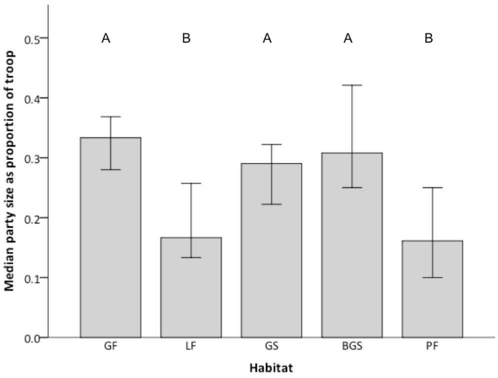


Figure 6.9: Comparisons of habitat-specific party size, taking into account the size of the troop. Party size was not significantly different between habitat types with the same letter. GF = gallery forest, LF = lowland forest, GS = Guinea savannah, BGS = burned Guinea savannah, PF = palm forest.

Season

Gamgam party sizes differed significantly by seasons (F (3, 135) = 3.99, p = 0.009) as did the proportion of the troop found in a party (χ^2 (3) = 8.07, p = 0.043). Seasonal comparisons are given in Figure 6.10 & Figure 6.11. Gamgam parties were largest at the end of the dry season, when on average 9.47 individuals (± 3.40) or 50% of the troop was seen together (*IQR* 0.34-0.61). No significant differences were found either between the absolute or the relative party size during the beginning of the wet, the end of the wet and the beginning of the dry season.

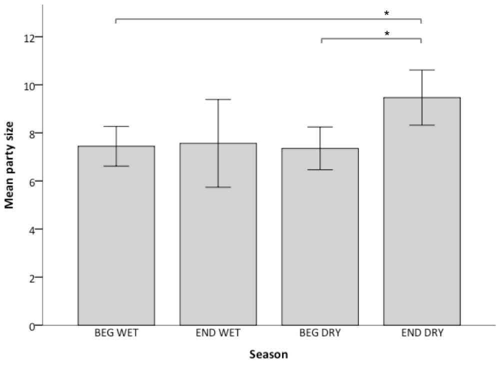


Figure 6.10: Results for seasonal comparison of Gamgam daily mean party size. * indicates $p < 0.05$.

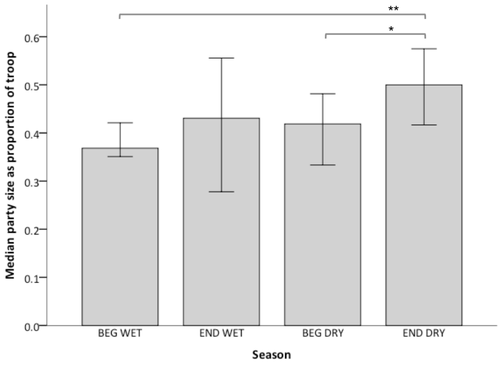


Figure 6.11: Results for seasonal comparison of Gamgam daily mean party size as a proportion of troop size. * indicates $p < 0.05$, ** indicates $p < 0.01$.

Season was found to affect absolute (χ^2 (3) = 8.54, p = 0.035) and relative party size (χ^2 (3) = 9.56, p = 0.022) in the Kwano troop. Comparisons between seasonal party sizes are given in Figure 6.12 & Figure 6.13. The seasonal differences in both absolute and relative party size were mainly driven by small parties in the end of the wet season, when 5.00 individuals (15% of troop) on average (*IQR* 3.00-6.50) were seen in a single party, significantly fewer than in the average party in the beginning of the wet (6.58; *IQR* 4.00-9.00; 21%) and the beginning of the dry season (5.67; *IQR* 3.50-9.33; 18%). Relative and absolute party size did not differ between any of the remaining seasons.

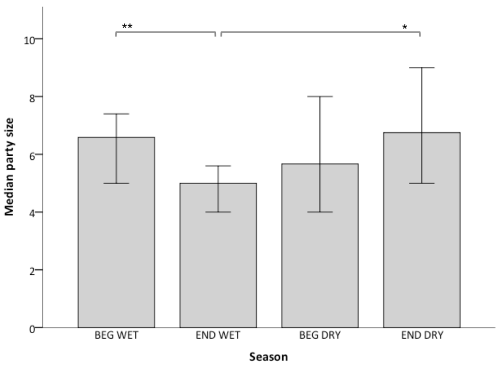


Figure 6.12: Results for seasonal comparison of Kwano daily mean party size. * indicates $p < 0.05$, ** indicates $p < 0.01$.

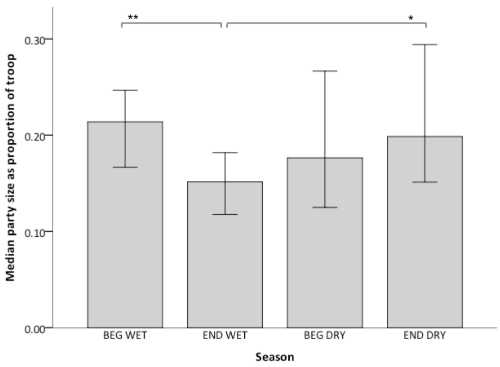


Figure 6.13: Results for seasonal comparison of Kwano daily mean party size as a proportion of troop size. * indicates $p < 0.05$, ** indicates $p < 0.01$.

Troop

Gamgam parties were significantly larger than Kwano parties (Independent t-test daily mean party size: $t = 4.24$, $df = 338$, $p < 0.001$). On average, Gamgam parties contained 42.50% of the troop (± 16.70), whereas Kwano parties contained 20.11% of the troop (± 11.15) and this difference was also significant (Independent t-test daily mean party size as proportion: $t = 13.42$, $df = 222$, $p < 0.001$).

As these results may be due to between-troop differences in habitat availability, comparisons were also made between troops within habitat types that the troops shared (*i.e.* gallery forest, lowland forest, Guinea savannah, burned Guinea savannah). Results are given in Table 6.8, Figure 6.14 and Figure 6.15. Gamgam parties were significantly larger than Kwano parties in all habitat types, apart from the lowland forest; parties contained a significantly larger proportion of the troop in Gamgam compared to Kwano in all habitat types that the troops shared.

Table 6.8: Results for between-troop comparisons within habitat types that the troops shared of a) daily mean party size; b) daily mean party size as a proportion of troop size. Bold values indicate a significant difference between troops.

a)

Habitat	Troop	*N*	Mean	SD	*t*	*df*	*p*
GF	Gamgam	165	**9.13**	**4.57**	**2.05**	**363.37**	**0.042**
	Kwano	201	**8.07**	**5.34**			
LF	Gamgam	20	6.20	3.89	0.37	100	0.713
	Kwano	82	5.87	3.57			
BGS	Gamgam	67	**8.19**	**3.55**	**2.09**	**103**	**0.039**
	Kwano	38	**6.68**	**3.58**			
GS	Gamgam	153	**7.37**	**3.78**	**3.40**	**290**	**0.001**
	Kwano	139	**5.94**	**3.42**			

b)

Habitat	Troop	*N*	Mean	SD	*t*	*df*	*p*
GF	Gamgam	165	**0.49**	**0.24**	**9.84**	**293.55**	**< 0.001**
	Kwano	201	**0.26**	**0.18**			
LF	Gamgam	20	**0.33**	**0.22**	**2.96**	**21.73**	**< 0.001**
	Kwano	82	**0.19**	**0.12**			
BGS	Gamgam	67	**0.43**	**0.18**	**6.95**	**10.32**	**< 0.001**
	Kwano	38	**0.22**	**0.12**			
GS	Gamgam	153	**0.40**	**0.21**	**10.94**	**239.66**	**< 0.001**
	Kwano	139	**0.19**	**0.11**			

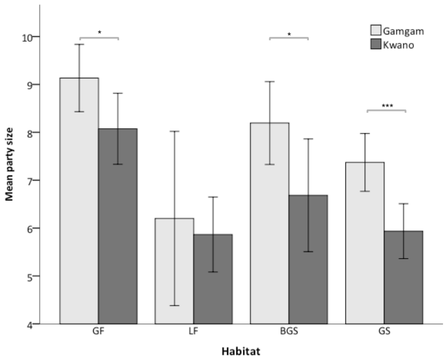


Figure 6.14: Comparison between troops of daily mean party size within habitat types which the troops shared. * indicates $p < 0.05$; *** indicates $p < 0.001$.

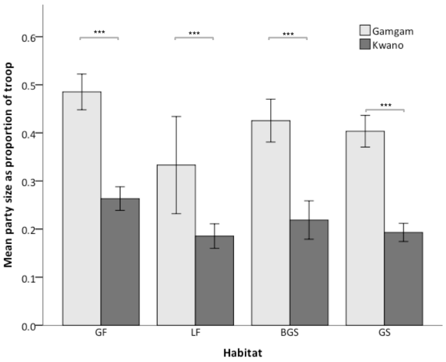


Figure 6.15: Comparison between troops of daily mean party size as a proportion of troop size within habitat types which the troops shared. *** indicates $p < 0.001$.

In sum, parties in the Gamgam troop were larger than in the Kwano troop across seasons, both in absolute terms, and relative to troop size. These between-troop differences were not due to differences in the availability of habitat types in the two home ranges.

6.3.3 What is the proximate mechanism for the formation of parties?

Three zero-truncated discrete frequency distributions were fitted to the party size frequency distribution for both troops to investigate which model for the formation and cohesion of parties receives most support. The frequency distributions of party sizes are given in Figure 6.16 and Figure 6.17, and Table 6.9 shows the estimated parameter values and the AIC for each model. For both troops the negative binomial was the best-fit model, while AICs of the Poisson and the exponential distributions are more than 10 units larger than the AIC of this best-fit model, which indicates that there is no support for the frequency distributions of the party sizes of either troop following those distributions (Burnham and Anderson 2002). The *G*-test for the goodness-of-fit (Sokal and Rohlf 1995) indicates that in both troops the observed distribution was not significantly different from the zero-truncated negative binomial (*G*-test of independence: Gamgam: $G = 99.75$, df = 252, $p > 0.05$; Kwano: $G = 116.60$, df = 315, $p > 0.05$), indicating that this model provided a good fit to the data.

Thus, in both troops there is evidence that individuals joined a party due to the attractiveness of larger groups, but were also more likely to leave a party when these were larger.

Table 6.9: Results for the fitting of the three zero-truncated discrete distributions to the party size data for the Gamgam and Kwano troops. Bold values indicate the model that best fits the data, as indicated by the lowest AIC.

		Mechanism underlying formation of party					
Troop	Distribution	Join	Leave	*df*	Estimated parameter values (SE)		AIC
Gamgam	**Negative binomial**	**Attraction to large party**	**Depart due to party size**	**2**	**2.29 (0.15)**	**1.23 (0.51)**	**123**
	Poisson	Random aggregation	Depart due to party size	1	2.30 (0.07)		141
	Exponential	Random aggregation	Random departure	1	0.09 (0.01)		2870
Kwano	**Negative binomial**	**Attraction to large party**	**Depart due to party size**	**2**	**2.43 (0.14)**	**1.15 (0.44)**	**148**
	Poisson	Random aggregation	Depart due to party size	1	2.44 (0.06)		179
	Exponential	Random aggregation	Random departure	1	0.10 (0.01)		3462

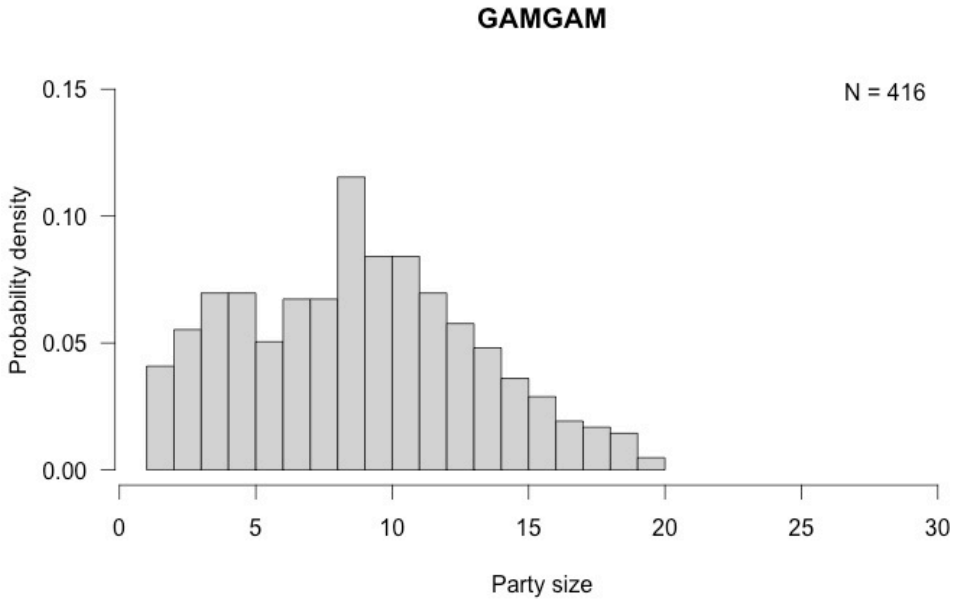


Figure 6.16: The observed probability density for the party sizes in the Gamgam troop.

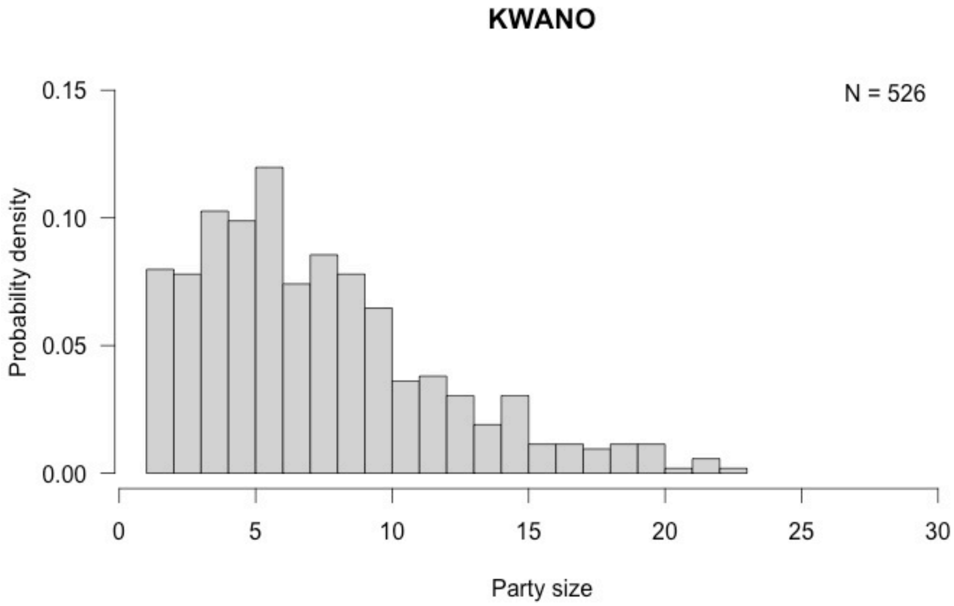


Figure 6.17: The observed probability density for the party sizes in the Kwano troop.

6.3.4 Does the rate of party composition change differ by season and by troop?

For the rate of party composition change it was not possible to examine the effect of habitat type, because this measurement was calculated over one hour, during which the party may have ranged in several habitat types.

Season

The rate at which Gamgam parties changed in composition was constant throughout the seasons, as neither the absolute rate of change, nor the rate of changes as a proportion of the maximum possible number of changes differed significantly by season (absolute rate: $\chi^2(3) = 3.46$, $p = 0.329$ - Figure 6.18; relative rate: : $\chi^2(3) = 3.57$, $p = 0.313$ - Figure 6.19). The rate of party composition change was most variable in the end of the wet season.

The rate at which Kwano parties changed in composition did differ by season, both when the absolute rate of change was considered (χ^2 (3) = 16.01, $p < 0.001$ - Figure 6.20) and when troop size was taken into account (χ^2 (3) = 17.23, $p < 0.001$ - Figure 6.21). Kwano parties changed at an average rate of 0.14 (*IQR* 0.09-0.17) individuals per minute during the end of the dry season, and this was significantly more than rates in any of the other seasons (BEG WET: median = 0.08, *IQR* = 0.06-0.10; END WET: median = 0.06, *IQR* = 0.04-0.09; BEG DRY: median = 0.06, *IQR* = 0.04-0.10). Rates did not differ significantly between the beginning of the wet, the end of the wet and the beginning of the dry seasons.

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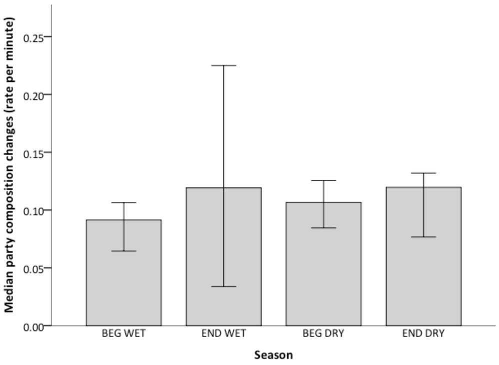


Figure 6.18: Comparison of the daily mean rate per minute of party composition changes across seasons in the Gamgam troop.

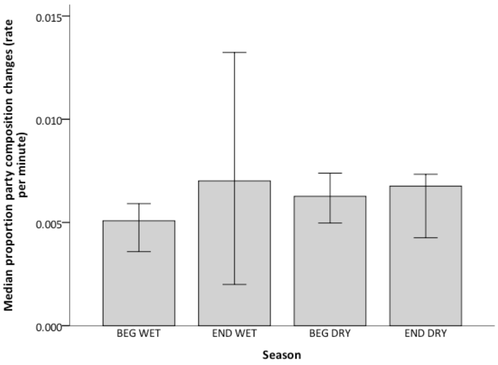


Figure 6.19: Comparison of the daily mean rate per minute of party composition changes as a proportion of the maximum possible number of changes across seasons in the Gamgam troop.

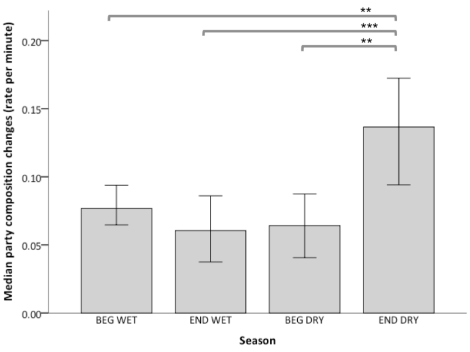


Figure 6.20: Comparison of the daily mean rate per minute of party composition changes in the Kwano troop across seasons. ** indicates < 0.01; *** indicates $p < 0.001$.

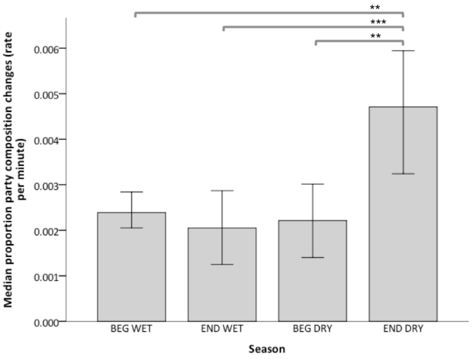


Figure 6.21: Comparison of the daily mean rate per minute of party composition changes as a proportion of the maximum possible number of changes in the Kwano troop across seasons. ** indicates < 0.01; *** indicates $p < 0.001$.

Troop

Despite this difference in the effect of season on the rate of party composition change, overall, troops did not differ significantly in the rate of party composition change; in the Gamgam troop, parties on average changed at a rate of 0.10 individuals per minute (± 0.05), whereas in the Kwano troop this was a rate of 0.11 individuals per minute (± 0.15) (Gamgam – Kwano: *t*(87.7) = -0.412, *p* = 0.681 - Figure 6.22). However, when troop size was controlled for, the Gamgam troop was found to have a significantly higher rate of party composition changes (mean: 0.006 ± 0.003) than did the Kwano troop (mean: 0.004 ± 0.005) (Gamgam – Kwano: *t*(108.7) = 3.037, *p* = 0.003 - Figure 6.23). Thus, relatively speaking Gamgam parties changed more rapidly in their composition than did Kwano parties.

Overall, the rate at which the composition of parties changed seems relatively stable, both over seasons, and between troops. Only when troop size was taken into account, was a difference found in the rate of change.

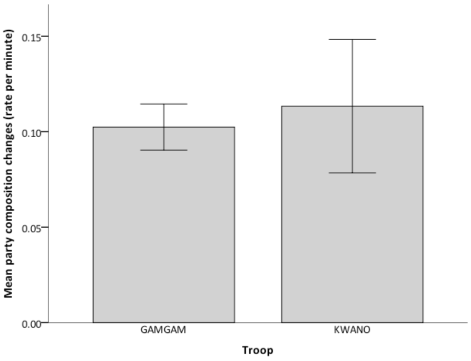


Figure 6.22: Comparison of the daily mean number of party composition changes per minute between troops.

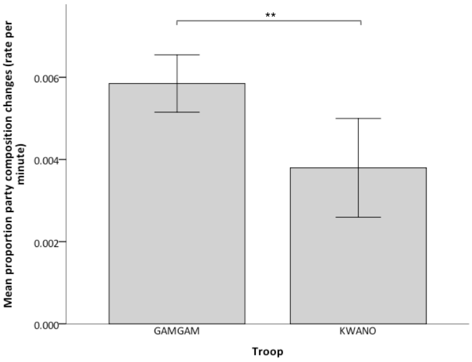


Figure 6.23: Comparison of the daily mean number of party composition changes per minute as a proportion of the maximum possible number of changes between troops. ** indicates *p* < 0.01.

6.3.5 How do spatial cohesion, party size, and party composition change relate to each other?

Correlations and partial correlations were run between each of the three components of fission-fusion dynamics to determine the relationships between these measurements. For the Gamgam troop party size co-varied positively with party composition change and negatively with spatial cohesion, but the latter two measurements were not correlated (Table 6.10). For the Kwano troop party size and party composition change also co-varied; while spatial cohesion did not co-vary with either party size or party composition.

Table 6.10: Results of correlations between the three components of fission-fusion dynamics. Correlations were run with daily mean values, with days on which all three measurements were known. Party size was defined as the proportion of the troop that was seen in a single party; spatial cohesion as the inter-individual distance between focal animals; the rate of change in party composition as the proportion of the maximum possible number of changes in party composition. Kendall's correlation coefficients (τ) are given along with *p*-values. Bold values indicate a significant association.

	GAMGAM (*N* = 18)		KWANO (*N*= 35)	
Correlation	*τ*	*p*	*τ*	*p*
Party size - party composition	**0.296**	**0.002**	**0.519**	**< 0.001**
Party size - spatial cohesion	**-0.346**	**0.045**	-0.166	0.160
Party composition - spatial cohesion	-0.137	0.426	-0.109	0.356

In both troops, the correlation between party size and party composition remained significant when spatial cohesion was controlled for (Table 6.11). Thus, when a larger proportion of the troop was together in a single party, the composition of the party was also more variable. This result is not an artefact of the greater number of individuals in larger parties, as changes in party composition were measured over all individuals in the troop, whether they were present or absent in the party. These results suggest that larger parties were less stable than smaller parties. The association between party size and spatial cohesion in the Gamgam troop was no longer significant when the rate of party composition change was controlled for.

Thus, these results show that in both troops large parties were more unstable, but that spatial cohesion varied independently from both party size and the rate of change in party composition.

Table 6.11: Results of partial correlations between the three components of fission-fusion dynamics. Correlations were run with daily mean values, with days on which all three measurements were known. Party size was defined as the proportion of the troop that was seen in a single party; spatial cohesion as the inter-individual distance between focal animals; the rate of change in party composition as the proportion of the maximum possible number of changes in party composition. Kendall's correlation coefficients (τ) are given along with *p*-values. Bold values indicate a significant association.

	GAMGAM (*N* = 18)		KWANO (*N*= 35)	
Correlation	*τ*	*p*	*τ*	*p*
Party size - party composition controlling for spatial cohesion	**0.585**	**0.014**	**0.617**	**< 0.001**
Party size - spatial cohesion controlling for party composition	-0.465	0.060	-0.058	0.746
Party composition - spatial cohesion controlling for party size	0.105	0.688	-0.209	0.236

6.3.6 Are variations in social interactions related to variations in spatial cohesion, party size, and party composition change?

Troops had generally similar rates of affiliative behaviour, and affiliative and agonistic vocalisations (Table 6.12). Gamgam individuals were aggressive at higher rates than Kwano individuals, whereas in Kwano contact calls were given significantly more frequently. To see if troops adjusted social interactions with grouping patterns, daily mean rates of affiliative and agonistic behaviours and affiliative, agonistic, and contact vocalisations were correlated with daily mean values for spatial cohesion, party size, and party composition change (Table 6.13) to investigate how social behaviours are associated with grouping patterns.

Table 6.12: Between-troop differences in the daily mean rates (rate per minute) of social interactions. Bold values indicate a significant difference.

	GAMGAM (*N* = 68)		KWANO (*N* = 91)				
Daily mean (rate per minute)	Mean	SD	Mean	SD	*t*	*df*	*p*
Affiliative behaviour	0.052	0.051	0.043	0.053	1.028	157	0.305
Agonistic behaviour	0.008	0.012	0.004	0.006	2.138	92.85	**0.035**
Affiliative vocalisation	0.167	0.140	0.127	0.202	1.421	157	0.157
Agonistic vocalisation	0.005	0.016	0.010	0.019	-1.667	157	0.097
Contact vocalisation	0.004	0.015	0.011	0.026	-2.091	147.49	**0.038**

Party size was not correlated with the rate of any of the social interactions considered in either troop. In the Kwano troop, when the composition of parties changed more rapidly, a higher rate of affiliative behaviours and vocalisations was observed. This was not seen in the Gamgam troop. Instead, when Gamgam parties changed more rapidly, the rate of contact calls was lower, and this was close to significance. Similarly, the association between spatial cohesion and affiliative behaviours was negative, and close to significance.

Thus, the association between grouping patterns and social interactions seems to occur on a broad scale, with differences occurring between troops in aggression and contact calls. Apart from the rate of affiliative behaviours and vocalisations changing with the stability of Kwano parties, troops did not seem to adjust social interactions to grouping patterns.

Table 6.13: Results for the correlations between the daily mean party size, party composition change and spatial cohesion on one hand, and the daily mean rate per minute of social interactions for the Gamgam and Kwano troops. Kendall's τ is given with the *p*-value in brackets. Bold values indicate a significant correlation, values in italics indicate a correlations with a trend towards significance.

		Behaviours		Vocalisations		
Troop	Fission-fusion component	Affiliative	Agonistic	Affiliative	Agonistic	Contact
GAMGAM	Party size (*N* = 64)	0.132 (0.124)	0.061 (0.503)	0.058 (0.498)	-0.035 (0.718)	-0.004 (0.970)
	Party composition changes (*N* = 54)	0.063 (0.506)	-0.082 (0.405)	0.012 (0.899)	-0.149 (0.159)	*-0.203* *(0.057)*
	Spatial cohesion (*N* = 18)	*-0.333* *(0.053)*	-0.264 (0.129)	-0.059 (0.733)	0.016 (0.931)	0.015 (0.935)
KWANO	Party size (*N* = 76)	0.031 (0.693)	-0.053 (0.525)	-0.074 (0.348)	-0.092 (0.265)	0.106 (0.202)
	Party composition changes (*N* = 73)	**0.257** **(0.001)**	0.066 (0.440)	**0.164** **(0.041)**	-0.025 (0.767)	-0.110 (0.195)
	Spatial cohesion (*N* = 36)	-0.148 (0.205)	-0.125 (0.305)	-0.119 (0.307)	-0.157 (0.190)	0.024 (0.845)

6.3.7 Does the degree of fission-fusion dynamics differ by season and troop?

The coefficients of variation (CV) for party size, party composition, and spatial cohesion were compared across seasons and troops to examine if the degree of fission-fusion dynamics was affected by season or troop.

Season

Seasonal fission-fusion dynamics of the Gamgam troop are given in Figure 6.24, and for the Kwano troop in Figure 6.25 .

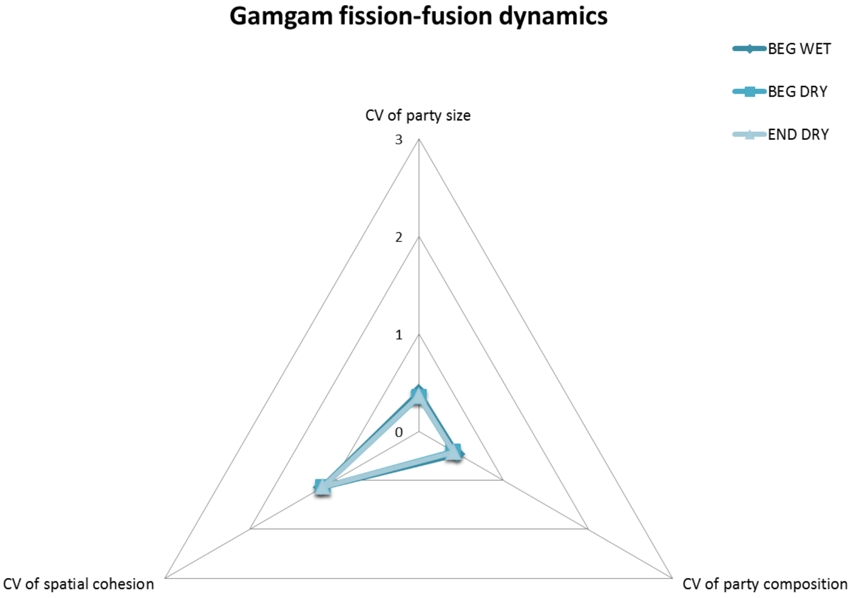


Figure 6.24: Fission-fusion dynamics of the Gamgam troop during the beginning of the wet, beginning of the dry, and the end of the dry seasons as measured by the CV in party size, spatial cohesion and party composition change.

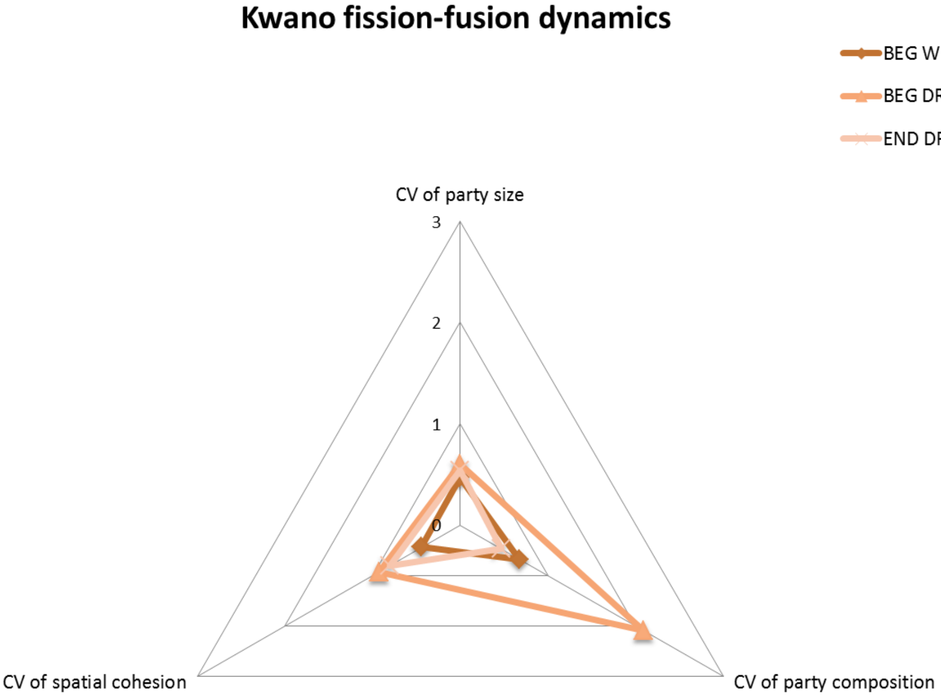


Figure 6.25: Fission-fusion dynamics of the Kwano troop during the beginning of the wet, beginning of the dry, and the end of the dry seasons as measured by the CV in party size, spatial cohesion and party composition change.

No significant seasonal effects were found on the degree of fission-fusion dynamics in the Gamgam troop, while the degree of fission-fusion dynamics was more variable across seasons in the Kwano troop, leading to an overall higher Fission-Fusion Dynamics Index (FFDI). The Kwano troop had the lowest degree of fission-fusion dynamics in the beginning of the wet season. The fission-fusion dynamics in the end of the dry season mainly differs from that of the beginning of the wet season in terms of the amount of variation in spatial cohesion. The troop showed the highest degree of fission-fusion dynamics in the beginning of the dry season, when the rate of party composition change was much more variable.

Troop

Between-troop differences in fission-fusion dynamics are given in Figure 6.26 and Table 6.14. The greater variability in the seasonal degree of fission-fusion dynamics gives Kwano a greater overall degree of fission-fusion dynamics; comparison of the CVs indicate that the Kwano troop showed greater variation in party size, party composition, and spatial cohesion than did the Gamgam troop and therefore, overall had a higher degree of fission-fusion dynamics.

6.3.8 Does party spread differ by habitat, by season, and by troop?

Rather than adjusting spatial cohesion at the level of the troop, the space over which parties are spread may instead be adjusted. The effect of habitat type, season, and troop on the volume (m3) over which parties are spread, and the number of individuals that were found in a 10m radius are examined here.

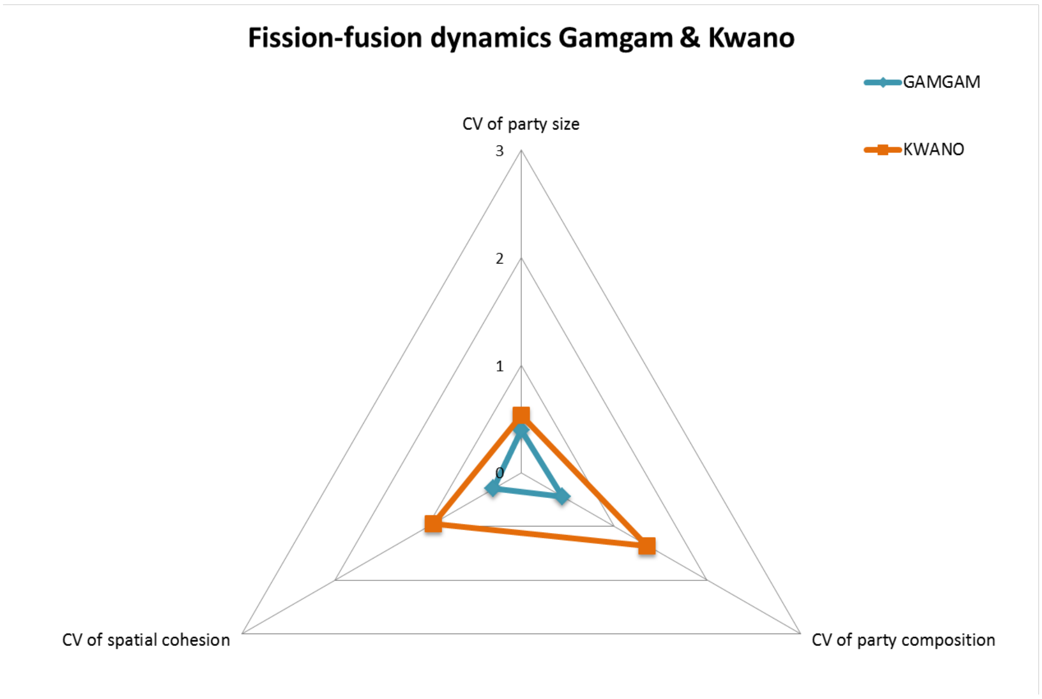


Figure 6.26: Fission-fusion dynamics of the Gamgam and Kwano troops over the entire study period as measured by the CV in party size, spatial cohesion and party composition change.

Table 6.14: The temporal variation in party size, party composition, and spatial cohesion as measured by the CV, along with the composite fission-fusion dynamics index (FFDI).

	Temporal variation			
TROOP	**Party size**	**Party composition**	**Spatial cohesion**	**FFDI**
GAMGAM	0.393	0.441	0.296	0.38
KWANO	0.537	1.355	0.943	0.95

Habitat

Habitat type significantly affected party spread and the space per individual in the party (3-dimensional space: χ^2 (4) = 59.06, p < 0.001; individual 3-dimensional space: χ^2 (4) = 59.20, p < 0.001). Results for *post hoc* Mann-

Whitney tests are given in Appendix D, Table D.3 – Table D.6. Party spread was highest in burned Guinea savannah, with parties spreading out, on average, over 14055 m^3 (IQR = 4042-41287; Figure 6.27), and each individual having on average 1893 m^3 (IQR = 558-3978; Figure 6.28). Party spread and individual space were greater in the gallery forest and Guinea savannah compared to both the lowland forest and palm forest. The availability of high trees seemed to have little influence on party spread, as higher trees were present in the lowland forest than in the Guinea savannah, and yet party spread was greater in the latter. Additionally, trees were of similar height in the burned and the not-burned Guinea savannah, and yet party spread was significantly greater in the burned Guinea savannah.

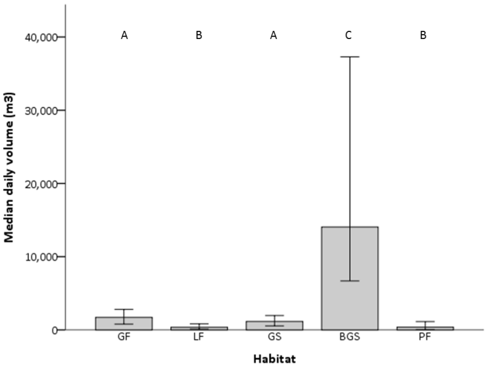


Figure 6.27: Comparisons of habitat-specific spatial cohesion measured by the volume (m^3) over which a party was spread. Volume was not significantly different between habitat types with the same letter. Different letters indicate a significant difference.

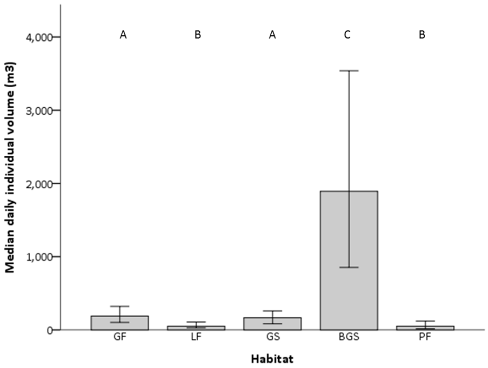


Figure 6.28: Comparisons of habitat-specific spatial cohesion measured by the volume (m^3) over which a party was spread, taking into account the size of a party. Individual volume was not significantly different between habitat types with the same letter. Different letters indicate a significant difference.

Both the number and the proportion of the party found in the centre 10m radius of the party were significantly affected by habitat type (number of individuals within 10m radius: χ^2 (4) = 30.57, $p < 0.001$; proportion of party within 10m radius: χ^2 (4) = 45.15, $p < 0.001$). This difference was largely due to low spatial cohesion in the burned Guinea savannah; the smallest number of individuals was found in the centre of the party in the burned Guinea savannah habitat (median = 2.00; *IQR* = 1.05-3.00; Figure 6.29). The number of individuals found in the central 10m of the party was also significantly higher in the gallery forest compared to the lowland and palm forests. Party spread did not differ across the remaining habitats. Similarly, when party size was taken into account, spatial cohesion was significantly lower in the burned Guinea savannah (median = 0.31; *IQR* = 0.16-0.45) compared to all other habitat types (Figure 6.30).

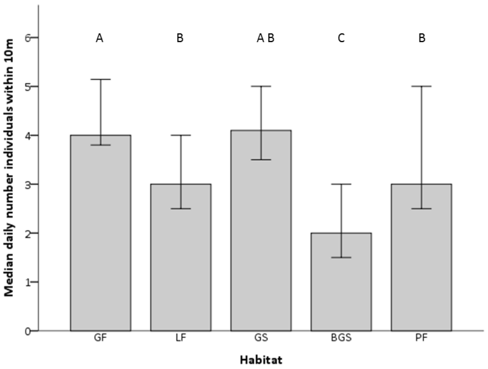


Figure 6.29: Comparisons of habitat-specific spatial cohesion measured by the number of individuals that were found within a 10m radius of the centre of a party. The number of individuals was not significantly different between habitat types with the same letter. Different letters indicate a significant difference.

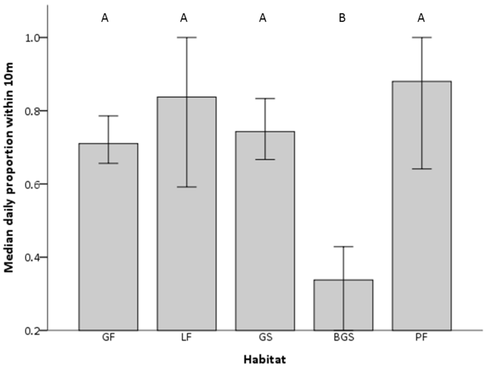


Figure 6.30: Comparisons of habitat-specific spatial cohesion measured by the proportion of a party that was found within a 10m radius of the centre of a party. The proportion was not significantly different between habitat types with the same letter. Different letters indicate a significant difference.

Season

In both troops, the absolute spread of parties and the 3-dimensional space per individual were significantly affected by season (Gamgam: 3-dimensional space: χ^2 (3) = 28.67, $p < 0.001$; individual 3-dimensional space: χ^2 (3) = 27.77, $p < 0.001$; Kwano: 3-dimensional space: χ^2 (3) = 29.73, $p < 0.001$; individual 3-dimensional space: χ^2 (3) = 26.19, $p < 0.001$). *Post hoc* Mann-Whitney tests showed Gamgam parties were most spread out during the end of the dry season (median = 9046m^3, IQR = 1776-24313 m^3 - Figure 6.31), followed by the beginning of the wet season (median = 5363 m^3, IQR = 1723-12564 m^3), and the beginning of the dry season (median = 1490m^3, IQR = 523-4019 m^3), and were most cohesive during the end of the wet season (median = 524 m^3, IQR = 114 - 3495 m^3). However, when party size was taken into account the spread of Gamgam parties was largest in the beginning of the wet and the end of the dry season (Figure 6.32), and parties were most cohesive during the end of the wet and the beginning of the dry seasons. In Kwano, party spread was highest during the end of the dry season, as indicated both by the area over which parties were spread out (Figure 6.33) and the 3-dimensional space per individual (Figure 6.34). Both median party area and median individual area were similar across the remaining seasons.

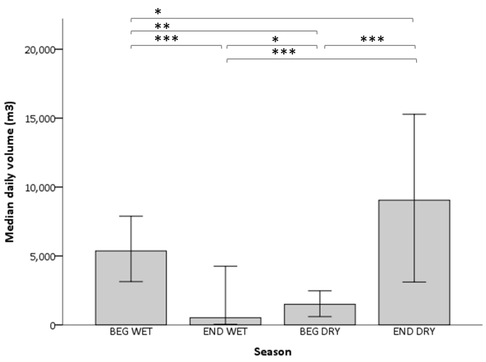


Figure 6.31: Comparison of Gamgam party spread across seasons. * indicates $p < 0.05$; ** indicates $p < 0.01$; *** indicates $p < 0.001$.

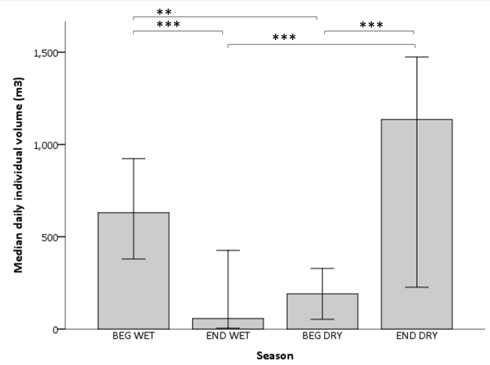


Figure 6.32: Comparison of Gamgam party spread across seasons, taking into account party size. ** indicates $p < 0.01$; *** indicates $p < 0.001$.

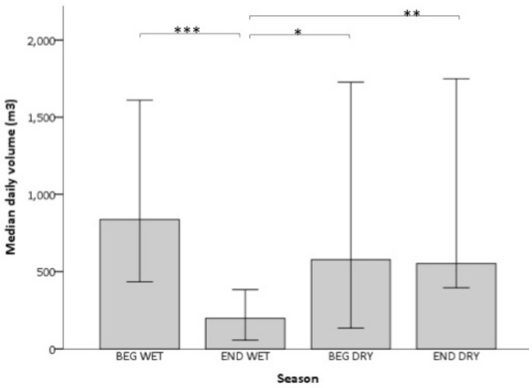


Figure 6.33: Comparisons of Kwano party spread across seasons. * indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$.

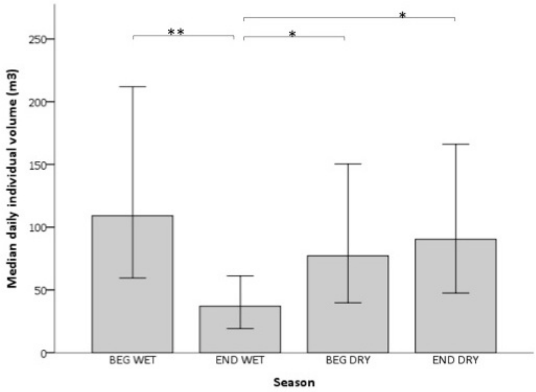


Figure 6.34: Comparison of Kwano party spread across seasons, taking into account party size. * indicates $p < 0.05$, ** indicates $p < 0.01$.

Season also significantly affected the number and the proportion of individuals in the party that were found within a 10m radius of the centre of the party in both troops (Gamgam: number within 10m radius: χ^2 (3) = 14.94, $p = 0.002$; proportion within 10m radius: χ^2 (3) = 41.60, $p < 0.001$; Kwano: number within 10m radius: χ^2 (3) = 14.56, $p = 0.002$; proportion within 10m radius: χ^2 (3) =

22.41, $p < 0.001$). *Post hoc* Mann-Whitney tests showed that, for the Gamgam troop, the seasonal difference in the number of individuals within a 10m radius from the centre of the party was driven by a lower density of party members in the beginning of the wet and the end of the dry season, and a higher density during the end of the wet and the beginning of the dry season (Figure 6.35). When seasonal differences in party size was taken into account (Figure 6.36) further distinctions could be made between the seasonal spatial cohesion; parties were least cohesive in the end of the dry season (median = 0.40, IQR = 0.20-0.50), followed by the beginning of the wet season (median = 0.49, IQR = 0.29-0.73), while being most cohesive in the end of the wet (median = 0.88, IQR = 0.57-0.88) and the beginning of the dry season (median =0.78, IQR = 0.48-0.95). These results thus largely confirm the seasonal differences in party spread measured by 3-dimensional space. For the Kwano troop, *post hoc* Mann-Whitney tests indicate that during the beginning of the wet season, fewest individuals were found within a 10m radius from the centre, but that this was only significantly different from the number in the beginning of the dry season (Figure 6.37). During the remaining seasons the number of individuals was similar. However, when party size was taken into account, parties were more cohesive during the end of the wet season compared to both the beginning of the wet season and the end of the dry season (Figure 6.38). The proportion of the party that was found within a 10 m radius was also significantly lower in the beginning of the wet season compared to the beginning of the dry season. These results are similar to the results found by comparing the spread of the parties, although the latter analysis allowed for further distinction between seasonal spatial cohesion.

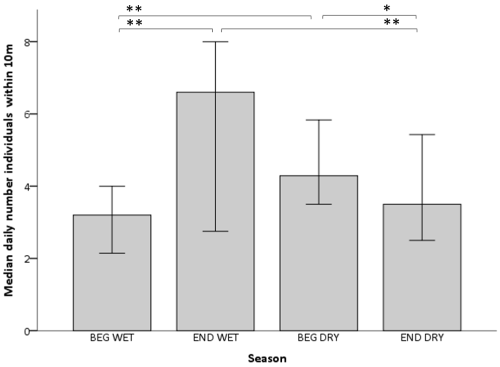


Figure 6.35: Comparison across seasons of Gamgam party spread as measured by the number of individuals that were found within a 10 m radius from the centre of the party. * indicates $p < 0.05$; ** indicates $p < 0.01$.

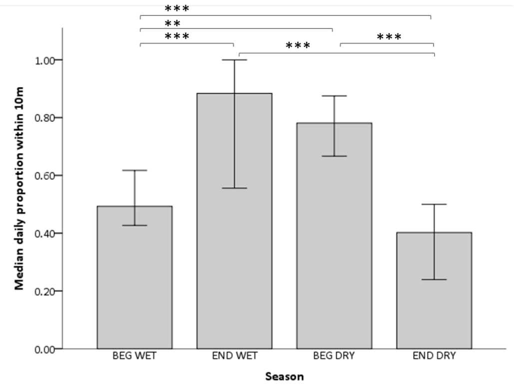


Figure 6.36: Comparison across seasons of Gamgam party spread as measured by the proportion of the party that was found within a 10 m radius from the centre of the party. ** indicates $p < 0.01$; *** indicates $p < 0.001$

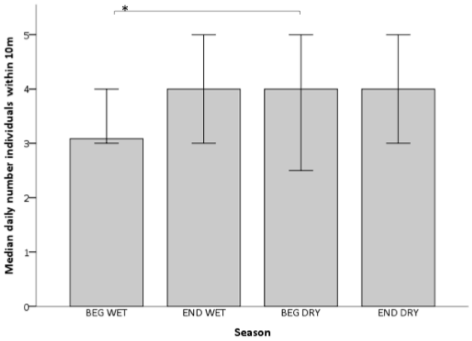


Figure 6.37: Comparison across seasons of Kwano party spread as measured by the number of individuals that were found within a 10 m radius from the centre of the party. * indicates $p < 0.05$.

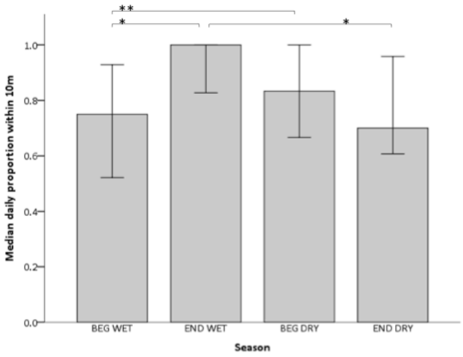


Figure 6.38: Comparison across seasons of Kwano party spread as measured by the proportion of the party that was found within a 10 m radius from the centre of the party. * indicates $p < 0.05$; ** indicates $p < 0.01$.

Troop

Parties in the Gamgam troop were spread over a significantly larger 3-dimensional space (11126 m^3 ± 27918 m^3) than were parties in the Kwano troop (4570 m^3 ± 13368 m^3) were (Independent t-test: $t = 2.57$, $df = 182$, $p =$

0.011). The spread of the Gamgam parties was also larger when the number of individuals in parties was taken into account; the 3-dimensional space per individual in parties was significantly larger for the Gamgam troop (1177 m^3 ± 2486 m^3) compared to the Kwano troop (493 m^3 ± 1492 m^3) (Independent t-test: $t = 2.90$, $df = 206$, $p = 0.004$).

As between-troop differences may be due to between-troop differences in habitat availability, comparisons were also made between the spread of parties in habitats that the troops shared. Again, Gamgam parties were found to be spread over a greater 3-dimensional space (Independent t-test: $t = 2.47$, $df = 289$, $p = 0.014$ - Figure 6.39), and individuals had a larger individual space (Independent t-test: $t = 2.65$, $df = 264.97$, $p = 0.009$ - Figure 6.40) than in Kwano parties, indicating that between-troop differences in party spread were not solely due to habitat differences.

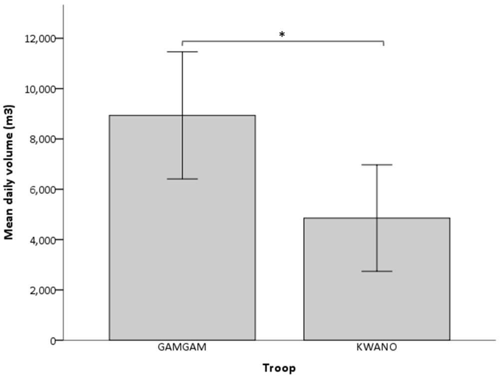


Figure 6.39: Comparison between troops of spatial cohesion as measured by the area over which parties were spread out, including only spatial cohesion measurements in habitat types which the troops shared. * indicates $p < 0.05$.

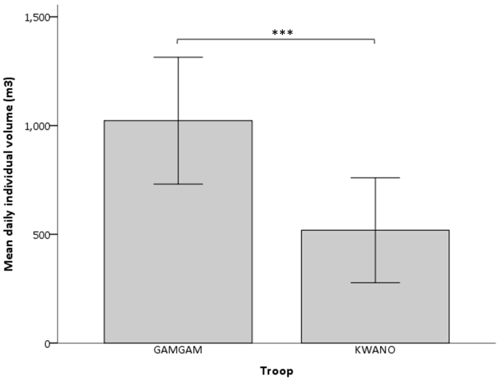


Figure 6.40: Comparison between troops of spatial cohesion as measured by the area over which parties were spread out, taking into account party size and including only spatial cohesion measurements in habitat types which the troops shared. *** indicates $p < 0.001$.

In both troops a similar *number* of individuals (Gamgam 4.02 ± 2.81; Kwano 4.15±2.70) was found within a 10m radius from the centre of the party (Independent t-test: t = -0.45, df = 338, p = 0.657). However, a significantly smaller *proportion* of Gamgam parties (0.54±0.31) was found within a 10m radius from the centre of the party compared to Kwano parties (0.72±0.31) (Independent t-test: t = -5.05, df = 338, p < 0.001). These results held when spatial cohesion was only compared between troops in habitat types that the troops shared (Independent t-test: number of individuals within 10m: t = -0.36, df = 282, p = 0.720; proportion within 10m: t = -4.28, df = 282, p < 0.001 - Figure 6.41).

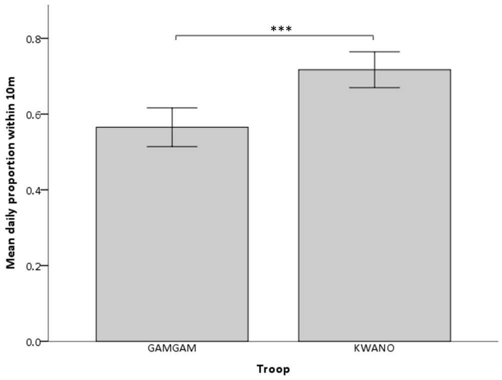


Figure 6.41: Comparison between troops in spatial party cohesion as measured by the proportion of the party that was found within a 10m radius from the centre of the party including only spatial cohesion measurements in habitat types which the troops shared. *** indicates p < 0.001.

In sum, the spread of individuals in parties differed by habitat type, by season, and by troop. Troops adjusted the spread of parties to the habitat; troops formed spatially cohesive parties in lowland and palm forest, whereas in burned Guinea savannah parties spread out over a larger 3-dimensional space. Spatial cohesion of parties in the gallery forest and Guinea savannah were in between these two extremes. Seasonal variation in spatial party cohesion showed a similar pattern of variation in the troops, with parties being least spatially cohesive during the end of the dry season. Overall, Gamgam parties were more spread out than Kwano parties were.

6.3.9 At what distance are individuals considered to be in different parties?

The fit of a single model of best fit was compared to the fit of a model with a mixture of two component distributions to establish whether a two-process model was a better description of the data than a single process model. When a mixture model provides a better fit to the frequency distribution of inter-individual distances, it indicates that a troop splits into parties, and the distance at which the mixture distributions cross is the distance at which individuals is considered to be in different parties. The distributions of the inter-individual distances and the best-fit distribution are given in Figure 6.42 & Figure 6.43. The AICs used for the model selection for single-process distributions are given in Table 6.15. The differences between several of the single-process models were relatively small, and it has been suggested that models that have an AIC up to 7 units larger than the best-fit model may have some support as well (Burnham *et al.* 2011). However, because in this analysis the improvement by a mixture model over a single model is what is of interest, rather than which *type* of distribution fit the data best, the model with the lowest AIC was used.

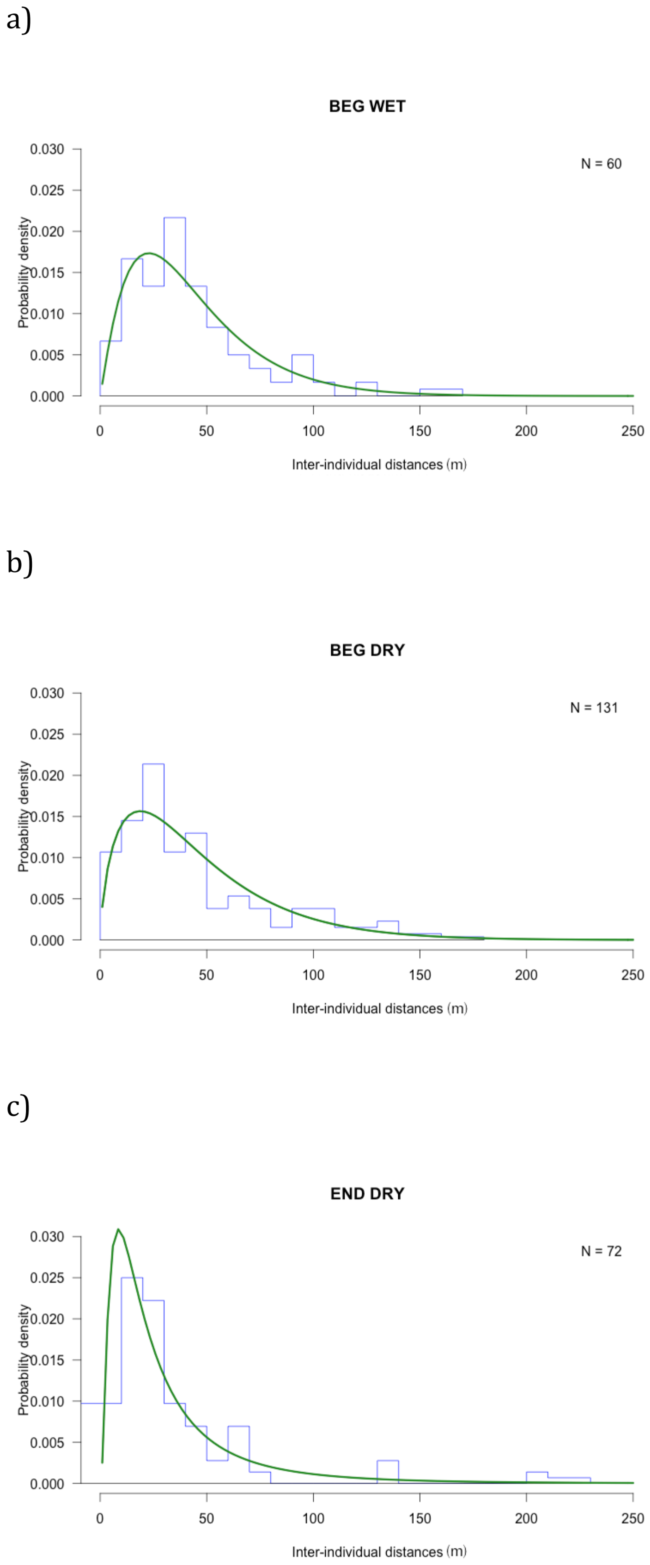


Figure 6.42: Distributions of inter-individual distances (blue outline) of the Gamgam troop with the best-fit distribution (red line). For the Gamgam troop a single gamma distribution best described the data in the beginning of the wet season (a) and in the beginning of the dry season (b), whereas data in the end of the dry season was best described by a single log-normal distribution (c).

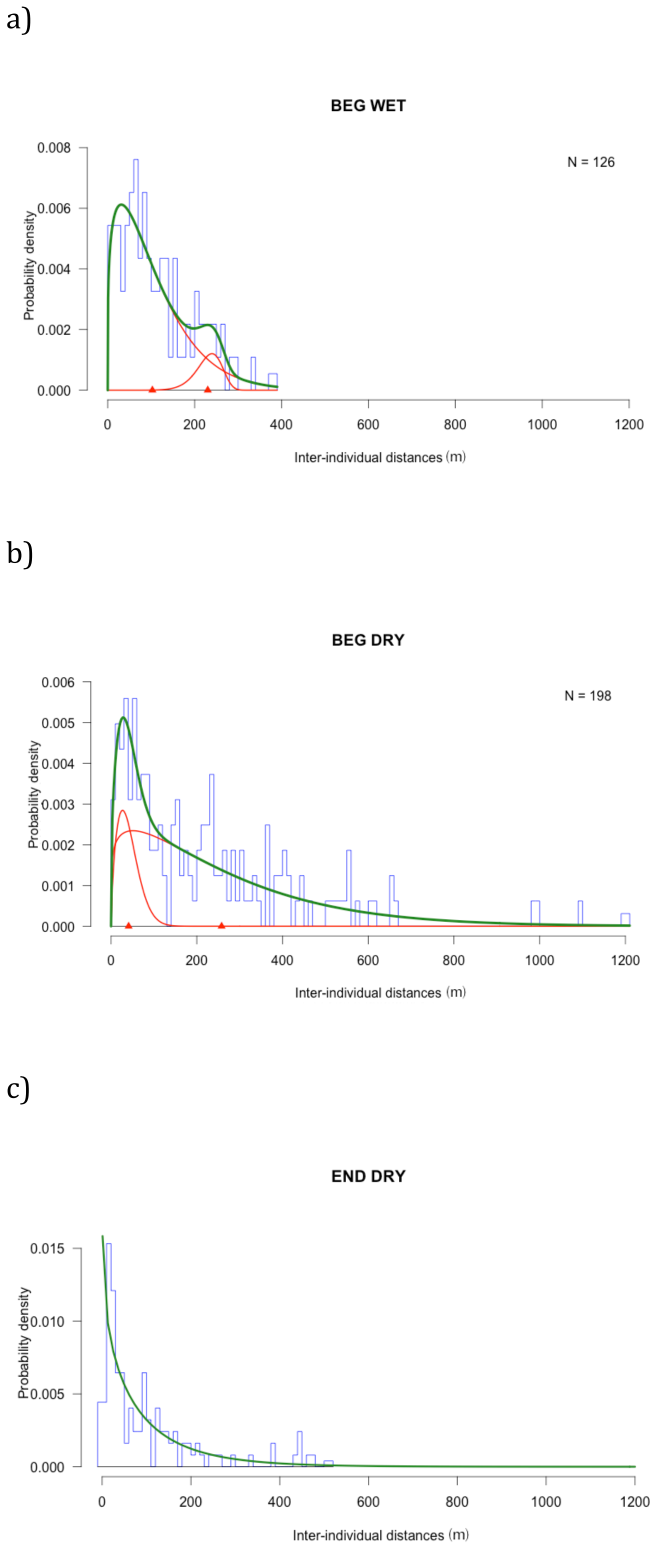


Figure 6.43: Distributions of inter-individual distances (blue outline) of the Kwano troop with the best-fit distribution. In the beginning of the wet season (a) and the beginning of the dry season (b) a two-process model was fitted (green line) and its two components of distribution curves (red lines). Means for each component distribution are indicated by triangles. In the end of the dry season (c) a single Weibull distribution (red line) best described the data.

Table 6.15: Model selection for single-process distributions. The Akaike Information Criterion (AIC) is given for each model fitted to the observed data per season. Bold values indicate the best-fit model.

GAMGAM			KWANO		
Season	Distribution	AIC	Season	Distribution	AIC
BEG DRY	Normal	1318.18	BEG DRY	Normal	2753.08
	Log normal	1256.07		Log normal	2535.52
	Weibull	1254.68		**Weibull**	**2533.24**
	Gamma	**1252.06**		Gamma	2534.58
	Exponential	1268.45		Exponential	2533.98
BEG WET	Normal	581.36	BEG WET	Normal	1465.76
	Log normal	561.95		Log normal	1436.98
	Weibull	560.16		**Weibull**	**1415.59**
	Gamma	**558.80**		Gamma	1416.59
	Exponential	573.11		Exponential	1425.52
END DRY	Normal	736.33	END DRY	Normal	1540.44
	Log normal	**642.70**		Log normal	1408.63
	Weibull	652.97		**Weibull**	**1396.43**
	Gamma	651.22		Gamma	1397.49
	Exponential	651.36		Exponential	1398.38

For both troops the frequency distributions of the inter-individual distances showed a positive skew in all seasons, indicating that individuals were frequently in close proximity of their troop members. For the Gamgam troop, the gamma distribution showed the best fit to the data in the beginning of the wet and the beginning of the dry seasons, whereas a log-normal distribution showed the best fit in the end of the dry season.

In the beginning of the wet and the beginning of the dry season the observed frequency distributions of the Gamgam troop did not differ significantly from a gamma distribution (Anderson-Darling test: BEG WET: $D = 0.19$, $p > 0.05$; BEG

DRY: $D = 0.60$, $p > 0.05$). Similarly, in the end of the dry season the observed distribution did not differ significantly from a log-normal distribution (Anderson-Darling test: END DRY: $D = 0.34$, $p > 0.05$). Inter-individual distances in the Gamgam troop are thus adequately described by a single distribution model, suggesting that the Gamgam troop did not split into spatially distinct parties.

For the Kwano troop the Weibull distribution showed the best fit to the data in all three seasons. In the end of the dry season the observed distribution did not differ significantly from a Weibull distribution (Anderson-Darling test: $D = 0.68$, $p > 0.05$); however, in both the beginning of the wet and the beginning of the dry season, the observed distributions deviated significantly from the Weibull distribution (Anderson-Darling test: BEG WET: $D = 0.36$, $p < 0.05$; BEG DRY: $D = 1.02$, $p < 0.05$). These results suggest that subgrouping did not occur during the end of the dry season, but may have occurred during the beginning of the wet and dry season. During the beginning of the dry season in particular spatial cohesion was low at times with individuals being over a kilometre apart (Figure 6.43b). Thus, a mixture of two Weibull distributions was fitted to the distance distributions for the beginning of the wet and the beginning of the dry season. In both seasons, the two-process model provided a better fit to the data than the single process model did (Table 6.16). Based on this mixture model, the distance at which individuals could be considered to be in different parties was 184 m in the beginning of the wet season, and 62 m in the beginning of the dry season.

Table 6.16: Comparisons of fit of single- and two-process models to the distribution of inter-individual distances of Kwano individuals in the beginning of the wet and the beginning of the dry season. Bold values indicate the model that provided a better fit to the data.

	AIC	
Season	Single process model	Two-process model
BEG WET	1416	**83**
BEG DRY	2533	**155**

A summary of all results described in this chapter is given in Table 6.17.

Table 6.17: Summary of the questions addressed in this chapter and the result of the analyses.

Question	Result
1a. Does spatial cohesion differ by season and by troop?	Season did not significantly affect spatial cohesion in either troop. The Gamgam troop was more spatially cohesive than the Kwano troop.
2a. Does party size differ by habitat, by season, and by troop?	The largest parties were found in the gallery forest, burned Guinea savannah and Guinea savannah. The smallest parties were found in the lowland and palm forest. Season had some affect on the party size of both troops; in Gamgam the size of parties was similar in the beginning of the wet, the end of the wet, and the beginning of the dry season, but parties were significantly larger in the end of the dry season. In Kwano, parties were similar in the beginning of the wet, beginning of the dry, and the end of the dry season, but were significantly smaller at the end of the wet season. Overall, Gamgam parties (absolute & relative) were larger than Kwano parties.
2b. What is the proximate mechanism for the formation of parties?	In both troops a zero-truncated negative binomial provided the best-fit to the frequency distribution of party sizes, indicating that individuals are attracted to larger groups, but are also more likely to leave larger groups.
3a. Does the rate of party composition change differ by season and by troop?	The rate of party composition change was constant in the Gamgam troop. In Kwano, the rate was similar across the beginning of the wet, end of the wet, and beginning of the dry seasons, but was significantly higher in the end of the dry season. The troops did not differ when the absolute rates were considered. However, when the rate of party composition changes was considered as a proportion of the maximum possible number of changes, the rate was higher in the Gamgam troop than in the Kwano troop.
4. How do spatial cohesion, party size, and party composition change relate to each other?	Larger parties change more rapidly in composition. Spatial cohesion varies independently from party size and party composition change.

Question (continued)	Result
5. Are variations in social interactions related to variations in spatial cohesion, party size, and party composition change?	Association between social interactions and grouping patterns may occur on a broad scale, with the Gamgam troop using more aggression and Kwano using more contact calls. In the Kwano troop the rate of affiliative behaviours and vocalisations increased when the composition of parties changed more rapidly. No other correlations were found between social interactions and grouping patterns.
6. Does the degree of fission-fusion dynamics differ by season and troop?	Gamgam's degree of fission-fusion dynamics did not vary across seasons. Kwano had the lowest degree of fission-fusion dynamics in the beginning of the wet season, followed by the end of the dry, and the beginning of the dry seasons. Overall, the Kwano troop thus had a higher degree of fission-fusion dynamics than the Gamgam troop.
7. Does party spread differ by habitat, by season, and by troop?	Parties were most cohesive in the lowland forest and palm forest, followed by the gallery forest and Guinea savannah, and were least cohesive in the burned Guinea savannah. Party spread also differed by season; Gamgam parties were least cohesive in the end of the dry season, followed by the beginning of the wet, beginning of the dry, and were most cohesive in the end of the wet season. Kwano parties were least cohesive in the beginning of the wet and the end of the dry seasons and most cohesive in the end of the wet and the beginning of the dry seasons. Overall, Gamgam parties were more spread out than Kwano parties.
8. At what distance can individuals be considered to be in different parties?	The Gamgam distribution was best described by a single process model, suggesting that the Gamgam troop did not form subgroups. Similarly, the Kwano distribution at the end of the dry season was best described by a single process model, indicating that the troop was cohesive during this season. However, during the beginning of the wet and the beginning of the dry season distributions were better described by a mixture model indicating that the troop formed parties in these seasons. The distance at which individuals can be considered to be in different parties was 184m in the beginning of the wet season, and 62m in the beginning of the dry season.

6.4 Discussion

This study is one of the first to quantify the degree of fission-fusion dynamics by measuring variation in party size, party composition and spatial cohesion. Estimates were compared across habitat, season, and troop within a population to investigate how grouping patterns vary.

Troops differed in the degree of fission-fusion dynamics; the Gamgam troop was more spatially cohesive and had larger parties than the Kwano troop, while the rate of party composition changes was similar in both troops. As the Gamgam troop showed less variation in each of these dimensions, the degree of fission-fusion dynamics was low compared to that of the Kwano troop. This was further supported by the fact that in a statistical sense the Gamgam troop did not actually form subgroups. Fitting of continuous models to the frequency distribution of inter-individual distances showed that the Gamgam troop was cohesive throughout the year. The large parties observed in Gamgam thus reflect a cohesive troop rather than subgroups. Nevertheless, Gamgam parties on average contained only 43% of the troop rather than the whole or the majority of the troop; therefore the *visual* definition of a party may not adequately estimate a party. The implications of the findings of this study for the quantification of fission-fusion dynamics are discussed in section 6.4.3. Statistically, the Kwano troop did form parties during the beginning of the wet and the beginning of the dry season but not during the end of the dry season. The smaller parties and increased spatial cohesion thus reflect the fragmentation of the Kwano troop into subgroups. Nevertheless, party size did not differ significantly between the beginning of the wet, the beginning of the dry and the end of the dry seasons, again suggesting that the visual definition of a party may not be a satisfactory description of a subgroup.

Season affected the three aspects of grouping patterns differentially; season did not affect spatial cohesion in either troop, whereas it did affect the rate of party composition change in Gamgam but not in Kwano. The sizes of parties on the other hand were adjusted seasonally. Furthermore, troops adjusted party size to habitat type.

Here, the effect of habitat, season, and troop on grouping patterns is discussed, along with the consequences of fission-fusion dynamics for social interactions, and the implications of these findings for the study of fission-fusion dynamics.

6.4.1 The socioecology of fission-fusion dynamics

Primate societies adjust grouping patterns to ecological conditions. Therefore, fission-fusion dynamics are likely to be affected by ecology. The availability of food may influence the size and composition of parties and the spatial cohesion of a troop. The size, density and distribution of food patches may also influence party size and a troop's spatial cohesion. The findings presented in this chapter suggest that the baboon troops at GGNP adjust grouping patterns to local ecological conditions. A difference was found in the troops' grouping patterns, which was in line with between-troop differences in local ecology. The Gamgam troop was relatively cohesive, and the large parties with a relatively unstable membership were associated with higher levels of food availability. Conversely, the Kwano troop fragmented into relatively small parties with a stable composition, and in the Kwano home range food availability was lower.

However, the relationship between seasonal variation in grouping patterns and seasonal variation in food availability was not straightforward. Both troops showed some seasonal variation in party size. In the Gamgam troop, parties were largest during the end of the dry season, when the availability of both fruit and leaves peaked, and when water may have been a limiting factor (chapter 3), while party size was smaller in the remaining seasons. Similarly, the Kwano troop did not fragment into subgroups during the end of the dry season, although in Kwano party size was not significantly larger in this season. In Kwano, the smallest parties were seen in the end of the wet season when the availability of flowers, seeds and leaves were all low (chapter 3). Similarly, the troops differed in some aspects of grouping patterns; only the Kwano troop showed seasonal variation in the rate of party composition change. Similarly, troops seemed to adjust party size to habitat-specific predation risk to some extent, as the smallest parties were found in the low-risk lowland forest and palm forest, whereas parties were larger in the higher risk Guinea savannah and burned Guinea savannah. However, parties were also large in the low-risk gallery forest.

These results suggest that there is some influence of food availability and predation risk on party sizes and the stability of party membership, but indicate that the relationships are not direct. There are several factors that were not controlled for in these analyses, which may have obscured the potential relationships between ecology and grouping patterns.

First, GGNP baboons were found to have habitat-specific preferences for certain activities (see chapter 3), which may have influenced the variation of grouping patterns across habitat types. For example, baboons were found to rest and engage in social activities preferentially in low risk habitats. When grooming, individuals necessarily are in close proximity, whereas when resting, spacing between individuals may be less important. During feeding on the other hand, individuals may be more spaced out to reduce competition for food (Cowlishaw 1999). Thus, some of the results found here may have been due to the activities that were performed in each habitat type.

Secondly, the between-troop differences in fission-fusion dynamics may be due to differences in the size and the composition of the troops. The size of a troop is likely to influence the degree of fission-fusion dynamics, as it influences the ability of a troop to form smaller subgroups. If the parties formed as a result of fissioning are below the minimum group size needed to reduce predation risk to acceptable levels, a troop may be unable to split. This may be especially important given that the benefits of group living are not a linear function of party size, but rather are logarithmically related (Jacobs 2010). Thus, if a troop splits in half, the benefits of group living to the individuals may reduce by more than half. An influence of community size on grouping patterns has for example been observed in chimpanzees; smaller chimpanzee communities form larger, more stable parties, in which there is greater association between males and females (Lehmann and Boesch 2004). The large parties observed in the Gamgam troop, resulting from the lack of fragmentation into subgroups, may be due to the smaller size of the troop. Conversely, the Kwano troop may be able to fragment into subgroups because the troop was larger. The development of null models could provide insights into how group size influences fission-fusion dynamics. Using agent-based modelling, it is possible to generate several groups of different sizes, and measure the degree of fission-fusion dynamics in each of these to give an indication of how group size influences grouping patterns.

Thirdly, troop demography may further influence fission-fusion dynamics, as individuals also have *social* motives for forming groups (Kummer 2008), which may become more important above a certain level of food availability (Newton-Fisher *et al.* 2000), or in a context other than feeding (Cowlishaw 1999). Male reproductive strategies and their effect on social relationships, for example, are the main factors influencing spatial cohesion in chacma baboons (Cowlishaw 1999), whereas the number of cycling females influences party size in chimpanzees (Sakura 1994; Matsumoto-Oda *et al.* 1998; Hashimoto *et al.* 2003; Lehmann and Boesch 2004). However, in the current study, males did not associate more frequently with cycling females compared to non-cycling females (chapter 4), suggesting this might not be an important factor in GGNP fission-fusion dynamics. Females did seem to form friendships with males, while avoiding immigrant males if they did not have some probability of having fathered their offspring (chapter 4 & 5), which may influence fission-fusion dynamics. In this study, too few matrilineal relationships were known to see how these affected relationships; however, kinship is likely to have an effect on fission-fusion dynamics. For example, female savannah baboons prefer to remain with close maternal kin at group fissions, providing the maternal kin group is large enough to oppose other matrilines (Van Horn *et al.* 2007). The size and number of matrilines may thus have some influence on the size and number of parties that are formed.

Finally, there may be other aspects of grouping patterns that help primates mediate the relationship between the environment and their society. For example, here it was found that parties in the generally cohesive Gamgam troop, were more spread out than Kwano parties. Thus, it may be that rather than splitting into subgroups, as the Kwano troop does, the Gamgam troop deals with their environment by adjusting the spacing between individuals within the same party. Moreover, it is possible that adjustments in the spatial cohesion of the party and the troop fall along a single continuum of spacing between individuals. Whether this spacing is between individuals in the same or in different parties may thus be largely due to the definition of a party, and when individuals are considered to be in the same party.

Nevertheless, both the proximate mechanism for the formation of parties and the frequency distribution of inter-individual distances at least give some indication of the influence of environmental factors. The observed frequency distributions of party size for both troops were best described by a zero-truncated negative binomial distribution. This provides evidence that the mechanism underlying fission-fusion is therefore not completely independent of the size or composition of the parties as expected if data followed a zero-truncated exponential model, nor is this a random process of joining, as predicted by the zero-truncated Poisson model. The negative binomial distribution indicates that the probability of an individual joining a party increases with party size, suggesting that individuals join a party because they are attracted to larger groups. Data indicates that departures from a party were also dependent on party size, which suggests that factors such as increased food competition in larger parties may play an important factor in the fissioning among GGNP baboons. Similar proximate mechanisms for joining and leaving parties have been found in chacma baboons (Cohen 1969), yellow baboons (Cohen 1975), and Guinea baboons (Patzelt *et al.* 2011). This type of proximate mechanism is in line with the traditional view that primate groups are the result of an optimisation process, in which the benefits of group living are traded off against its costs. Individuals may be attracted to groups to reduce predation risk to acceptable levels (Hamilton 1971; Terborgh 1983; van Schaik and van Hooff 1983; van Schaik *et al.* 1983; Dunbar 1988) and to avoid infanticide (Sterck *et al.* 1997), while within-group competition acts as a constraint on group size (Terborgh 1983), with individuals trying to minimise the cost of feeding competition (van Schaik 1983; Dunbar 1988).

Similarly, the shapes of the frequency distribution of inter-individual distances give further insights into grouping patterns and individual motivations. In all seasons in the Gamgam troop, and in the end of the dry season in the Kwano troop, distributions showed a single peak and were skewed to the right, this indicates that during these seasons, troops did not frequently split into smaller subgroups and that individuals did not move independently of each other. When the movements of two animals are completely independent, the frequency distribution of inter-individual distance does not show a skew (Sugiura *et al.* 2011). A distribution that is skewed to the right, where short distances are more frequent between individuals, occurs when the movements of individuals are not completely independent (Sugiura *et al.* 2011), either when they start at the same location and move apart, or start at different locations and move towards each other. Thus, these results also give some indication of the processes of attraction and repulsion from other troop members.

Thus, the Gamgam troop was found to have a lower degree of fission-fusion dynamics, but showed greater seasonal differences in their patterns of associations, which, as suggested in chapter 4, maybe due to a stronger seasonality in food availability. While the Kwano troop was found to have a higher degree of fission-fusion dynamics, association patterns and food availability were found to be more stable across seasons for this troop. This disparity in the results between association patterns and fission-fusion dynamics is likely to be due to the different time spans over which analyses were conducted. It seems that the few changes in the Gamgam troop took place in a time period greater than three months (*i.e.* in a period greater than the time period over which data for the seasonal association networks were collected). As a result, the overall degree of fission-fusion dynamics is low, but each association network differs from the previous network. The Kwano troop on the other hand, seemed to have changed frequently over short time periods, for example within a day, or over several days, leading to a high degree of fission-fusion dynamics. The frequency of these changes was, however, stable over the seasons, and therefore, association networks were not found to differ across seasons. These results suggest that grouping patterns on different time scales may be linked to different aspects of ecology. Gamgam individuals seemed to adjust individual association strategies seasonally, indicating that grouping patterns and associations were linked closely to ecology. In other words, small troop size, high predation risk and high food availability all played a part in the day-to-day stability of Gamgam associations and grouping patterns. However, seasonal changes in the availability of food seemed to have led individuals to change some of their associations. In Kwano, associations and grouping patterns changed more frequently. It seems that lower food availability causes the Kwano troop to avoid competition by fragmenting, which is possible because of the lower level of predation risk. It was suggested that this is also the reason the Kwano troop has fewer agonistic relationships (chapter 5). What is not yet clear is why the Kwano troop remains cohesive at all. In chapter 4, social factors were shown to have little influence on association patterns. However, some indication was given that infanticide avoidance may have had an effect on the formation of substructures in the Kwano troop. Therefore, it may be that Kwano individuals associate in larger groups to avoid harassment and infanticide, factors suggested as being important drivers of primate sociality in socioecological models (Wrangham 1979; Sterck *et al.* 1997; van Schaik and Kappeler 1997; Kappeler and van Schaik 2002). Alternatively, it may be that Kwano individuals meet up at sleeping sites. While trees were found throughout the Kwano home range, animals chose to sleep in the palm forest for the majority of observations (Appendix D Figure D.2). By comparison, Gamgam sleeping sites were more spread out over the home range (Appendix D Figure D.1). Thus, Kwano individuals may associate in smaller parties during the day, but meet at the sleeping sites in the palm forest at dusk.

In sum, differences were found in fission-fusion dynamics across habitat types, across troops, and across seasons, and the results discussed above give some indication of the effects of local environmental factors on this. While it was not possible to separate out the influence of food availability, predation risk, troop size and demography in this study, results do give some indication of the influence of each of these factors and the complexity of determinants of fission-fusion dynamics, as well as highlighting the need for developing null models (Hemelrijk 2004) against which observed fission-fusion degrees can be compared. The proximate mechanism underlying the formation and cohesion of parties in both troops, as well as the spacing between individuals, seem to reflect individuals' conflicting socioecological motives.

6.4.2 Implications of fission-fusion dynamics for social interactions

Social interactions are expected to be affected by fission-fusion dynamics (Aureli *et al.* 2008a) because the extent to which a group temporarily splits into smaller parties influences the opportunities and context of social interactions. Ultimately, this may have important consequences for both the social structure and the mating system of a group. Here, between-troop differences in social interaction rates are related to differences in fission-fusion dynamics, and within-group quantitative differences in social interactions are related to the three estimates of grouping patterns.

Troops were found to differ in the daily mean rates of aggression and contact calls. Contact calls are long-distance calls given by animals that have been separated from the troop, or from certain individuals (Byrne 1981; Ransom 1981; Cheney *et al.* 1996; Rendall *et al.* 2000; Fischer *et al.* 2001). Here, it was found that the daily mean rate of contact calls was significantly lower in the more cohesive Gamgam troop compared to the Kwano troop. These results are as expected, as individuals are more likely to be separated from others when the troop is fissioned.

The daily mean rate of aggression on the other hand was significantly higher in the Gamgam troop compared to the Kwano troop, suggesting that the avoidance of conflict may be an important factor driving fission-fusion dynamics. Aggression may be due to competition for food, and fissioning may be an effective way of reducing food competition, as it is a way of producing a 'dynamic ideal free distribution' (Grove 2012), in which animals distribute themselves according to varying resource availability. For example, in spider monkeys the rate of aggression and fission are associated (Suarez 2001) and fissioning has been shown to reduce both scramble and contest competition (Asensio *et al.* 2008). It may be that individuals in the Kwano troop avoided food competition escalating into aggression by fissioning, although the results presented here are not conclusive due to several factors. Firstly, while these results show that rates of aggression were lower in a troop with a higher degree of fission-fusion dynamics, it does not show whether aggression occurred during periods when the troop was cohesive. Thus it is not clear if aggression was reduced due to fissioning, or due to other factors. Secondly, while there was some indication that party size differed with the availability of fruit and leaves, these relationships were not straightforward, which may be expected if troops used fissioning to reduce their competition for food. Furthermore, in this study no distinction was made between aggression over food and other types of aggression, and consequently factors other than food availability may have influenced the rate of aggression.

Fissioning may also reduce aggression by providing a solution to conflicts of interests between individuals, particularly those concerning spatial decisions (Sueur *et al.* 2011b). Conflict may occur in a group when individuals differ in their energetic needs, and consequently differ in preferences for activity or location (Sueur *et al.* 2011b). In these instances, by fissioning, individuals can avoid group decisions that are not in their own favour (Kerth *et al.* 2006). However, again it is not known if aggression occurred when groups were fissioned or cohesive. Future research should therefore include information on the timing of fission events in relation to aggression, to determine if rates of aggression are indeed lower when a troop has fissioned, and if this is a strategy for avoiding conflict. Comparisons of aggression over food, the direction of individuals' movements, and behavioural synchrony between times when troops are fissioned and when troops are cohesive would further help distinguish if fissioning helps to reduce conflicts over food or conflicts over group decisions.

Apart from these between-troop differences, some associations were also found between social interactions and grouping patterns within troops. In Kwano, individuals that were in parties that changed more rapidly in their composition had higher rates of affiliative vocalisations and behaviours. This may be because affiliative behaviours, which included behaviours such as grooming, lip smacks, and embraces, are used to reinforce social bonds and update social information after a period of absence. For primates it is important to assess not only changes in their own relationships with others, but also changes in the relationships between others (Barrett *et al.* 2003). Therefore, when part of the troop has been out of sight for some period, individuals may need to assess third-party social relationships (Barrett *et al.* 2003). Greetings are used to reinforce social bonds after a period of separation for example by spotted hyenas, a species with a high degree of fission-fusion dynamics (Smith *et al.*

2011), and have been suggested to be a bond testing behaviour in Guinea baboons (Whitham and Maestripieri 2003).

Alternatively, affiliative behaviours and vocalisations may be ways to manage conflict; when parties fuse, tensions may arise due to conflicts over resources and party-level decisions (Aureli and Schaffner 2007). For example, spider monkeys have been found to use embraces as a way to reduce tension at fusions of subgroups in the wild (Aureli and Schaffner 2007) and for the regulation of social relationships in captivity (Schaffner and Aureli 2005). Grooming may reduce tension in both the recipient (Schino *et al.* 1988; Aureli *et al.* 1999) and the actor (Shutt *et al.* 2007; Aureli and Yates 2010) of grooming, and may reduce the risk of aggression (Silk 1982; Aureli and Yates 2010) and increase tolerance (Kapsalis and Berman 1996; Barrett *et al.* 2002). Affiliative behaviours are often accompanied by grunts (affiliative vocalisations in this chapter) as a way to signal benign intent and facilitate social interactions (Cheney *et al.* 1995; Rendall *et al.* 1999; Silk 2002a). Thus, individuals may use affiliative behaviours more when party composition changes rapidly to reduce tension, and use grunts to facilitate those affiliative interactions.

Whether affiliative behaviours and vocalisations are used to reinforce social bonds or manage conflict, no association was found between these interactions and the rate at which Gamgam party membership changed. It may be that, because the rate of party composition change was relatively stable across seasons, the other contexts in which these behaviours were used have become more important. For example, affiliative behaviours are also used to signal benign intent prior to infant handling (Henzi and Barrett 2002; Silk 2002a; Frank and Silk 2009).

Regardless, the overall lack of associations between grouping patterns and social interactions is what is perhaps more surprising, as grouping patterns influence the number of individuals that are available for social interactions. The lack of associations may be due to the use of daily mean rates for both the three grouping pattern components and the social interactions, which might have obscured more small-scaled adjustments. If troops fission and fuse several times during a day, taking the daily mean averages may mask the variation in rates of social interactions associated with these different grouping patterns. To investigate finer associations between social interactions and grouping patterns, future researchers should use estimates calculated over shorter time frames, such as hourly rates.

This study shows that an intra-specific difference in the degree of fission-fusion dynamics is associated with a quantitative difference in social behaviours and vocalisations. The difference between the degrees of fission-fusion dynamics of troops within a population is likely to be relatively fine-grained. Future research should focus on quantifying the degree of fission-fusion dynamics and its effects on vocalisations and social interactions across a wide range of populations and species, to test if the degree of fission-fusion dynamics also affects social behaviours and vocalisations in a *qualitative* way. For example, it has been suggested that conflict resolution behaviours may be less prevalent in groups or species that have the option of fissioning, as conflict can be avoided rather than resolved (Aureli *et al.* 2008a).

6.4.3 Implications for quantification of fission-fusion dynamics

The quantification of fission-fusion dynamics is crucially important for the exploration of the continuum of variation in primate social systems (Aureli *et al.* 2008a; Coles *et al.* 2012). Here, a method for the estimation of the degree of fission fusion dynamics was suggested by calculating the CV for inter-individual distances, party size, and the rate of party composition change. Several issues with the estimation of each of the fission-fusion dimensions and how they relate to each other are discussed below, which may inform future studies into fission-fusion dynamics.

First, to allow for a comparison across species, the distances in the spatial cohesion measure should be standardised for example by taking into account the average body size of a species. Alternatively, the spatial cohesion measure could be given as a proportion of home range size, which itself is related to body size (Dunbar 1988), or could take into account the average locomotory velocity of a species, to indicate the speed at which individuals would be able to reach each other.

The way a party is defined will have great consequences for the estimation of party size and the rate of party composition change. Here, a visual definition of a party was used in the majority of analyses. While such a definition is practical to the observer, some methodological problems may be associated with this definition. Habitat visibility may have some influence on how well individuals can be located (Chapman *et al.* 1993; van Elsacker *et al.* 1995) and therefore on party size or party composition. In this study, observers moved around the area for several minutes before each scan so that individuals could be located better, minimizing the effect of habitat visibility on the individuals included in a party. Nevertheless, the influence of habitat visibility on party size and party composition change cannot completely be ruled out. In this study, this may have had some effect on between-troop comparisons as the availability of habitat types differed between troops. The effect of habitat visibility would, however, have a greater impact when comparing between populations or between species. A more objective definition of a party would be one based on the analyses presented in section 6.3.9, where it was determined at what distance individuals could statistically be considered to be in separate parties. The difficulty with using such an operational definition is that sufficient data on inter-individual distances need to be collected during an initial study to determine this cut-off value, which is, as was the case in this study, not always possible until the data collection is over.

Furthermore, the visual and statistical definition of a party may not always overlap. Using the operational definition, the Gamgam troop was cohesive, yet using the visual definition on average only 43% of the troop was observed in a single party. Similarly, in Kwano, while statistically the Kwano troop was cohesive in the end of the dry season and fragmented during the beginning of the wet season and the beginning of the dry season, party size did not differ significantly between these seasons. Individuals may be in a subgroup with individuals that are all in visual contact (*i.e.* a visual definition of a party) but if these subgroups travel in the same direction, under the statistical definition these coordinated subgroup may be classified as a single party. This is further supported by the lack of two distinct peaks in the frequency distribution of inter-individual distances, which may be expected in a primate group with a high degree of fission-fusion dynamics. In chimpanzees for example, parties are expected to move more independently, therefore creating the two distinct distributions. If parties are coordinated, however, the distribution of distances between individuals in different parties may not be completely distinct from distance between individuals within a party. Therefore, it would be very interesting to analyse not only the distance between individuals but also whether they are travelling in the same direction. Additionally, a comparison with a nomadic party, *i.e.* all individuals seen in a day, may be useful here.

Furthermore, it may also be valuable to compare parties defined by various cut-off distances that reflect aspects of the species' communication systems. The distance at which individuals are no longer able to hear, or smell each other may be a useful cut-off point for when individuals are no longer considered to be in the same party, as individuals may no longer be able to coordinate travel. Definitions of a party that take into account some species-specific characteristics in this way may make results more comparable across species.

Estimates of party size and the rate of party composition change did not correlate with estimates of spatial cohesion, indicating that these estimates varied independently from each other, and therefore quantify different dimensions of primate grouping patterns. However, party size and rate of party composition change were not found to vary independently from each other; in both troops, larger parties were more variable in composition. Larger parties may be more unstable in their composition because in these parties there is greater opportunity to fission and to fuse, or because there is a wider range of opinions on group decisions. Additionally, small parties may consist of related individuals who may be more likely to remain in the same party. In this study, too few of the matrilineal relationships were known to investigate the effect of kinship on association patterns (see chapter 4). However, kinship is likely to have an effect on the cohesion of individuals in a party, and this should therefore be taken into account in future studies.

The co-variation between party size and rate of party composition change may be a particular characteristic of GGNP baboons' fission-fusion dynamics, or may be inherent to the two estimates if these are essentially estimating the same underlying phenomenon. Future research into the fission-fusion dynamics of other populations or species would give further insights into whether these measurements do vary independently, and therefore if the estimates suggested here provide a good indication of fission-fusion dynamics. Modelling may be a particularly useful approach here, as parameters can be manipulated experimentally. For example, by creating agents that join and leave parties following particular ecological rules we can measure both party size and the rate at which party composition changes. This way, it is possible to determine if the correlation between these two estimates is particular to GGNP baboons, or a general phenomenon of fission-fusion dynamics.

Taking these issues into account, the CV for the relative inter-individual distances, party size and party composition change provides a good standardised estimate of the relative degree of fission-fusion dynamics. The composite index here may be useful in that it allows for an easy comparison of a troop's degree of fission-fusion dynamics. However, by using this index some information is also lost, as it does not indicate on which of the three axes the variation lies. The radar charts shown in Figure 6.24 and Figure 6.25 may therefore be a better way to represent and compare these data, as they indicate the CV for each of the three fission-fusion dynamic components.

Results reported in this chapter indicate that there is a between-troop difference in the degree of fission-fusion dynamics. However, it was not possible to determine if this was a large or a fine-scaled difference. In order to place the results in a context, and thus evaluate how large the difference in the degree of fission-fusion dynamics is, it is necessary to determine the degree of fission-fusion dynamics of a wide range of species across and beyond the primate order. Initially, investigations should focus on those species that are thought to fall on either end of the fission-fusion spectrum, *i.e.* vervet monkeys (*Chlorocebus spp*.) that are likely to have low levels of fission-fusion dynamics, and chimpanzees (*Pan troglodytes*) or spider monkeys (*Ateles spp.*) that are thought to have high degrees of fission-fusion dynamics. Once the fission-fusion dynamics of a larger number of species have been quantified, this would provide a context in which differences in the degree of fission-fusion dynamics between troops, populations, or species, can be evaluated.

6.5 Summary of chapter

- The results presented here give some indication of the influence of environmental factors on fission-fusion dynamics; differences were found in the degrees of fission-fusion dynamics across habitat types, and between troops. These differences were in line with between-habitat and between-troop differences in local ecology. However, the relationship between seasonal variation in food availability and seasonal variation in grouping patterns was not straightforward. Troop size, demography, and the activity of individuals in a party are likely to influence grouping patterns, and, in order to tease out the influence of local ecology on fission-fusion dynamics, these factors should be controlled for. These results emphasize the importance of developing null models against which observed fission-fusion dynamics can be compared.

- Evidence was provided that the proximate mechanism of the formation of parties was similar in the two troops, and seems to reflect the underlying costs and benefits of group living. Individuals join larger parties because they are attracted by their size, most probably to avoid predation and infanticide, while they leave larger parties potentially to reduce within group competition.
- There was evidence that grouping patterns influenced social interactions, which ultimately affects the social system. Between-troop differences in the rates of aggression suggest the avoidance of conflict may be an important factor in driving fission-fusion dynamics; individuals may leave a party to reduce food competition or to avoid group decisions that are not in their own interests. A between-troop difference was also found in the rate of contact calls. In Kwano, but not in Gamgam, parties that changed more rapidly in composition had higher rates of affiliative behaviours and vocalisations, which may be used to reinforce social bonds and update social information after a period of

absence, or as a way to manage conflict and reduce tension at fusion events.

- A method for quantifying fission-fusion dynamics was suggested by calculating the CV for inter-individual distances relative to home range size, for the number of party composition changes relative to the maximum possible number of changes, and for party size relative to troop size. As this is a standardised measure, it would be possible to make comparisons across populations and species. An objective way of defining a party is spatially, by determining the statistical cut-off point at which two individuals are no longer considered to be in the same party. Further research is needed to see if party size and the rate of party composition change vary independently, and thus if they estimate different aspects of primate grouping patterns. Furthermore, to be able to put the observed between-troop difference in context, the fission-fusion dynamics of a range of other populations and species should be quantified.

Chapter 7

Discussion

Understanding fission-fusion dynamics is crucial to understanding primate social systems, as the degree to which a group can split and reform not only affects its social organisation, but can also have far-reaching consequences for its social structure and mating system (Kerth 2008), and for shaping cognitive abilities (Aureli *et al.* 2008a). In this thesis, a method for the quantification of fission-fusion dynamics was developed and applied, generating new insights into the flexibility of the social system of olive baboons. Two aspects of the social system were investigated in particular: patterns of associations and of social interactions were analysed using a social network approach.

The structure of networks based on associations was analysed and compared across troops and seasons. Variations in network structures were related to variations in food availability, predation risk, and habitat use, to examine the influence of ecological factors on association patterns. Individual association preferences and the influence of social factors on association patterns were also investigated. Additionally, social networks were generated from five types of social interactions. Differences in behavioural network structures were related to patterns of associations, and the influence of social factors on the structure of social relationships was also examined. Established statistical methods were used to evaluate the extent to which olive baboons are flexible in their grouping patterns, and to determine the degree of fission-fusion dynamics.

In this final chapter, the broader implications of the study findings are discussed, and directions are suggested for future research.

7.1 Implications for socioecology

Savannah baboons are generally said to form cohesive troops (Anderson 1981; Swedell 2011). However, in some marginal habitats these baboons may form smaller foraging parties that do not have a set composition (Anderson 1981; Barton *et al.* 1996; Henzi and Barrett 2003; Henzi and Barrett 2005; Swedell 2011). Such fragmentation of troops has, for example, been observed in chacma baboons in the Suikerbosrand Nature Reserve in South Africa where this fragmentation has been suggested to be a strategy to cope with food scarcity (Anderson 1981). It should be noted that baboons at Suikerbosrand live in habitats that are extremely seasonal in terms of food availability and temperature (Anderson 1982). In the current study it was shown that another of the savannah baboon subspecies, olive baboons, also show some degree of flexibility in their grouping patterns, and that the subgroups that are formed are not set 'subtroops', but rather are fluid in composition. Fission-fusion dynamics and association patterns differed between the two study troops, and were adjusted, to some extent, to seasonal variations in the environment. However, unlike Suikerbosrand, GGNP does not seem to present a marginal and seasonal habitat for baboons in terms of food availability; plant diversity and productivity are high in GGNP all year round, which means that, compared to other baboon populations, the diet of GGNP baboons contains a high proportion of preferred foods, such as fruits and seeds (Ross *et al.* 2011). Furthermore, forested habitats are generally less seasonal than for example, savannah habitats (Alberts *et al.* 2005). Thus, even in a habitat that does not have extreme fluctuations in food abundance, baboons show some flexibility in their grouping patterns. A similar kind of flexibility was found in another West-African population of olive baboons; in the Comoé National Park in Ivory Coast, similarly small troops of olive baboons were found to split into parties for one or several days (Kunz and Linsenmair 2008). The diet of this population also contains a large proportion of fruit and seeds, and predation risk is low (Kunz and Linsenmair 2008). It may be that this high degree of frugivory among olive baboon populations in West Africa, coupled with a lower density of predators (Bauer *et al.* 2003; Kunz and Linsenmair 2008), has allowed these troops to split and reform temporarily. Thus, West African baboons may be more flexible in their grouping patterns and social behaviour than East or southern African populations, because the abundance of fruit and the low risk of predation release them to some extent from the constraints of group living. Much of our current knowledge about savannah baboons stems from studies on population in East and southern Africa (Kunz and Linsenmair 2008; Higham *et al.* 2009), which may be why the GGNP baboons do not readily fall into the ‘cohesive’ category outlined for savannah baboons (Barton *et al.* 1996). These apparent differences in the flexibility of grouping patterns of West African compared to other savannah baboon populations may be an example of selected responses to 'restricted, local evolutionary conditions' (Henzi and Barrett 2005). Taking a phylogenetic approach to population differences seems to be a promising way to help understand how local evolutionary histories may affect current patterns of sociality. The baboon socioecological model should thus incorporate the flexibility of grouping patterns that has been observed here, and this study therefore highlights the need for further studies of West African baboon populations.

Moreover, the socioecological model more generally should place more emphasis on within-species variation (Chapman and Rothman 2009). Here it was shown that the demographic and environmental factors proposed in the socioecological model go some way to explaining not only between-troop variation of grouping patterns, but also the seasonal variation of grouping patterns within olive baboon troops. While the concept of small-scale variation in the social structure of a primate group in response to small-scale variation in demography, food availability, or predation risk, is implicit in the socioecological model, this small-scale variability may be lost because of the use of modal categories. In other words, nuances are lost by using categorical variables in both the ecological driving factors and the resulting social systems, such as low or high competition, or an egalitarian versus a despotic system. In the past it was suggested that "the use of categorical variables is justified because, although the underlying ecological variation is continuous, the social responses are more or less discrete" (Sterck *et al.* 1997: 294). This study has shown that social responses are more flexible than previously thought, and along with the increasing number of field studies showing intra-specific variation (reviewed in Chapman and Rothman 2009), there is now growing evidence that social responses may not be discrete. Therefore, the socioecological model should be modified to take this variation into account.

Rather than adding more parameters to the model, the best way to incorporate this variation may be to abandon the use of distinct categories. As the environmental factors that underlie social systems vary continuously rather than categorically (Sterck *et al.* 1997), splitting the social response into distinct categories is rather arbitrary (Kasper and Voelkl 2009). Instead, network metrics could be used to characterise the structure of a group, which, because network metrics are continuous, allows for a much finer comparison of the structure of primate groups (Kasper and Voelkl 2009). For example, rather than classifying a group as egalitarian or hierarchical, the dominance style of a group could be measured using the *network centralisation*, or a combination of the *reciprocity* and *transitivity* of relationships. In chapter 5 it was shown that agonistic relationships were more reciprocal in Kwano and more transitive in Gamgam, suggesting that the dominance hierarchy was more linear and stronger in Gamgam compared to Kwano. Because these measures are a ratio, they can easily be used to estimate dominance style along a gradient. Rather than simply identifying whether nepotism is present or absent in a group, with a social network approach it also possible to measure to what extent kin is an assortative force on the network. In the current study, too few kin relations were known to perform such an analysis, but in essence this would be similar to the analyses of the effect of female reproductive state on relationships in chapter 4 and 5. The *density* and *average tie weight* can give an indication of the overall strength and number of relationships, which could be used instead of classifying societies as cohesive or flexible. Equally, the *weighted clustering coefficient* or *compactness* could be used to give an indication of the cohesion of a network as a ratio rather than discrete categories.

Such an approach to the classification of primate social systems is especially interesting given the recent developments in multi-dimensional social networks (Barrett *et al.* 2012), in which several behavioural dimensions can be added as layers in a single network. This makes it possible to consider associations, grooming and other affiliative behaviours, aggression, and vocalisations simultaneously in the characterisation of primate social structures.

Presently, the use of network metrics as a means of characterising social structures may not yet be practical, as currently a large proportion of global network metrics are affected by network size, making direct comparisons between networks of different sizes difficult (Anderson *et al.* 1999). In chapter 5, conditional uniform graph tests were used to make comparisons between the networks of the Gamgam and Kwano troops. While the number of metrics that can be tested with this procedure is currently limited (Butts 2011), methods are continually being improved and it is therefore likely that in the near future comparisons of a greater number of network metrics will be possible.

As was discussed in chapter 6, the timescale at which the temporal variation in grouping patterns is measured influences the estimation of the degree of fission-fusion dynamics. In this study, the grouping patterns in the Kwano troop changed over a shorter time period than in the Gamgam troop. When using methods that considered relatively short time periods, such as the inter-individual distances measured every 15 minutes (chapter 6) or the daily mean of the size and change in the composition of parties calculated from the scan sample measures taken every hour (chapter 6), the Kwano troop was considered to have a higher degree of fission-fusion dynamics than the Gamgam troop. However, when using a method that spanned a longer time period, such as social networks over three months or a year (chapter 4), Kwano showed less variation than the Gamgam troop. Currently, it is not clear at what timescale fission-fusion dynamics should be considered, and this may differ across species. For example, a species' cognitive capacities may be important for determining such a timescale, as the period over which individuals can remember group members may limit fission-fusion dynamics. For example, while cotton-top tamarins recognise calls of relatives after four years of separation (Matthews and Snowdon 2011), elephants still recognise calls up to 12 years after separation (McComb *et al.* 2000). Taking species-specific cognitive abilities into account may thus make the estimate of fission-fusion dynamics more relevant to the study species. In this thesis, grouping patterns were found to differ slightly depending on the methods and thus the timescale used, and it is difficult to know which of these gives the best approximation of the degree of fission-fusion dynamics. The implications of these findings for the use of social network analysis in the estimation of fission-fusion dynamics are discussed in section 7.2.

Finally, while the results in this thesis indicate the relative differences between two troops of olive baboons, it is not yet known if this represents a large or a relatively fine-grained difference. More generally, it is also not yet clear at what point of the fission-fusion spectrum these troops fall. Given the level of fluidity observed in the grouping patterns of chimpanzees (Symington 1990; Lehmann and Boesch 2004), spider monkeys (Symington 1990; Suarez 2001), and southern muriquis (Coles *et al.* 2012), this is likely to be at the lower to intermediate end of the fission-fusion continuum. However, fission-fusion dynamics need to be quantified in a range of species to be able to put the results found here in to context.

7.2 Measuring fission-fusion dynamics using social networks

The social network approach, in combination with association indices, has been suggested to be a good method to quantify the degree of fission-fusion dynamics (Kerth 2008). As was discussed in chapter 1, the method has proven valuable in the study of association patterns in animals that are thought to have a high degree of fission-fusion dynamics (Cross *et al.* 2005; Lusseau *et al.* 2006; Ramos-Fernández *et al.* 2006; Sundaresan *et al.* 2007; Wolf *et al.* 2007; Lehmann and Boesch 2009) because it may be difficult to understand the social relationships amongst individuals that are frequently dispersed. However, some of the analyses in this thesis have highlighted limitations in the use of social network analysis for quantification of fission-fusion dynamics. First, in order to construct a social network that accurately describes the social relationships between individuals in a troop, it is necessary that all individuals have had some opportunity to interact. Usually, this means data are needed from an extended period, although the exact length of time depends, amongst other things, on the data collection protocol. For example, in chapter 4, association networks could be constructed for each three-month period, because these were based on data taken during hourly scans in which data were recorded on several dyads simultaneously. Conversely, in chapter 5, networks were constructed over the whole study period because these were based on data from individual focal follows and not all individuals were sampled during a three-month period. As was highlighted in the previous section, the timescale over which data are collected may have a large impact on the estimation of the degree of fission-fusion dynamics. Thus, after an appropriate timescale has been determined for quantifying the degree of fission-fusion dynamics, the data collection protocol needs to be adjusted so that sufficient data can be collected on all individuals.

Second, crucially, fission-fusion dynamics are concerned with the amount of temporal variation in grouping patterns. While social networks are generated from data over a certain time period (*e.g.* here three months, or one year) network metrics do not explicitly measure variation over time, and in fact may mask the variation within a group. For example, the network structure of a group that always associates as a single group may not be that different from the network structure of a group that is extremely flexible in their associations, providing that all individuals associate with all group members at some point. Even in an extremely fluid society all individuals are likely to interact, but a longer time period is needed to observe all these interactions than in a society that is more cohesive. This suggests that when using a social network approach to estimate fission-fusion dynamics, networks should in fact be generated and compared over small slices of time, rather than over several months or a year, as has often been the case in characterisations of the social structures of species that are thought to have a high degree of fission-fusion dynamics (Cross *et al.* 2005; Sundaresan *et al.* 2007; Wolf *et al.* 2007; Wolf and Trillmich 2008; Lehmann and Boesch 2009; Ramos-Fernández *et al.* 2009). Recent developments in proximity logging technology, such as interactive tags or tags that work with fixed receivers, can increase the quantity and quality of association data that is collected (Ryder *et al.* 2012). Such technology can thus help ensure sufficient data is collected over short time periods, particularly so that each individual in the group has been adequately sampled, to construct social networks over very short time periods.

Future research should investigate if such short-term networks may in fact characterize fission-fusion dynamics more accurately than social networks generated from data collected over a longer period. Specifically, research is needed into how various degrees of fission-fusion dynamics may produce different network structures and how the time frame over which data for the social network were collected may interact with this structure. For example, agent-based modelling (Hemelrijk 2004) can be used to develop null models for the structure of social networks at varying degrees of fission-fusion dynamics and timespans against which networks generated from empirical data can be compared.

Until more is known about the timescale over which fission-fusion dynamics should be measured, and more weighted network metrics and null models have been developed, more traditional measures such as the coefficient of variation used in chapter 6, may provide the best available estimate of fission-fusion dynamics.

7.3 The cognitive demands of fission-fusion dynamics

Primates have strong social bonds that are often, although not always, maintained through grooming (Kudo and Dunbar 2001; Dunbar and Shultz 2007a). Such strong bonds have also been observed in species that are not always spatially cohesive (Lehmann and Boesch 2009; Mitani 2009). It is not yet known how animals in groups that frequently split into subgroups of variable composition are able to recognise members of their social group that have been absent for some time, maintain stable social relationships with them, and thus maintain a distinct social group (McComb *et al.* 2001; Barrett *et al.* 2003; Amici *et al.* 2008b; Kerth *et al.* 2011). Both adjustments in behaviour and evolutionary adaptations in cognitive skills may help primates adapt to particular degrees of fission-fusion dynamics.

It has been suggested that individuals may alter their behaviour to maintain social bonds in response to the degree of fission-fusion dynamics (Amici *et al.* 2008a; Aureli *et al.* 2008a). The current study shows for the first time that quantitative differences in social behaviours are indeed linked to differences in fission-fusion dynamics. The Kwano troop, with a higher degree of fission-fusion dynamics, had a more focused grooming network and a stronger, more cohesive, and more reciprocal affiliative network. This suggests that affiliative behaviours were used more in the Kwano troop to help 'update' social relationships after the individuals had been separated. The spatially more cohesive Gamgam troop had a cohesive and well-connected grooming network and contact calls were made frequently. It was suggested that these behaviours may have helped the Gamgam troop to maintain cohesion. In Gamgam, agonistic behaviour was more common and widespread, which may be a result of the inability to avoid conflict by spatially separating. This study thus gives some insight into how social relationships are maintained in a population with a low/medium degree of fission-fusion dynamics, and, importantly, how individuals may have to adjust their behaviour to the degree of fission-fusion dynamics. However, cognitive abilities may limit the extent to which primates can maintain social relationships in a dispersed society and consequently their degree of fission-fusion dynamics.

Higher degrees of fission-fusion dynamics have been suggested to be the driving factor behind the increased cognitive abilities of apes compared to monkeys (Barrett *et al.* 2003). For primates in general, the complexity of living in permanent and cohesive social groups has been proposed to have selected for greater social skills and cognition (Humphrey 1976). Neocortex volume and social complexity, approximated by group size, have been found to correlate positively across the primate order (Dunbar and Shultz 2007b). Further behavioural indices of social complexity, such as coalition formation (Kudo and Dunbar 2001) or the occurrence of tactical deception (Byrne and Corp 2004) are also predicted by the size of the neocortex. It has been assumed that social complexity increases with higher degrees of fission-fusion dynamics, and therefore increases cognitive demands. A number of factors may underlie this link between fission-fusion dynamics and cognitive abilities.

First, in groups that have a high degree of fission-fusion dynamics, part of the social group may be out of sight for extended periods. Individuals in such groups need to be able to retain information about members of their community that they do not regularly come into contact with over a long time period (McComb *et al.* 2001; Barrett *et al.* 2003). Moreover, individuals have to be able to predict how the presence or absence of certain individuals may affect the behaviour of others (Barrett *et al.* 2003). Chimpanzees, for example, seem to understand and remember which individuals were present at an event, and can act on that information (Hare *et al.* 2001). While all anthropoids may be able to recognise third party relationships (Barrett *et al.* 2003), the ability to reason causally about how the presence or absence of individuals may influence behaviours is likely to be more cognitive demanding.

Second, animals that live in groups with a high degree of fission-fusion dynamics may need to have greater cognitive control (Barrett *et al.* 2003), *i.e.* the ability to retain information and use this to guide and control behaviour appropriately, because the effectiveness of a response may change with the composition of the social group. For example, challenging a troop member may be more effective when fewer of that individual's kin are around to intervene. A relationship between fission-fusion dynamics and cognitive control has been shown in studies of primate species with varying degrees of fission fusion dynamics. For example, one study compared the performance of individuals in a series of tests that assessed inhibitory control across seven primate species (Amici *et al.* 2008a). Spider monkeys were found to have a level of inhibitory control similar to that of chimpanzees, bonobos, and orang-utans, while the performance of gorillas was similar to that of capuchins and long-tailed macaques (Amici *et al.* 2008a); in other words, species that are thought to have a high degree of fission-fusion dynamics, all had high levels of inhibitory control, whereas species that are thought to have a low degree of fission-fusion dynamics had a low inhibitory skills. In another study, the ability to withhold information was compared across three monkey species (Amici *et al.* 2009). While all species were able to withhold information about the location of food when a dominant animal was present, spider monkeys were better able than capuchin monkeys and long-tailed macaques to wait for a favourable setting before taking the food (Amici *et al.* 2009). This study thus also suggests that a higher degree of fission-fusion dynamics may increase the degree of inhibitory control.

Finally, animals in groups with a high degree of fission-fusion dynamics need to track and update social information after a period of absence (Barrett *et al.* 2003). As changes in a social relationship may have occurred during the period of absence, individuals need to be able to deal with these relationship uncertainties (Connor 2007) and renew the information about their relationships with group members. For example, individuals may engage in certain interactions on reunion, such as risky intimate contact, to gain reliable information about the quality and strength of social bonds (Zahavi 1977; Zahavi and Zahavi 1997; Whitham and Maestripieri 2003). Furthermore, individuals also need to track any changes in the social relationships of others, which they may do, for instance, by picking up on subtle cues in the interactions between others (Aureli *et al.* 2008a). It has been suggested that species with a high degree of fission-fusion dynamics have enhanced inferential skills (Engh *et al.* 2005) to gather information about third-party relationships.

Species with a lower degree of fission-fusion dynamics may not have experienced the selection pressures on cognition outlined above. It would for example be much more likely that individuals witnessed events or interactions in their groups, and therefore there is less demand for inferential skills. There is also some indication that individuals in groups with lower fission-fusion dynamics show less inhibitory control. Japanese macaques, for example, continue challenging individuals in their group, even when their own kin are not able to provide support because they have been removed from the group (Chapais 1992).

Varying degrees of fission-fusion dynamics may thus impose different selective pressures on cognitive skills, and primates may be cognitively limited in the extent to which they are able to maintain social relationships in a group that is spatially dispersed. In order to understand better the relationship between fission-fusion dynamics and cognitive skills, future research should include a phylogenetic comparative approach (Harvey and Pagel 1991; Nunn 2011). Such a method can help to establish whether there is a phylogenetic signal in the degree of fission-fusion dynamics, and thus if closely related species have a tendency to have a similar degree of fission-fusion dynamics (Hillis and Huelsenbeck 1992). If no phylogenetic signal is found in the degree of fission-fusion dynamics, this suggests that the current environment has a greater influence on fission-fusion dynamics than does phylogenetic inertia. Moreover, using this method it is possible to investigate the co-evolutionary relationships of fission-fusion dynamics and various cognitive skills, and the relative timing of the evolution of those traits. From such analyses it is possible to infer the presence and direction of the causal relationship between cognitive capacities and fission-fusion dynamics. While the cognitive abilities of species across the primate order have been well studied, the degree of fission-fusion dynamics has not been quantified before. In this study a method for the quantification of fission-fusion dynamics that can be applied across the primate order was suggested. Quantifying the degree of fission-fusion dynamics in a wide range of species would be the first step in understanding the cognitive demands of fission-fusion dynamics. Using the degree of fission-fusion dynamics, rather than a binary characterisation of primate societies, is particularly important in phylogenetic comparative analyses, because the use of continuous variables greatly increases the power of these tests by increasing the amount of evolutionary change that is reconstructed (Nunn 2011). Understanding the cognitive demands of fission-fusion dynamics may be especially important as the demands of maintaining social relationships over distance and time have been suggested to be an important driving factor in human evolution (Foley and Gamble 2009).

7.4 Implications for the evolution of human societies

Fission-fusion dynamics have been suggested to be key during human evolution (Gowlett 2008; Foley and Gamble 2009; Grove 2012; Grove *et al.* 2012; Malone *et al.* 2012), and may be one of the factors that have allowed humans to live in a wide range of environments. More specifically, during two time periods a high degree of fission-fusion dynamics may have helped hominins adapt to a changing environment. The first was 6-4 million years ago, when early hominins, such as Ardipithecines and Australopithecines, were adapting to a cooling environment (Foley and Gamble 2009). During the end of the Miocene and the Early Pliocene the global climate cooled, which led to a drier, more seasonal, climate in Africa, in which areas of closed forest gave way to more open woodland savannah (Potts 1998; Gowlett 2008). A drier, more seasonal environment may have increased the range size of these early hominins (Gowlett 2008), while this mosaic of habitats would have made the distribution of food more patchy (Foley and Gamble 2009). A higher degree of fission-fusion dynamics may have allowed Australopithecines to feed more efficiently (Gowlett 2008) by keeping travel costs low (Grove 2012; Grove *et al.* 2012). The second period when fission-fusion dynamics were likely to have been important in hominin evolution was around 400,000-300,000 years ago, when changes in technology allowed *Homo heidelbergensis* to hunt mid-sized ungulates (Foley and Gamble 2009). It has been suggested that this change to the exploitation of ungulates led to more seasonal variation in foraging patterns and an "explosion of the scale of fission-fusion" (Foley and Gamble 2009: 3275). Furthermore, an increase in the degree of fission-fusion dynamics during this time is thought to have led to encephalisation in both Neanderthals and modern humans, as an adaption to the cognitive demands of maintaining social relationships in a spatially and temporally dispersed group (Foley and Gamble 2009).

In this study it was shown that olive baboons show some degree of flexibility in their grouping patterns in response to local ecology and demographic pressures. These findings may help to improve understanding of how fission-fusion dynamics could have helped early hominins to adjust to their changing environment. Baboons in general have been suggested to be a good model for early hominin adaptation to the environment (Jolly 1970; Jolly 2001; Elton

2006) because their functional morphologies have certain parallels (Jolly 1970; Jolly 2001; Codron *et al.* 2008). The taxa are related closely enough to have traits that are homologous, but equally are related sufficiently distantly for derived traits to be recognisable too (Jolly 2001). The baboons at GGNP seem to be a particularly good model for human evolution, because they are thought to live in very similar habitats to early hominins. It is now thought that the earliest hominins lived in varied, patchy habitats (Leakey *et al.* 2001; Gowlett 2008). Reconstructions of the habitats of both *Ardipithecus* and *Australopithecus* species, based on the morphological adaptations of mammalian assemblages found with these hominins, indicate that they lived in habitats with ample water and trees, which were a mix of closed to open woodland, bushland and grassland and patches of forest (Reed 1997; White *et al.* 2009). Such an environment is very similar to the mosaic of woodland savannah, forests, and grassland and the numerous rivers seen at GGNP (Dunn 1999; Sommer and Ross 2011).

Baboons at GGNP were found to have some degree of flexibility of grouping patterns, which appeared to be adjusted in response to ecological variation. Similar to GGNP baboons, early hominins may have minimised within-group competition and avoided aggression in this patchy environment by temporarily splitting into smaller subgroups. These smaller subgroups may have been possible because the various woodland habitats would have provided abundant refuges, making perceived predation risk low.

The scarcity of safe sleeping sites and watering holes is thought to play an important role in the formation of Hamadryas baboons' troops (Kummer 1968;

Stammbach 1987). This study suggests that such resources need not be scarce to influence grouping patterns; it was, for example, shown here that even in a region with very high rainfall and numerous rivers, water may be a limiting factor on the ranging patterns of baboons in some seasons. Similarly, it was shown that baboons may have specific preferred sleeping sites, even though safe sleeping places could be found throughout the home range and are thus not limited. This suggests that hominin foraging subgroups may have convened at areas were water was available or at specific sleeping sites, even if such areas were not scarce. This 'central place foraging', *i.e.* returning to a central place following foraging, may have facilitated 'central place provisioning' where food is brought back to the central place, which may have had far-reaching implications for human social organisation, such as a sexual division of labour and sharing of food (Marlowe 2005; Marlowe 2006).

In this study it was also shown that even for an animal with a relatively low risk of infanticide (Lemasson *et al.* 2008), the avoidance of infanticide might have some influence on the structuring of associations, as females were only part of network modules that contained males that had some probability of having fathered their offspring. The risk of infanticide is likely to have been greater in Australopithecines compared to olive baboons; across primates, whenever the period of lactation is longer than gestation, there is a risk of infanticide (van Schaik and Kappeler 1997). Because the ratio between lactation and gestation is well above one in all great apes, it is likely that Australopithecines also faced a high level of infanticide risk. Compared to GGNP troops, infanticide avoidance may thus have played a greater part in the structuring of early hominin groups, and may have been important in shaping the composition of subgroups.

Apart from providing a model for the evolution of human societies, this study also suggests that the patterns of fission-fusion dynamics in hominins may not have been new behaviours but were instead enhancements of a pre-existing trait. Previously it has been suggested that the ability for flexible grouping patterns was a trait of the 'African ape' that was our last common ancestor with chimpanzees and bonobos (Foley and Gamble 2009), and this was first extended in Australopithecines and later 'exploded' in *Homo sapiens* and *Homo neanderthalensis*. More recently it was suggested that these were modifications made to traits that were already present in the last common ancestor of all hominoids (Malone *et al.* 2012). In this study, evidence was provided that ecology and demography have an influence of the grouping patterns of olive baboons, suggesting that the flexibility of grouping patterns may also not have been a new trait in the apes, but that instead this was an enhancement of a trait that may have been present in the last common ancestor of all Catarrhines. What is more, a degree of flexibility of grouping patterns may have been a characteristic of primate species throughout evolutionary history. Quantitative changes in the degree of this flexibility may have occurred at various points in primate evolution and the extent of these changes may have been limited by brain size. Successive enhancements of this plasticity ultimately may have led to the enormous flexibility of human societies we see today. Quantifying fission-fusion dynamics across the primate order, including humans, would allow for a comparative analysis using phylogenetic methods (Harvey and Pagel 1991; Nunn 2011) which could give greater insights into the evolution of the continuum of primate sociality.

7.5 Conclusion & summary

This study has demonstrated the flexibility of grouping patterns of olive baboons at Gashaka-Gumti National Park, and the implications of this flexibility for social relationships. Results highlight the importance of focussing on intra-specific and temporal variation in primate social systems. By using discrete categories to classify primate societies, much of the nuances of this continuum of primate sociality have been overlooked. Socioecological models should incorporate this variation by using continuous measures of social systems, for example by using social network metrics. However, some limitations to the social network approach in the study of fission-fusion dynamics were highlighted, and it was suggested that networks constructed from data over short time-periods may be more useful than networks generated from data collected over weeks or months. However, future research should focus on developing null models against which networks can be tested. While this study shows that a difference in fission-fusion dynamics is associated with a quantitative difference in social behaviour, more research is needed to understand the cognitive adaptations to varying degrees of fission-fusion dynamics; for this a phylogenetic comparative approach seems a promising method. Such research is particularly important given the potential role of fission-fusion dynamics during human evolution. An increase in the degree of fission-fusion dynamics may have helped early hominins to adapt to a global cooling of the climate, and groups may have met at sleeping sites or water sources, even in an environment where such resources are not scarce. However, to understand better the continuum of fission-fusion dynamics, the cognitive demands of fission-fusion, and the role it played in human evolution, it is crucial that future work focuses on the quantification of fission-fusion dynamics in a wide variety of species.

Appendix A

Supplementary material to chapter 3

Table A.1: List of the plant and tree species found in the home ranges of the Gamgam and Kwano troop, and whether these were monthly staples. Only the phenology of monthly staples was monitored in each troop, and therefore only these species were entered into the FAI calculations.

	Present in home range		Monthly staple	
SPECIES	**Gamgam**	**Kwano**	**Gamgam**	**Kwano**
Anona senegalensis	✓	✓	✓	✓
Bridelia ferruginea	✓	✓	✓	✓
Daniellia oliveri	✓	✓	✓	✓
Elaus guineansis	✓	✓	✓	✓
Erythrophleum suaveolens	✓	✓	✓	✓
Landolphia macrantha	✓	✓	✓	✓
Mangifera indica	✓	✓	✓	✓
Parkia biglobosa	✓	✓	✓	✓
Piliostigma thonningi	✓	✓	✓	✓
Prosopis africana	✓	✓	✓	✓
Syzgium guineense var littorale	✓	✓	✓	✓
Uapaca togoensis	✓	✓	✓	✓
Vitex doniana	✓	✓	✓	✓
Dialum spp	✓	✓	✓	✗
Ficus sur	✓	✓	✓	✗
Gramineae	✓	✓	✓	✗
Pandanus candelbarum	✓	✓	✓	✗
Parinari excelsa	✓	✓	✓	✗
Pterocarpus erinaceus	✓	✓	✓	✗
Rottboelia exaltata	✓	✓	✓	✗
Terminalia latifolia	✓	✓	✓	✗
Terminalia spp2	✓	✓	✓	✗
Amaranthus spinosus	✓	✗	✓	✗
Borassus aethiopium	✓	✗	✓	✗
Gardenia nitida	✓	✗	✓	✗
Liana	✓	✗	✓	✗
Mucuna poggei	✓	✗	✓	✗
Panicum maximum	✓	✗	✓	✗
Alchornea cordifolia	✓	✓	✗	✓
Cynometra megalophylia	✓	✓	✗	✓
Landolphia sp1	✓	✓	✗	✓
Landolphia sp2	✓	✓	✗	✓
Pseudospondias microcarpa	✓	✓	✗	✓
Tricalysia oligonvera	✓	✓	✗	✓
Ficus polita?	✗	✓	✗	✓
Manilkara obovata	✗	✓	✗	✓
Phoenix reclinata	✗	✓	✗	✓
Xylopia spp	✗	✓	✗	✓

Table A.2: Species that occurred in the home ranges of both troops, but for which the phenology was only monitored in one troop, and thus were entered in the FAI calculations of only one troop. The numbers of months that each food item was a staple food, and the average time troop spent feeding on each item were taken from Warren (2003).

	Entered in FAI calculations			
SPECIES	**Gamgam**	**Kwano**	**Number of months food is staple**	**Average monthly feeding time (%)**
Dialum spp FRUIT	✓	✗	1	1.1
Ficus sur FRUIT	✓	✗	3	1.3
Gramineae SEED	✓	✗	2	5.9
Pandanus candelbarum FRUIT	✓	✗	1	4.0
Parinari excelsa SEED	✓	✗	2	5.5
Parinari excelsa FRUIT	✓	✗	1	9.2
Pterocarpus erinaceus FLOWER	✓	✗	1	5.3
Rottboelia exaltata SEED	✓	✗	2	20.9
Terminalia latifolia FLOWER	✓	✗	0	<1
Terminalia spp2 LEAF	✓	✗	1	2.5
Alchornea cordifolia FRUIT	✗	✓	1	1.7
Cynometra megalophylia LEAF	✗	✓	1	11.8
Cynometra megalophylia EXUDATE	✗	✓	1	1.1
Landolphia sp1 FRUIT	✗	✓	1	1.9
Landolphia sp2 FRUIT	✗	✓	1	3.1
Pseudospondias microcarpa FRUIT	✗	✓	1	2.6
Tricalysia oligonvera FRUIT	✗	✓	1	1.1

Seasonal activity budgets

Activity budgets were determined from focal observations. Behaviours recorded during focal observations were classified into five behavioural categories (Dunbar 1992). Feeding and foraging, and drinking were classified as 'forage'; resting, eating items from cheek pouches, sleeping and nursing were classified as 'rest'; giving and receiving grooming, aggression, play, sex, subordinate and other social behaviours were classified as 'social'; locomotion was classified as 'travel' and other behaviours as 'other' (see chapter 2 for a full description of these behaviours). Activity budgets determined for each individual (Gamgam *N* = 6; Kwano *N* = 8) in each of four seasons, and seasonal time budgets components were compared using repeated measures ANOVAs. When data were not spherical, the Greenhouse-Geisser statistic is reported instead. Planned contrasts were used to investigate the differences between seasonal time budget components further.

Table A.3: Results for the repeated measures ANOVAs comparing seasonal time budget components of the Gamgam troop. Bold values indicate that season had a significant effect on the proportion of time that was allocated to that activity. *N* = 6 individual time budgets.

TIME BUDGET COMPONENT	*F*	*df*	*p*
Forage	**15.16**	**3, 15**	**< 0.001**
Travel	1.16	3, 15	0.357
Rest	**5.10**	**3, 15**	**0.012**
Social	1.22	1.07, 5.36	0.321

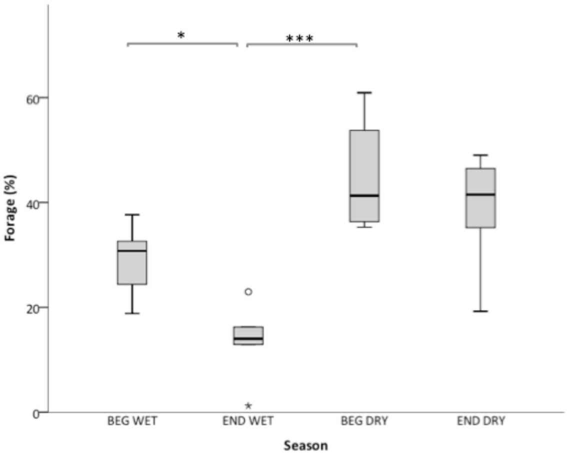


Figure A.1: Comparison of the proportion of time Gamgam baboons spent foraging in each season. * indicates $p < 0.05$, *** indicates $p < 0.001$.

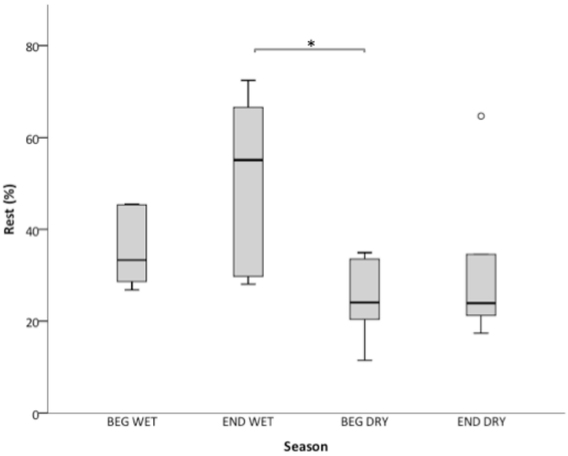


Figure A.2: Comparison of the proportion of time Gamgam baboons spent foraging in each season. * indicates $p < 0.05$.

Table A.4: Results for the comparison of seasonal time budget components of the Kwano troop. Bold values indicate that season had a significant effect on the proportion of time that was allocated to that activity. *N* = 8 individual time budgets.

TIME BUDGET COMPONENT	*F*	*df*	*p*
Forage	1.42	3, 21	0.264
Travel	**7.68**	**3, 21**	**0.001**
Rest	2.62	3, 21	0.078
Social	0.93	3, 21	0.443

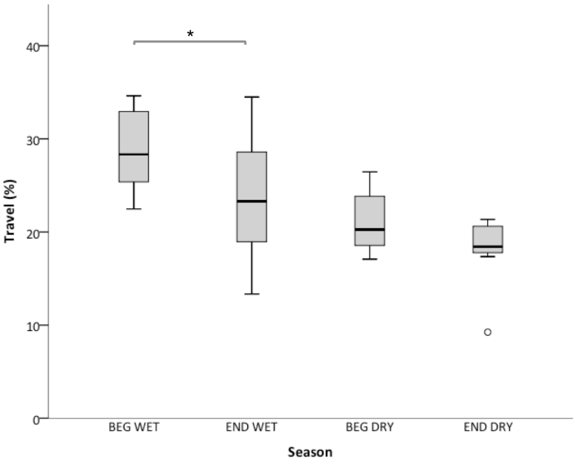
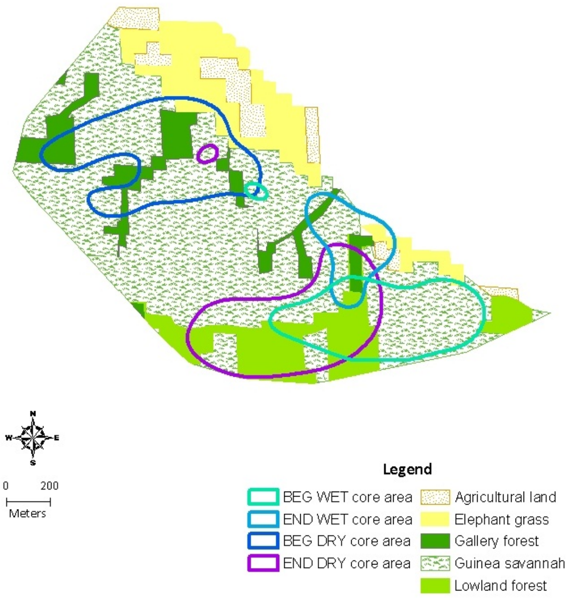


Figure A.3: Comparison of the proportion of time Kwano baboons spent travelling in each season. * indicates $p < 0.05$.

Core areas

Fixed density kernels were used to determine core areas within the home range using the GPS locations of the focal animal taken every 15 minutes. Kernel density estimation can give an indication of how intensely animals use different parts of their home range (Rodgers and Kie 2007). The kernel density estimation is a non-parametric method in which the probability of finding an animal in a particular part of the home range is estimated. For these analyses the Home Range Tool extension for ArcGIS (Rodgers *et al.* 2007) was used, and the focal GPS locations for each season. The smoothing factor or bandwidth (*h*) determines how wide the kernel is for each observation. Here, *h* was set to *href*, in which the optimum value of *h* is chosen with reference to the bivariate normal distribution (Rodgers and Kie 2007). Core areas were defined as those areas within the home range in which the probability of finding an animal is 0.5.

a)



b)

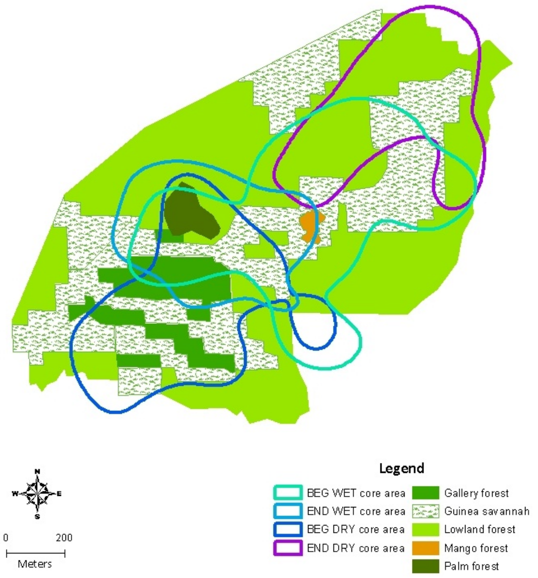


Figure A.4 a & b: The home ranges with seasonal core areas for a) the Gamgam troop and b) the Kwano troop. Core areas are fixed density kernels estimates and give an indication of how intensely animals used different parts of their home range. Core areas were defined as areas in which the probability of finding an animal was 0.5.

Appendix B

Supplementary material to chapter 4

Table B.1: Matrix showing dominance relationships of adult and subadult females in the Gamgam troop. Cells indicate the number of aggressive and submissive interactions between individuals. Individuals on rows were dominant in the interactions, individuals in columns were subordinate. Individuals are ranked from high to low, with highest ranking female in first row and column.

	MMK	KAN	GLO	BUW	STR	MMW
MMK	*	18	9	12	28	16
KAN	0	*	24	19	48	20
GLO	1	12	*	9	27	5
BUW	2	5	5	*	9	7
STR	1	10	20	6	*	18
MMW	1	4	4	1	1	*

Table B.2: Matrix showing dominance relationships of adult and subadult females in the Kwano troop. Cells indicate the number of aggressive and submissive interactions between individuals. Individuals on rows were dominant in the interactions, individuals in columns were subordinate. Individuals are ranked from high to low, with highest ranking female in first row and column.

	DRK	LMI	YMK	SAD	MOM	TJL	BRA	LDI	RAB	KYE	FDI	KRM
DRK	*	2	2	7	5	1	0	5	10	2	10	4
LMI	1	*	3	2	1	2	3	2	1	1	5	2
YMK	0	0	*	5	2	0	2	1	1	9	4	0
SAD	0	1	0	*	2	1	0	3	5	7	13	3
MOM	0	0	0	0	*	3	3	1	4	3	2	6
TJL	0	0	0	0	0	*	0	0	1	2	4	0
BRA	0	0	0	0	0	0	*	0	3	0	0	2
LDI	0	2	0	0	0	0	0	*	9	7	1	5
RAB	0	0	1	0	0	0	0	4	*	2	0	2
KYE	0	1	1	0	2	0	0	1	1	*	1	2
FDI	0	0	0	0	0	1	0	3	0	0	*	0
KRM	0	0	0	0	0	0	0	0	0	1	0	*

Drinking sites and core areas

Core areas are defined as those areas within the home range in which the probability of finding an animal was 0.5 (see Appendix A for details). The GPS location of the focal animal was recorded when it was observed to drink, in order to obtain information on drinking sites. The locations of permanent rivers and seasonal streams were determined by walking in the riverbed, and taking GPS readings at regular intervals.

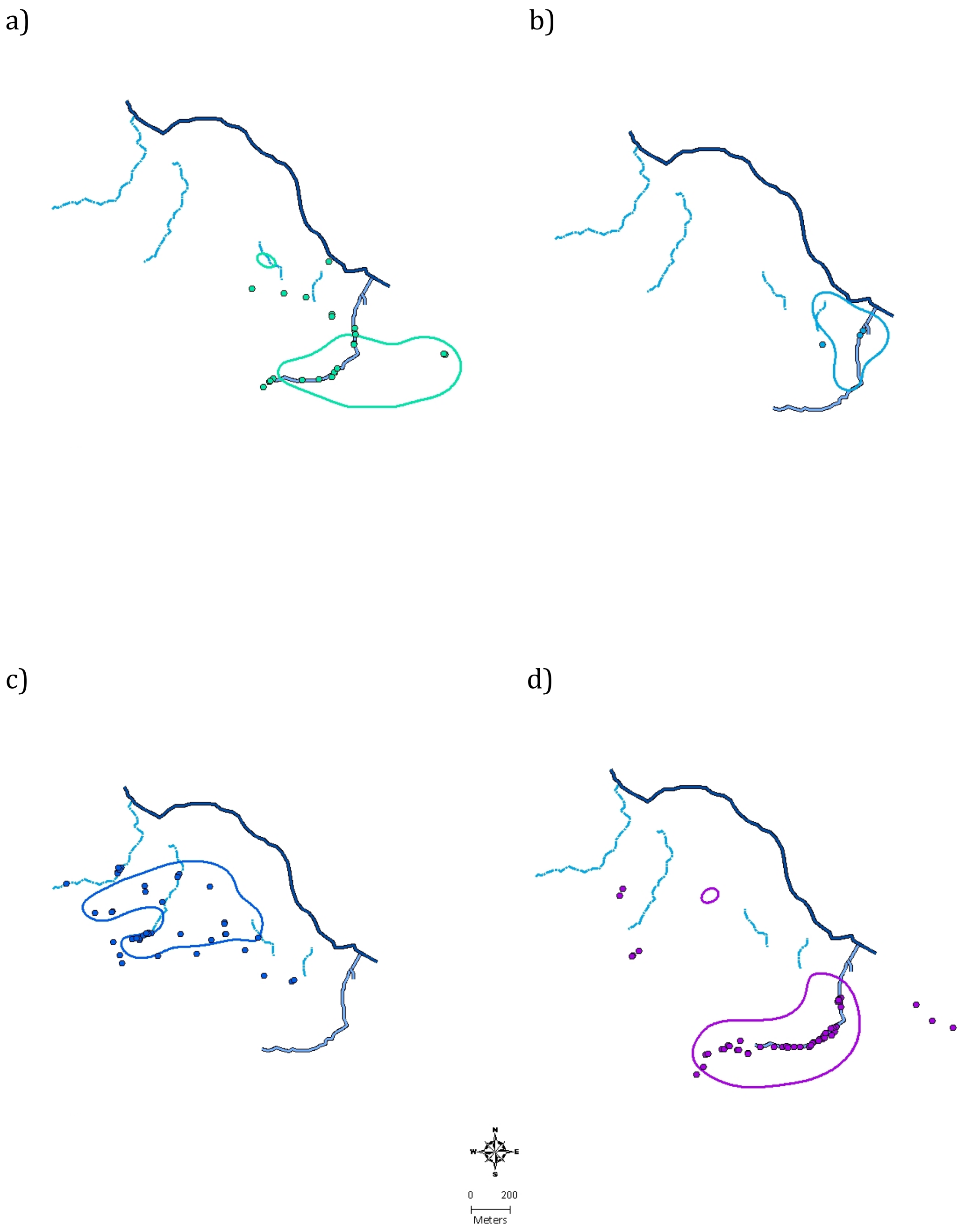


Figure B.1 a-d: Maps showing the river *Gamgam* (solid dark blue line), the *Tapare tributary* (solid light blue line), and seasonal streams (dashed lines) in the Gamgam home range, along with drinking sites (circles) and the outlines of seasonal core areas for a) the beginning of the wet season; b) the end of the wet season; c) the beginning of the dry season; d) the end of the dry season.

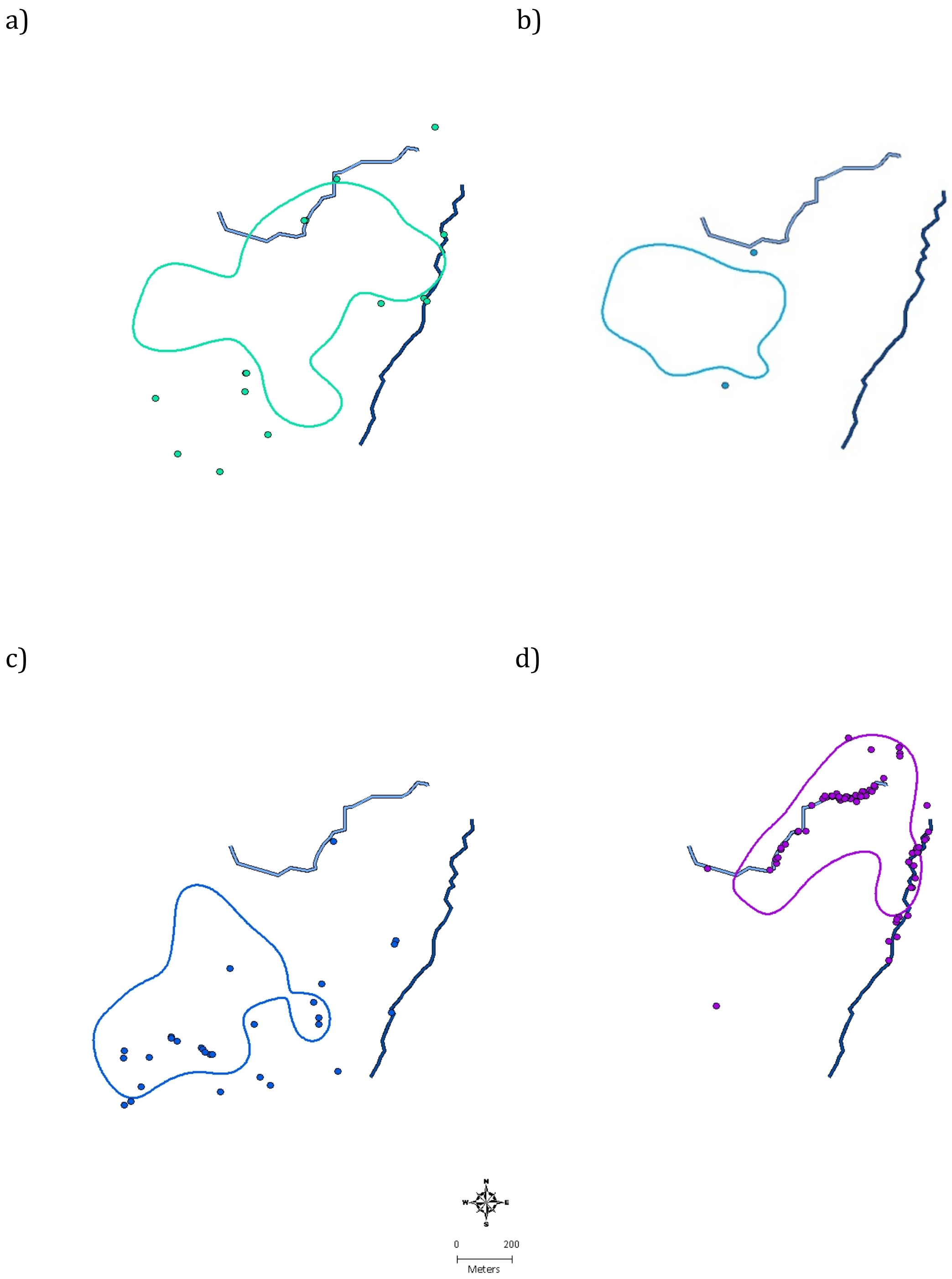


Figure B.2 a-d: Maps showing the *Mayo Be* (solid light blue line) and the *Mayo Dim* (solid dark blue line) rivers in the Kwano home range, along with drinking sites (circles) for the Kwano troop and the outlines of seasonal core areas for a) the beginning of the wet season; b) the end of the wet season; c) the beginning of the dry season; d) the end of the dry season.

Appendix C

Supplementary material to chapter 5

Activity budgets

Methods for the estimation of activity budgets are given in Appendix A. Here, activity budgets calculated for each individual (Gamgam: n = 9; Kwano: n =20) over the entire study period were used. Between-troop comparisons were made using independent t-tests. Results are given in Table C.1.

Table C.1: Results for the between-troop comparison of time budget components. Time budgets were calculated for each focal animal over the entire study period.

	Mean time budget allocation (%)				
	GAMGAM (N = 9)	KWANO (N = 20)	t	df	p
Forage	43.47	45.37	-0.40	9.63	0.697
Rest	27.45	25.46	0.61	27	0.550
Social	8.32	5.80	1.52	27	0.141
Travel	20.15	22.89	-1.81	27	0.081
Other	0.61	0.48	0.45	27	0.655

Appendix D

Supplementary material to chapter 6

Table D.1: Comparisons of habitat-specific mean daily party size. Mann-Whitney *U* values are given with *p*-value in brackets, and the habitat type in which party sizes were larger. Bold values indicate a significant difference.

	Gallery forest	Lowland forest	Guinea savannah	Burned Guinea savannah	Palm forest
Gallery forest	-	**1918 (0.002) GF**	**4346 (0.045) GF**	1908 (0.933) BGS	**1201 (0.005) GF**
Lowland forest		-	2026 (0.070) GS	**607 (0.007) BGS**	785 (0.607) LF
Guinea savannah			-	1394 (0.075) BGS	1245 (0.057) GS
Burned Guinea savannah				-	**406 (0.023) BGS**
Palm forest					-

Table D.2: Comparisons of habitat-specific mean daily party size as a proportion of troop size. Mann-Whitney *U* values are given with *p*-value in brackets, and the habitat type in which a larger proportion of the troop were seen together. Bold values indicate a significant difference.

	Gallery forest	Lowland forest	Guinea savannah	Burned Guinea savannah	Palm forest
Gallery forest	-	**1623 (< 0.001) GF**	4443 (0.076) GF	1857 (0.750) GF	**835 (< 0.001) GF**
Lowland forest		-	**1746 (0.003) GS**	**511 (< 0.001) BGS**	716 (0.253) LF
Guinea savannah			-	1424 (0.103) BGS	**920 (< 0.001) GS**
Burned Guinea savannah				-	**257 (< 0.001) BGS**
Palm forest					-

Table D.3: Results for the comparisons of habitat-specific spatial cohesion measured by the volume (m^3) over which a party was spread. Mann-Whitney *U* values are given with *p*-value in brackets, and the habitat type with a greater area. Bold values indicate a significant difference.

	Gallery forest	Lowland forest	Guinea savannah	Burned Guinea savannah	Palm forest
Gallery forest	-	**1730** **(< 0.001)** **GF**	4799 (0.348) GF	**827** **(< 0.001)** **BGS**	**1053** **(< 0.001)** **GF**
Lowland forest		-	**1658** **(< 0.001)** **GS**	**245** **(< 0.001)** **BGS**	801 (0.708) LF
Guinea savannah			-	**707** **(< 0.001)** **BGS**	**1022** **(0.002)** **GS**
Burned Guinea savannah				-	**145** **(< 0.001)** **BGS**
Palm forest					-

Table D.4: Results for the comparisons of habitat-specific spatial cohesion measured by the volume (m^3) over which a party was spread, taking into account the size of a party. Mann-Whitney *U* values are given with *p*-value in brackets, and the habitat type with a greater area. Bold values indicate a significant difference.

	Gallery forest	Lowland forest	Guinea savannah	Burned Guinea savannah	Palm forest
Gallery forest	-	**1798** **(< 0.001)** **GF**	5043 (0.726) GF	**729** **(< 0.001)** **BGS**	**1103** **(< 0.001)** **GF**
Lowland forest		-	**1676** **(< 0.001)** **GS**	**238** **(< 0.001)** **BGS**	807 (0.754) LF
Guinea savannah			-	**681** **(< 0.001)** **BGS**	**1031** **(0.003)** **GS**
Burned Guinea savannah				-	**154** **(< 0.001)** **BGS**
Palm forest					-

Table D.5: Results for the comparisons of habitat-specific spatial cohesion measured by the number of individuals that were found within a 10m radius of the centre of a party. Mann-Whitney *U* values are given with *p*-value in brackets, and the habitat type with a greater area. Bold values indicate a significant difference.

	Gallery forest	Lowland forest	Guinea savannah	Burned Guinea savannah	Palm forest
Gallery forest	-	**2061** **(0.012)** **GF**	4818 (0.381) GF	**777** **(< 0.001)** **GF**	**1365** **(0.049)** **GF**
Lowland forest		-	2071 (0.102) GS	**588** **(0.004)** **LF**	816 (0.809) PF
Guinea savannah			-	**876** **(< 0.001)** **GS**	1381 (0.235) GS
Burned Guinea savannah				-	**363** **(< 0.004)** **PF**
Palm forest					-

Table D.6: Results for the comparisons of habitat-specific spatial cohesion measured by the number of individuals that were found within a 10m radius of the centre of a party, taking into account the size of a party. Mann-Whitney *U* values are given with *p*-value in brackets, and the habitat type with a greater area. Bold values indicate a significant difference.

	Gallery forest	Lowland forest	Guinea savannah	Burned Guinea savannah	Palm forest
Gallery forest	-	2456 (0.303) LF	5181 (< 0.984) LF	**580** **(< 0.001)** **GF**	1415 (0.078) PF
Lowland forest		-	2226 (0.316) LF	**330** **(< 0.001)** **LF**	780 (0.560) PF
Guinea savannah			-	**650** **(< 0.001)** **GS**	1306 (0.108) PF
Burned Guinea savannah				-	**174** **(< 0.001)** **PF**
Palm forest					-

Sleeping sites

Sleeping sites were recorded at sites at which the focal baboon was found at dawn (*i.e.* around 6-6:30) or at dusk when the focal entered the trees for the night (*i.e.* around 18:00). These sleeping sites were imported into the home range map for each troop in ArcGIS (ESRI 2011), which included vegetation types and the seasonal core areas.

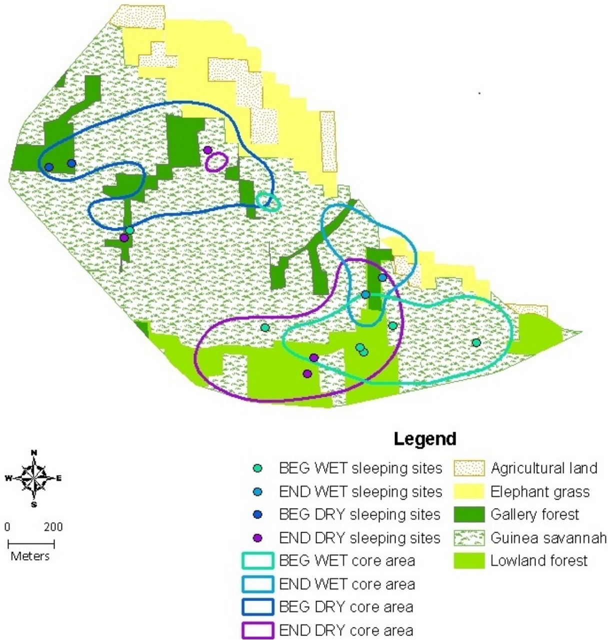


Figure D.1: Map showing the Gamgam sleeping sites for each season, along with the seasonal core areas. Core areas were defined as areas within which the probability of finding an individual of the Gamgam troop was 0.5.

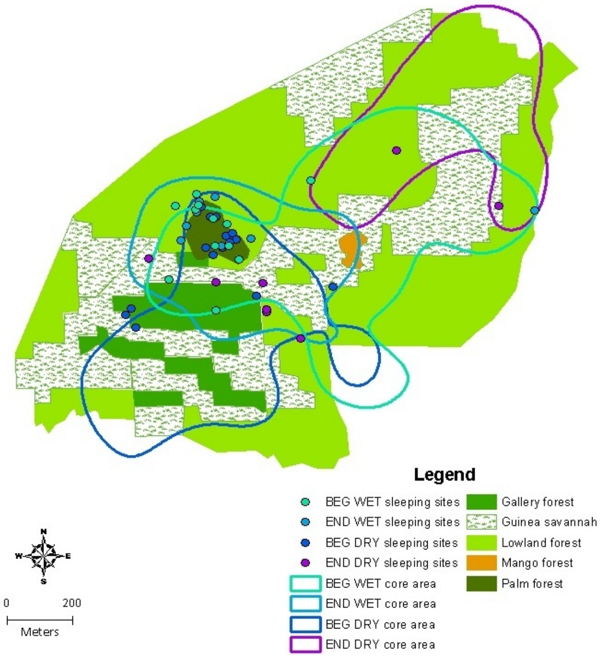


Figure D.2: Map showing the Kwano sleeping sites for each season, along with the seasonal core areas. Core areas were defined as areas within which the probability of finding an individual of the Kwano troop was 0.5.

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