Leadership, coordinated behaviour, and information use in a social primate

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Abstract

A substantial body of work has addressed why animals live in groups. However, few studies have described how group-living vertebrates are able to coordinate their actions and make collective decisions; crucial if individuals are to maximise the benefits and minimise the costs of grouping. In this thesis, I apply observational, experimental, and theoretical methods to address this paucity of knowledge, using a social primate – chacma baboons (*Papio ursinus*) – as a model system. Specifically, I investigate three concepts upon which group-living is reliant: information use, coordinated behaviour and leadership. I address each of these concepts in turn. First in the case of information use, I show that the foraging decisions of individual baboons meet the predictions of 'producer-scrounger games' – evolutionary models developed to predict when a social forager should find its own food patch, or join the discovery of a group-mate. I also use a simple theoretical model to show that social information can allow less well-informed members of large groups to reach a correct decision with the same probability as more well-informed members of small groups. Second, in the case of coordinated behaviour, I show that individual state and the environment (both social and ecological conditions) can influence levels of behavioural synchrony in baboons. Moreover, behavioural synchrony in baboon groups was seen to positively influence the behaviour of another species: rock kestrels (*Falco rupicolus*) derived foraging opportunities by associating with baboons as they travel-forage together in desert vegetation 'flushing' kestrel prey items. Finally, I examined leadership behaviour. I used an experimental design that allowed me to test between two alternate decision-making modes: despotism (i.e. leadership) and democracy (i.e. a majority rule, voting). Baboon group foraging decisions were consistently led by the individual who acquired the most benefits from those decisions, namely the dominant male. Subordinate group members followed the leader despite considerable costs, and follower behaviour was mediated by social ties to the leader.

Declaration

I, Andrew James King, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Andrew King

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Chapter 1 – Introduction

Colonies, schools, flocks, herds, and troops – the formation of groups is a universal phenomenon in the Animal Kingdom. Such incredible diversity of sociality has intrigued behavioural and evolutionary biologists, and there is a rich and diverse literature that strives to explain the origins and maintenance of group living.

Individuals from almost any animal species will be found in association with conspecifics at certain points in their lives. At one end of the spectrum solitary individuals, if successful enough to find a mate, will have temporarily belonged to a pair. At the other extreme, individuals can spend their entire lives, from the moment they are born until the moment they die, in close proximity to many other individuals. Most animals however, fall somewhere in between, forming and breaking groups with remarkable frequency (Couzin, 2006; Lehmann et al., 2007a; Van Schaik, 1999). Current ideas on the evolution and ecology of group living are therefore the result of researchers scrutinizing the interactions that occur when individuals come into contact with one another, and trying to understand the short- and long-term consequences of such interactions (Krause and Ruxton, 2002; Parrish and Edelstein-Keshet, 1999).

Two most commonly cited reasons for grouping in animals are that it can reduce predation risk, and increase foraging opportunities. In the case of reduced predation risk, several studies have demonstrated that larger groups are more effective at detecting predators (Elliot, 1985; Roberts, 1996; Treves, 2000). This classical 'many-eyes theory' is generally considered to be a consequence of an increased number of individuals scanning for predators (Childress and Lung, 2003; Lima and Bednekoff, 1999), and an increased potential for information transfer between individuals (Fernandez-Juricic and Kacelnik, 2004; Jackson and Ruxton, 2006). Grouping can also 'dilute' predation risks (Beauchamp and Ruxton, 2008; Krause and Ruxton, 2002). Dilution is the reduced probability of a given individual being predated as the presence of more conspecifics increases the likelihood that another individual will be targeted. Individuals belonging to groups can also actively deter or mob predators to reduce the chances of being preyed upon (Graw and Manser, 2007; Owings and Coss, 1977; Shields, 1984).

Foraging benefits to grouping are also widely studied (Giraldeau and Caraco, 2000; Krause and Ruxton, 2002). The first foraging benefit relates to resource defence. Larger groups can gain foraging advantages over smaller groups by better acquiring or defending high-quality food resources (Cant et al., 2002; Isbell et al., 1998; Spong, 2002). However, grouping also introduces a cost of intra-group feeding competition (see discussion of costs later). A second major foraging benefit derived from grouping is the behaviour of other group members: which enables individuals to make faster, more accurate assessments of potential food sources through the information that group-mates provide (Giraldeau and Caraco, 2000; Valone, 2007; Valone and Templeton, 2002) . This can be most usefully applied to situations where animals forage in ephemeral patches. Individuals that interact with conspecifics can thus exploit their food discoveries (Vickery et al., 1991). This can even be achieved remotely: when individuals habitually return to a specific location after foraging – e.g. where birds return to a roost site before travelling back to a discovered food source – such locations can act as information centres (Brown, 1986; Ward and Zahavi, 1973). Other variants can also be identified, e.g. informed individuals can consistently lead groups to food sources (Couzin et al., 2005; Reebs, 2000). However, this may only occur when the informed animals have sufficient incentives (Foley et al., 2008), which I will discuss in more detail later (see below and Chapter 7). Finally, in the case of cooperative hunting, large group size can also allow predators to capture prey too large for a single individual (Boesch, 1994; Creel and Creel, 1995; Packer and Ruttan, 1988).

Other well-studied benefits of grouping include increased mating opportunities as a consequence of individuals gathering within sight of each other to court and compete (Kappeler and van Schaik, 2002; Kirkpatrick and Ryan, 1991; Lank and Smith, 1992); conserving heat by huddling together and reducing the fraction of their surface area exposed to cold (Beauchamp, 1999; Roverud and Chappell, 1991; Yahav and Buffenstein, 1991); and reduced energetic costs during movement as a result of individuals placing themselves behind conspecifics (Drucker and Lauder, 1999; Owsianowski and Kesel, 2008).

In contrast, relatively less is known about the costs of grouping (Krause & Ruxton). Competition over food resources is one cost that has been better studied. Feeding competition can take many forms; I will mention the two main ones here: 1) scramble competition, and 2) contest competition. Scramble competition occurs when groups of socially foraging animals feed on food types that are not easily monopolised, and which are thus often dispersed relatively evenly across the habitat (Schwagmeyer and Woontner, 1986; Van Schaik and Van Noordwijk, 1988). Contest competition occurs where food sources can be monopolised, and is a direct form of feeding competition in which individuals act to secure a greater share of the resources (Kazahari and Agetsuma, 2008; Koenig, 2000; Utami et al., 1997). It is also sometimes referred to as direct competition (Janson and van Schaik, 1988), and can involve aggression over food, prey stealing and displacement from good feeding sites (Barton et al., 1996; Morand-Ferron et al., 2007; Watts, 1994).

There are other less obvious costs to grouping too. Aggression may not necessarily be associated with food, but a consequence of competition over other resources, such as mates (Cowlishaw and Dunbar, 1991; Garcia et al., 2006). Misdirected parental care (Price et al., 1983; Roulin, 2002; Wisenden, 1999) where males provide parental care to offspring which they have not sired as a consequence of confused paternity (see Heistermann et al., 2001; Nunn, 1999), or an increased potential for pathogen transfer as a consequence of density effects in larger groups (De Koeijer et al., 1998; Reno, 1998; Wilson, 2003) can each introduce substantial costs to an individual. Also, larger groups may be easier for predators to detect, although there are only limited tests of this cost to grouping (see Cresswell, 1994).

Traditional research has therefore adopted a cost-benefit approach to understanding the trade-offs associated with group living (Hoare et al., 2004; Molvar and Bowyer, 1994; Van Schaik, 1999). This has allowed researchers considerable insight into the question of why, and when, animals should form groups (Krause and Ruxton, 2002). While it is safe to say that there is no such thing as a typical animal group, the unifying concepts regarding grouping behaviours allow us to discuss the processes that govern the evolution and maintenance of grouping behaviour throughout the Animal Kingdom

(Ebenspherger and Cofre, 2001; Kappeler and van Schaik, 2002; Lindstrom, 1986).

In this thesis I focus on three unifying concepts upon which the maximisation of the aforementioned benefits – and minimisation of many of the costs – of grouping are reliant. These are information transfer (Galef and Giraldeau, 2001; Sumpter et al., 2008), coordinated behaviour (Lima, 1995; Pays et al., 2007; Stewart and Harcourt, 1994) and leadership (Couzin et al., 2005; Leca et al., 2003; Reebs, 2000). I will provide a brief overview of each of these unifying concepts in turn (Sections A, B, and C below). Many of the examples I draw upon are deliberately biased toward vertebrate systems, since my focal species is a social primate, the chacma baboon, *Papio ursinus* (see Chapter 2). In the final section of the Introduction (Section D), I will outline the organisation of my thesis and my chapter objectives.

A. Information transfer

A key benefit of being near to others is access to information (Sumpter et al., 2008; Ward et al., 2008). Individuals that are able to monitor and use the information that other individuals provide ('social' or 'public' information: Dall et al., 2005; Valone, 2007; Valone and Templeton, 2002) can increase their own rate of finding food (Fernandez-Juricic and Kacelnik, 2004; Reader et al., 2003; Ryer and Olla, 1991) or detecting a predator (Cordi et al., 2005; Fairbanks and Dobson, 2007; Fernandez-Juricic et al., 2004). The use of social information can therefore be thought of as a force that drives patterns of grouping behaviour. Indeed, theoretical, empirical, and comparative studies have shown that the use of social information can promote the evolution of sociality (Beauchamp et al., 1997; Buckley, 1997a; Buckley, 1997b; Safi and Kerth, 2007). Nevertheless, the investigation of social information use has largely been confined to species which only form ephemeral groups – potentially for the very reason of acquiring information (e.g. Brown, 1986; Ward and Zahavi, 1973). Investigations into use of social information for animal groups in which group-living evolved for other reasons (see Wrangham, 1980), but in which social information can offer yet another benefit, remain scarce (though see Bicca-Marques and Garber, 2005 for an example). Moreover, assumptions are commonly made about the type of information that can be collected, its accuracy, and the costs associated with collecting it (Krause and Ruxton, 2002; McLinn and Stephens, 2006). The validity of these assumptions remains largely untested, at least in stable social groups (Valone, 2007).

While social information may be highly beneficial when it is reliable, it may equally incur costs when it is unreliable. The magnitude of these costs may be variable. For instance, unreliable information regarding the quality of a food source may have a relatively small cost: the individual will simply be required to restart its search effort. Yet if information is unreliable concerning the approach of a predator, the cost may be ultimate – being preyed upon. Thus, it may pay for individuals to react to any possible threat even if it turns out to be harmless, on the basis that the costs of an incorrect alarm are much lower than the costs of failing to give/respond to a genuine alarm. This 'better safe than sorry' strategy appears common (Haftorn, 2000; Hare and Atkins, 2001), but can also result in costs; conspecifics and heterospecifics can give false alarm calls in order to usurp food discoveries (Beauchamp and Ruxton, 2007; Tramer, 1994; Whiten and Byrne, 1988).

The range at which information can be detected also varies enormously dependent on species and context. For example, in relatively small (and stable) groups, like those found in primates or carnivores, group members can usually communicate directly with all other members (e.g. Boinski, 1993; Stewart and Harcourt, 1994). This has been termed ‘global communication’ (Conradt and Roper, 2003). In contrast, for relatively large (and often ephemeral) groups such as large flocks of birds (Ballerini et al., 2008), fish shoals (Couzin and Krause, 2003; Levin and Grillet, 1988), colonies of social insects (Lindauer, 1957; Visscher, 2007; Visscher and Seeley, 2007), or herds of ungulates (Gueron and Levin, 1993), group members cannot communicate directly with all other members. Here, the group is dependent on ‘local communication’ (Conradt and Roper, 2003) with only their spatial neighbours (Couzin and Krause, 2003; Halloy et al., 2007; Sumpter et al., 2008). The consequence of these different levels of communication can have profound affects, not least for the fundamental maintenance of groups, but also upon their synchrony of behaviours and coordination of activities. Which takes me on to the next concept which I address in this thesis: coordinated behaviour (Dostalkova and Spinka, 2007; Martinez et al., 2007; Visscher and Seeley, 2007).

B. Coordinated behaviour

For individuals to accrue the benefits and minimise the costs of group living (see above) they are required to be at least partially coordinated in their activities and travel directions. At the most fundamental level, this requires that some individuals do not go and forage while the rest of the group remains at their sleeping site, for example (Conradt and Roper, 2000). Group-living animals must therefore 'co-ordinate to act in unison' (Sumpter et al., 2008; Sumpter, 2006). This process has been termed behavioural synchronisation (Calhim et al., 2006; Dunbar and Shi, 2008).

The benefits of behavioural synchronisation are not only limited to preventing stragglers from getting lost. It can be beneficial for animals to be in periodic synchronisation with respect to a variety of behaviours. Synchronising periods of activity and rest in ant colonies can increase their output (Cole, 1991a; Cole, 1991b), while close within-group birth synchrony can reduce the predation of vulnerable offspring (predator swamping), in a variety of species (Boinski, 1987; Gregg et al., 2001; Rutberg, 1984). Equally, anti-phase synchronisation, where one or a number of individuals do the opposite to the rest of the group can also be an efficient way of scheduling activities. Classic examples involve sentinel behaviour, where one or a few animals (normally the most satiated) take the duty of anti-predator vigilance behaviour (Clutton-Brock et al., 1999), allowing others to decrease their individual vigilance and thus increase foraging time (Bednekoff and Woolfenden, 2003; Hollen et al., 2008; Wright et al., 2001).

Activity synchronisation (and asynchrony) can nevertheless be costly to individuals if it requires them to postpone an activity that would be personally more profitable in order to do what the rest of the group (or opposite of what the rest of the group) is doing (Conradt and Roper, 2000). This scenario will be more common in more stable social groups (e.g. primates: Wrangham, 1980), where groups can be particularly heterogeneous as a consequence of dominance (Cowlishaw and Dunbar, 1991; Rands et al., 2006), relatedness (Csillery et al., 2006; Silk, 2002), internal state (Lendvai et al., 2004; McNamara and Houston, 1996; Rands et al., 2003), and levels of information (Biro et al., 2006; Couzin et al., 2005; Dyer et al., 2008). Specifically, it means that individuals are required to balance their desired actions and behaviours with that of their neighbours (Biro et al., 2006; Dussutour et al., 2008). Such costs could influence the individual's decision to remain in the group. Indeed, where between-individual variation in the timing of activities becomes too large then animals may not be able to reach a 'consensus' (Conradt and Roper, 2003) on their activities and coordination is predicted to break down (Conradt and Roper, 2007; Kuramoto, 1984). So how do animal groups coordinate themselves under such conflict of interests?

C. Leadership

Models by Rands and colleagues (Rands et al., 2003; Rands et al., 2004) provide a straightforward resolution to the problem of group coordination where individuals' interests differ. They use a game-theoretic, state-dependent, individual-based approach to model the foraging behaviour of a pair of animals. Their models predict that differences in the energetic reserves of the two players spontaneously develop, as a result of stochastic processes, leading them to adopt different behavioural roles. The individual with lower reserves tends to emerge as the leader, since the individual with the higher reserves will always prefer to minimise predation risk by foraging only when the other player is doing so. However, this approach only considers small groups (two animals), and while the effects of the decision rule derived from this model have been explored in larger groups (Rands et al., 2004; Rands et al., 2006), these explorations have not specifically addressed the question of how groups reach a consensus, on the timing of activities and travel directions for example. For this, alternative approaches are needed.

Much of the coordination in the timing of activities and travel directions evident in biological systems can be the result of relatively simple interaction patterns among group members (Couzin and Franks, 2003; Halloy et al., 2007; Visscher, 2007). In such 'self-organising systems' (Bonabeau et al., 1997; Couzin and Krause, 2003; Sumpter et al., 2008) multiple individuals following simple movement rules can produce complex collective behaviours (Ballerini et al., 2008). Such emergent collective behaviours can therefore be explained without invoking complex decision-making abilities at the level of the individual (Couzin, 2007; Couzin et al., 2002). But whilst self-organising models can be usefully applied to a variety of group behaviours and in many study systems (Bonabeau et al., 1997; Couzin and Franks, 2003), such models tend to work best where groups are composed of individuals with identical interests, and which only communicate locally. Typical examples are decisions made by eusocial insects about choosing a new nest site (Britton et al., 2002; Lindauer, 1957; Visscher, 2007), or by navigating birds about travel routes (Guilford and Chappell, 1996; Simons, 2004). For many of the groups that we see in nature, however, individuals and their interests will differ (see above).

To specifically address the problem of conflicts of interests, Conradt and Roper (2003) examined consensus decisions: "when the members of a group choose between two or more mutually exclusive actions with the aim of reaching a consensus". They specifically address the issue of 'consensus costs', which are the costs (in terms of reduced fitness) of animals forgoing their own optimal action to comply with the group consensus (Conradt and Roper, 2005). Thus, if there is a large conflict of interest involved in a consensus decision, the consensus costs will be equally large. They modelled two alternative decision processes. First, decisions may be made in a democratic manner, where the average behaviour of individuals is adopted. Second, decisions may be made by a single animal or minority of animals in a more despotic manner (Conradt and Roper, 2003; Conradt and Roper, 2005; Conradt and Roper, 2007). Conradt and Roper's models show that both democratic and despotic decision-making can evolve through, and be maintained by, individual selection (Conradt and Roper, 2007). However, they predict that under most conditions the costs to subordinate group members, and to the group as a whole, are considerably higher for despotic than for democratic decisions. As a consequence, they suggest that democratic decisions are more likely to evolve. Conradt and Roper's models further indicate that democratic decisions can even evolve when groups are heterogeneous in composition; when alternative decision outcomes differ in potential costs and these costs are large; when grouping benefits are marginal; or when groups are close to, or above, optimal size (Conradt and Roper, 2007).

Empirical tests of consensus decision-making in vertebrate groups have largely concentrated on decisions about travel routes or the timing of activities (Conradt & Roper 2005). Within this body of research, evidence for both democratic and despotic decision-making has been presented, e.g. primates (Boinski and Campbell, 1995; Byrne, 2000; Leca et al., 2003; Schaller, 1963), ungulates (Dumont et al., 2005; Fischhoff et al., 2007; Prins, 1996; Squires and Daws, 1975; Stine et al., 1982), and birds (Biro et al., 2006; Black, 1988; Radford, 2004). Yet insights into why democratic or despotic decisions might occur remain scarce (Conradt and Roper, 2005). Additionally, why despotism appears to be as widespread as democracy – contrary to theoretical predictions – remains unclear.

New insights into the emergence of despotic systems in vertebrate groups may be acquired by understanding how leaders arise and why others follow them. There are conceivably several different types of animal that might emerge as a leader. In eusocial insects, it has been shown that very few individuals within a group may actually possess pertinent information with respect to the decision in hand (Franks et al., 2002; Seeley, 2003), and thus become crucial to coordinating behaviour and the decision process. In vertebrates too, a minority of informed individuals (often elders) are seen to guide entire groups to specific resources. These include golden shiner fish *Notemigonus crysoleucas* (Reebs (2000)), elephants *Loxodonta africana* (Foley et al. (2008), ravens *Corvus corax* (Wright et al. (2003), and broad-winged hawks *Buteo platypterus* (Maransky and Bildstein (2001). Specific animals may also lead groups on the basis that they are hungriest, or because of the feeding benefits they derive from leading groups to food resources (Erhart and Overdorff, 1998; Overdorff et al., 2005; Overdorff et al., 2002).

But the incentive or information required to create leaders does not necessarily generate following, and both processes are necessary for effective leadership. Consider long-lived and cognitively-complex organisms, like primates, that display intricate social interactions. These create higher-order properties of groups that can be studied and quantified as dominance hierarchies and social networks (Cowlishaw and Dunbar, 1991; Krause et al., 2007). Given that such higher-order properties can modify individual behaviour, should we expect all individuals to have an 'equal say' where group coordination and decision-making is concerned (sensu Conradt and Roper, 2003)? Concerning dominance, high-ranking individuals are known to hold a particularly strong influence over the behaviours of group-mates (Deaner et al., 2005; Gould, 2004). Where members of families (or matrilines) coexist together, specific individuals may also have larger influence according to the relative number of kin relations (i.e. size of matriline) (de Ruiter and Geffen, 1998; Kappeler, 1993; Pope, 2000). Similarly, given the amount of time invested in social relationships, and the established importance of social networks to individual fitness (e.g. Silk et al., 2003), individuals with stronger and/or more social bonds within groups may be in a better position to generate follower behaviour (Chapter 7 of this thesis). The impact of social constraints can therefore not be ignored with regard to their critical roles on group decision-making (Sueur and Petit, 2008).

The growing number of theoretical and empirical studies is building a more complete understanding of group decision-making, but as I have outlined, there are still some important gaps. In this study, I hope to explore some of these less well understood areas.

D. Chapter organisation and objectives

In this thesis, I present five research papers investigating various aspects of group-living, with a focus on a well-researched social primate, the chacma baboon (*Papio ursinus*). Each chapter contains an introduction and rationale specific to the topic addressed. The thesis divides naturally into three sections, relating to the three unifying concepts explored in this Introduction. Thus, the first section examines how information is used in complex social groups (chapters 3 and 4), the second section tackles the issues of behavioural synchrony and coordinated group action (chapters 5 and 6), and the third section deals with group decision-making and more specifically leadership (chapter 7). A summary outline for each chapter is provided below.

Chapter 1 has provided an introduction to the study of group-living animals. It has identified three unifying concepts that are critical to advancing our understanding of animal sociality, and that form the focus of this thesis.

Chapter 2 will provide an introduction to the study species and site at which the field component of this research was carried out. It will also present basic ecological and behavioural data relevant to the understanding of the more-detailed data chapters that follow.

Chapter 3 will investigate the conditions under which individual baboons rely on the information provided by group-mates (rather than their own personally-acquired information) with reference to food sources. It will explore whether individuals alter their decisions when foraging, adopting either a 'producer' (find own food source) or 'scrounger' (attend the discoveries of group-mates) strategy according to the predictions of producer-scrounger games.

Chapter 4 will then explore the opportunities and constraints associated with the use of personal information versus information obtained from group-mates, i.e. 'social information'. Specifically, I investigate the relative value of social information for individuals that belong to groups of different sizes, where information available is of varying reliability.

Chapter 5 will examine what factors constrain or promote behavioural synchrony in baboon groups. It will first compare the behavioural synchrony observed by empirical observations to that expected by a statistical null model. I will then test hypotheses about the effects of activity budgets, habitat constraints, and group spatial properties on the observed patterns of behavioural synchrony.

Chapter 6 will look at how the synchrony of activities in one species (baboons) can affect the behaviour of another (kestrels), and consider the possibility that commensal relationships (specifically foraging associations) can vary in their frequency as a consequence of the behavioural synchrony of the species involved.

Chapter 7 will present the results of a series of foraging experiments on wild baboons designed to gain new insights into despotic group decision-making. The chapter tests the hypotheses that the acquisition of foraging benefits by one or a minority of individuals can create incentives for them to lead; and that despotic decisions can then result through the genetic and/or social ties that compel other group members to follow.

Chapter 8 will provide a summary of my thesis and synthesise the main findings.

Chapter 2 – Details of field research & baboon ecology

Abstract

The field work component of this study was conducted at Tsaobis Leopard Park in a semi-desert region of Namibia where two groups of chacma baboons were studied over a two-year period. In this chapter I provide summaries of the field site and study subjects. I then present basic data collection protocols and descriptive results necessary to provide background information to the detailed data chapters that follow. First, basic group demography data are presented. Second, data on social, dominance, and kin relationships are given. Third, patterns of group home-range and daily travel distances are provided. Fourth, I describe general activity budgets, a description of baboon habitats, and the temporal changes in baboon food preferences.

Study subjects

The subjects of study in this research were wild chacma baboons (*Papio ursinus*) (Figure 2.1). Chacma baboons are found throughout southern Africa in south-western Angola, southern Zambia, southern Mozambique, Namibia, Botswana, Zimbabwe, South Africa, Swaziland and Lesotho (Nowak, 1999).

Their social system consists of a matriarchal lineage in which females are philopatric and males typically disperse once they reach sexual maturity (Altmann and Altmann, 1970; Clarke et al., 2008). The mating system is multi-male (although uni-male groups do occur), with the alpha male generally gaining the greatest share of mating opportunities (Bulger and Hamilton, 1987; Weingrill et al., 2000). Females breed throughout the year: their oestrous cycle lasts a mean of 35.6 days (range 29 – 42 days), they have a gestation period of around 6 months, and on the vast majority of occasions give birth to one infant (Altmann and Altmann, 1970; Nowak, 1999). Leopards are their main predator (Cowlishaw, 1994).

Chacma baboons are a good model species in which to develop our understanding of information use, coordinated behaviour, and leadership in vertebrate social groups (Chapter 1), as many intricacies of their group social structure, behaviour and ecology can be easily recorded. For example, individuals are easily recognisable and can be simply categorised with respect to their age-sex class, dominance rank (Altmann and Altmann, 1970; Henzi and Barrett, 2005), social relationships (Henzi and Barrett, 2002; Henzi et al., 2000; Henzi et al., 1997), reproductive state (females) (Huchard et al., 2008; Setchell et al., 2006; Weingrill et al., 2003), and occurrence of mate-guarding or *consortships* (Weingrill et al., 2000), all by direct observation. Genetic samples can also be collected from faeces and tissue samples for determining relatedness between individuals (Altmann et al., 1996; Huchard et al., 2006; St George et al., 1998).

Study site and population

Fieldwork was carried out at Tsaobis Leopard Park, Namibia, from May to December 2005 and 2006. The park is in the semi-desert Pre-Namib region located at 15° 45′E, 22° 23′S, and consists of mountains that descend to an ephemeral riverbed (the Swakop River). The riverbed is dry all year apart from the few days following any heavy rain in the region. Underground water below the riverbed supports woodland groves consisting mainly of *Prosopis glandulosa*, *Salvadora persica* and *Faidherbia albida*. Elsewhere vegetation is sparse; the landscape is open with scattered dwarf trees (mainly *Commiphora virgata*) and shrubs (Figure 2.2; Figure 2.3). See Cowlishaw and Davies (1997) for more details. The altitudinal range of the park is 683 – 1445 m. The climate is arid: mean annual rainfall is 122mm (n=66 years), and falls only in the austral summer (October – April). The mean minimum and maximum daily shade temperatures during the study periods were 17-32°C, and 14-32°C, for 2005 and 2006 respectively.

The baboons at this study site were the subject of behavioural and ecological research during the beginning of the 1990's, and have been studied continuously since 2000, under the direction of Guy Cowlishaw (e.g. see Cowlishaw, 1997a; Cowlishaw, 1997b; Cowlishaw, 1999). Two focal groups, J (large group) and L (small group), were used in this study (see Table 2.1 for group sizes, and age-sex class breakdowns). Group L has been under observation since 2003 and so were relatively well habituated to the presence of human observers. Group J, however, had not been followed directly by observers and considerable time at the beginning of the 2005 field season was spent habituating this group to observer presence. Following these periods of habituation, focal individuals in both groups could be followed on foot and watched from close range (typically a distance of 5m), during which they would pay little if any attention to the observers. Hereafter and in the data chapters that follow (Chapters 3-7) these two study groups will generally be referred to simply as the 'large' and 'small' group.

These focal groups were also the subject of a concurrent PhD project by Elise Huchard investigating patterns of baboon mate choice (Huchard, 2008). Therefore, much of the general data presented in this chapter have been collected in collaboration with Elise Huchard, together with a small team of volunteer field workers who assisted with data collection on both projects.

Figure 2.1
Study subject: sub-adult chacma baboon sat on a rocky outcrop at Tsaobis. Photo credit: Tim Davies, Tsaobis Baboon Project Volunteer, 2006.

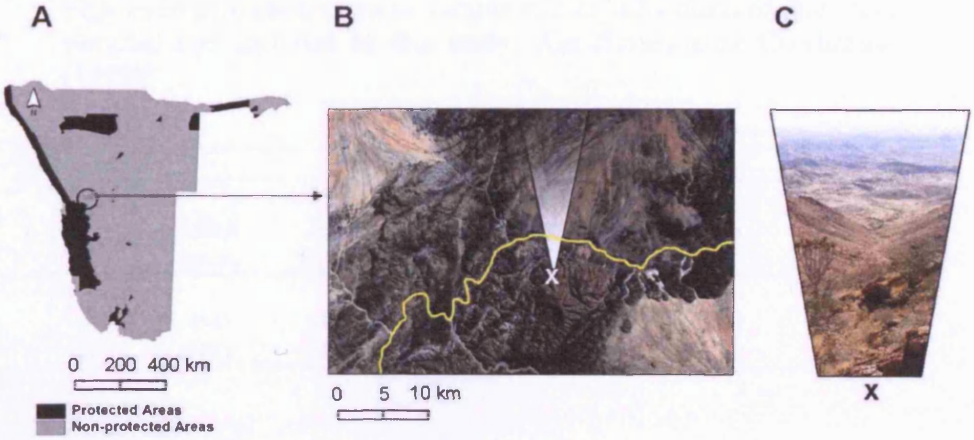


Figure 2.2
(A) Map of Namibia, with study site region in the semi-desert Pre-Namib region indicated, located at 15° 45´E, 22° 23´S. (B) Satellite photograph of study region. The area consists of mountains that descend to an ephemeral riverbed (the Swakop River: outlined in yellow). 'x' marks the location of the photograph taken that is shown in (C). (C) Photograph taken at the centre of the study site looking north to the Swakop River which is the tree-lined strip running across the top of the photograph.

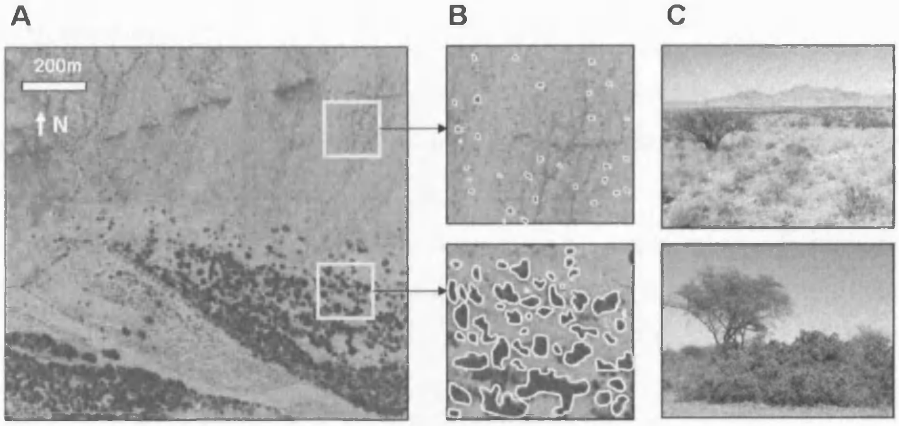


Figure 2.3
(A) Aerial photograph showing part of study site: the (dry) Swakop River is shown in the lower half of the image, bounded on either side by riparian woodland groves, and a flat rocky desert area to the north. (B) Enlarged portions of each habitat (desert and woodland). Potential baboon food patches are marked with a white outline. (C) Photographs of typical vegetation in each of the habitats shown in (B).

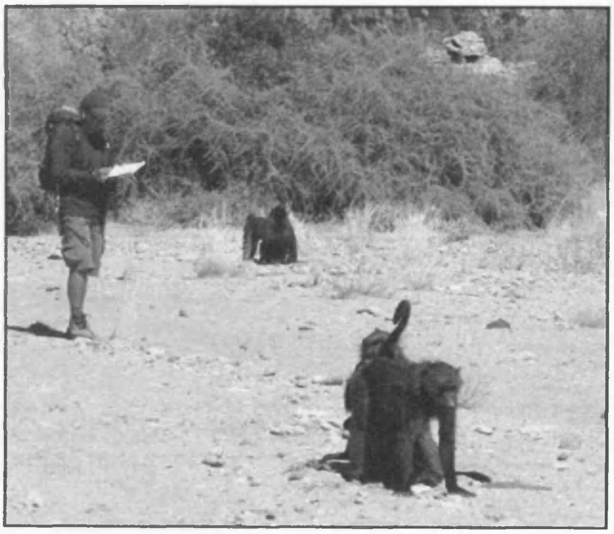
Table 2.1
Study group compositions (modal values across study period). Figures in parentheses denote sample size of individuals of that class sampled and included in this study. Age-classes after Cowlishaw (1999).

Group	Composition of groups					Group size
	Adult males	Adult females	Sub-adults	Juveniles	Infants	
J	4(4)	18(18)	9	16	10	57
L	4(4)	10(10)	3	10	5	32

Data collection

The baboon focal groups were followed on almost a daily basis (n_{large}=287; n_{small}=273 days) over the two field seasons. Group follows would begin at dawn, at the previous night's sleeping cliff, and finish at dusk at the new sleeping site location. These day follows would be carried out by a team of two field workers on foot, and the baboons studied by direct observation (Figure 2.4). Following a training period during which the identification of individuals baboons and their behaviours were learnt by all observers (approximately two weeks), a variety of data collection protocols were implemented (that also required a short training period). Protocols were each aimed at gathering appropriate data relevant to answering the questions that will be developed in this thesis. In the following sections of this chapter, I provide details of the data collection protocols related to: (1) group demography; (2) social, dominance and kin relationships; (3) home range and daily travel distances; and (4) general activity budgets and foraging behaviour. I also summarise the basic behavioural patterns of the two baboon groups in each of these areas, to provide background information and context for the analyses that follow in the subsequent chapters.

Figure 2.4
Direct observation of baboon group by AJK. Photo credit: Hans Kelstrup, Tsaobis Baboon Project Volunteer, 2005.



(1) Group demography

Demography data were collected each day a group was observed. This included recording the number of individuals in the group and noting any births, deaths, injuries, immigrations, emigrations, or baboons that were absent. The sexual state of adult females was categorised in terms of whether the female was pregnant, lactating, cycling with no sexual swelling (non-fertile phase), or cycling and swollen (fertile phase). Pregnancy was indicated by a scarlet colouration of the paracalossal skin adjacent to the ischial callosities (Saayman, 1970; Smuts, 1985; Weingrill et al., 2003), i.e. the skin around the anal region. All females suckling infants were categorised as lactating (Smuts, 1985). The fertile versus non-fertile phase of each female was identified by the state of her ano-genital skin which, as in many catarrhine primate species, gradually swells during each oestrous cycle, reaching its maximal size around the time of ovulation (fertile phase), before rapidly returning to its non-swollen state (non-fertile phase) (Domb and Pagel, 2001; Higham et al., 2008; Setchell and Wickings, 2004). Thus, sexually-swollen females were easily identified by their ano-genital swelling. Females 'cycling with no swelling' had no infants, no sexual swelling and their paracalossal skin was grey (Smuts, 1985). Female reproductive state can have a strong influence on male behaviour, and also potentially the behaviour of other females, in baboon groups. I will investigate such effects in relation to patterns of information use (Chapter 3), behavioural synchrony (Chapter 5), and leadership (Chapter 7) subsequently in this thesis.

(2) Social, dominance, and kin relationships

(a) Social relationships.

The level of affiliation between individuals is commonly assessed through grooming behaviour, which is widely accepted as measure of social affiliation in primates (Barton et al., 1996; Henzi and Barrett, 2002; Henzi et al., 2000). I used a matrix of grooming frequencies observed during *ad libitum* samples (n_{large}=2,535 and n_{small}=1,727) to generate two different measures of social affiliation.

The first measure was concerned with only the relative 'strength' of dyadic relationships, i.e. how evenly social contacts were distributed across dyads. This was termed the grooming strength index. For this measure, the grooming matrix was first folded across the main diagonal and corresponding cells summed to yield a triangular matrix. I then calculated the frequency of grooming for each possible dyad *ij*, and divided by the mean frequency of grooming for all dyads in the group (after Silk et al., 2006a). This gave me a distribution of scores for which 1.0 was the average, and for which higher values represented dyads with stronger bonds than expected and lower values those that had weaker bonds. The distribution of these scores was strongly skewed to the left, comparable to that found by Silk et al. (2006a) for a similar index that combined grooming strength with patterns of spatial proximity (Figure 2.5a and 2.5b).

Using these data I was also able to determine the grooming clique size held by each group member. This was the number of individuals with whom that group member shared a 'strong' grooming relationship, i.e. >1.0 (Kudo and Dunbar, 2001). This absolute clique size was comparable across both groups (Figure 2.6a), and so represented a greater proportion of the total group size for the small group compared to the large group (Figure 2.6b). This is a commonly reported phenomenon with respect to group size. Henzi et al. (1997) found that when the demands of grooming all other females reduce bout length to a point when no reciprocated bouts are possible, female clique size is capped. This in turn leads to weakening of the overall female network. Henzi et al. (1997) cites this as a reason for groups to fission in support of Dunbar's hypothesis (1992) concerning the mechanism underpinning fission. I suggest an amendment, which may be important to this process, in Chapter 7.

The second measure of grooming was concerned with the balance of grooming given and received within a dyad. This was termed the grooming symmetry index. For this measure, the whole matrix was used. I calculated the proportion of total grooming that was performed by each partner in a dyad, i.e. $i_g/(i_g+j_g)$ and $j_g/(i_g+j_g)$. This gave a value between 0 and 1 for the relative contribution to total grooming in a dyad. For a completely equitable relationship both partners in dyad *ij* would score 0.5. In contrast, if dyadic relationship *ij* was maintained almost completely by individual *i*, then *i* would score close to 1 and *j* close to 0. See Figure 2.5c and 2.5d. For dyads with very weak social relationships (i.e. strength < 0.1, see above) grooming events occurred so rarely between these individuals that it was not possible to reliably assess the relative balance in grooming in that dyad. Additionally, the infrequence of grooming observed between these individuals suggests that they do not 'invest' in these relationships. On this basis, for dyadic relationships scoring less that 0.1 on the strength of grooming index, those individuals involved were not assigned a symmetry score, and were not included in any subsequent analysis exploring the effect of this measure. The symmetry scores are normally distributed around 0.5, but show much variation about this mean (Figure 2.5c and 2.5d).

One school of thought has suggested that grooming may be seen as a commodity on a 'biological market', that can be traded for grooming (in reciprocation) or other services, such as coalitionary support (see Barrett et al. 1999 for a discussion). The distribution of the grooming symmetry index in the groups under study here, demonstrating a peak at 0.5, i.e. balanced reciprocation, suggest that individuals tend to preferentially groom those group mates that groom them most (Schino and Aureli, 2008; Silk, 2007c). According to the biological markets theory, this would suggest that grooming is being traded for grooming. However, there is also considerable variation around 0.5, indicating that grooming may also be traded in exchange for other services (sensu biological markets theory: Noe and Hammerstein, 1994; Noe and Hammerstein, 1995).

As a measure of social affiliation in primate groups, I will be exploring patterns of grooming behaviour in a variety of contexts in this study. In particular, these analyses, which will include both grooming strength and grooming symmetry indices, will explore the importance of social affiliation for both information use (producer-scrounger behaviour) and leadership (Chapters 3 and 7 respectively).

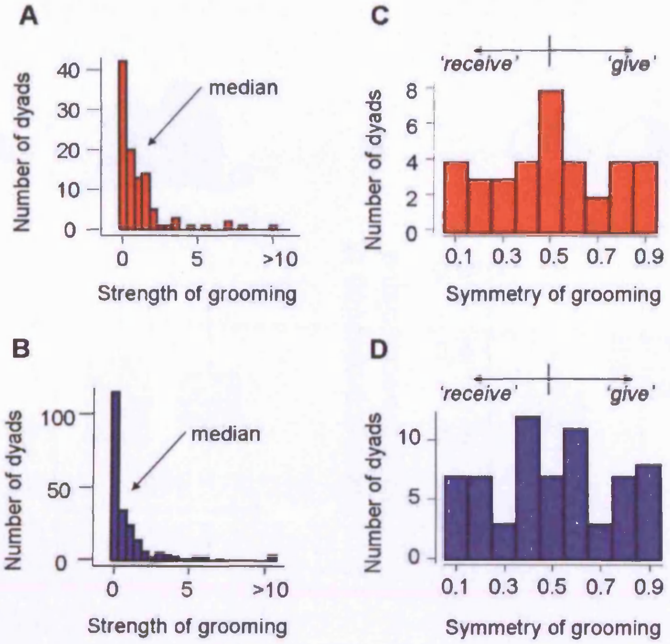


Figure 2.5
(A) and (B) shows the frequency distribution of the strength index for the large group (blue) and small group (red). The median value of the sociality index was 0.45 (L) and 0.20 (J). The grooming relationship exceeded 2.0 for less than 10% of all dyads in each group. Panels (C) and (D) show the frequency distribution of the symmetry index for each group. Grooming direction is indicated on the x-axis: 0.5 represents an equitable relationship; values above this indicate that individual *i* grooms individual *j* more, while values below this indicate that individual *j* is groomed more by individual *i*.

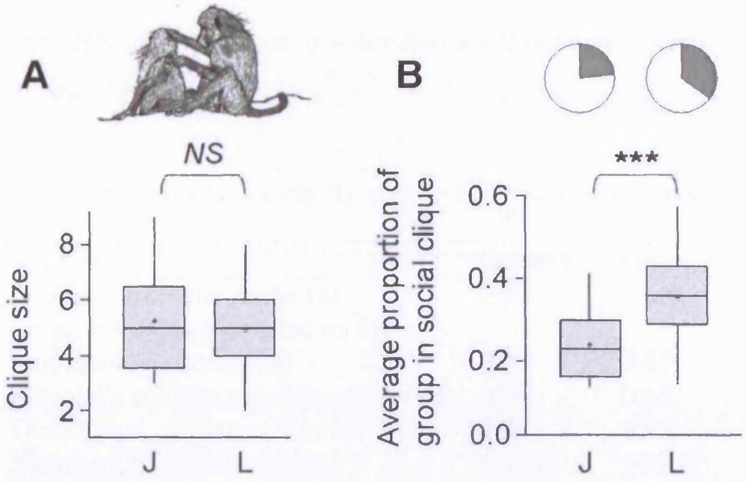


Figure 2.6
Comparisons of individual grooming clique sizes in the large (J) and small (L) study group. (A) absolute clique size, after Kudo & Dunbar (2001). (B) proportional clique size (relative to group size; also shown in accompanying pie charts). Samples sizes (individuals) N= 21 for J, N=14 for L. T-tests of differences between groups were performed, and results indicated: NS=$P>0.05$; ***=$P<0.001$. Means are shown by dots, horizontal lines indicate medians, the bars indicate interquartile ranges, and the vertical lines indicate the full range.

(b) Dominance

To determine the dominance relationships between all subjects, frequencies of all agonistic and approach-avoid interactions between baboons were collected using *ad libitum* and focal observations across the entire study period ($n_{large}=1698$; $n_{small}=1485$) (Silk et al., 2006a; Silk et al., 2006b). These were subsequently entered into actor-recipient matrices. The dominance hierarchy of each group was then determined using Matman software (Devries et al., 1993): statistically significant linear hierarchies were found in both groups, and all adult males out-ranked all adult females (see Table 2.2 for test statistics).

Linear dominance hierarchies are common in primate species, and are a common characteristic of group-living. An individual's dominance rank in the hierarchy correlates with its ability to compete and gain access to limited resources (e.g. Barton et al. 1996). In primates, as in most mammals, females compete primarily for access to food resources, while males compete primarily for access to mates (Cowlishaw and Dunbar, 1991). Later in this thesis, I investigate the role of dominance in individual-level (Chapter 3) and group-level (Chapter 7) foraging decisions.

Table 2.2 Dominance hierarchy statistics for each study group.

Statistics	Group L	Group J
Landau's linearity index (h)	0.93	0.65
Linearity index h' (corrected for unknown relationships)	0.95	0.67
Kendall's coefficient of linearity (K)	0.93	0.65
Directional consistency index	0.94	0.88
Number of Randomizations	10000	10000
Chi-square value	63.62	93.55
Right-tailed probability	<0.0001	<0.0001

(c) Kinship

Kin relationships were determined using DNA derived from tissue and faecal samples collected from all individuals during routine capture procedures. Three capture operations were carried out during this study: The large group (J) was captured in 2005, and both groups were captured in 2006. These operations relied upon the involvement of all Tsaobis Baboon Project members. The capture sites were baited with dry maize, and their locations were chosen on the basis of proximity to a waterhole—which ensured that the groups would find them quickly. The baboons were captured in individual cages, which were gradually introduced to the trapping location over a number of weeks, so that all individuals would get used to their presence (Figure 2.7). Once all group members regularly visited to feed on the artificial food provided, and would enter into the cages to retrieve food items, the cages were 'set' the night before capture.

Each baboon group was then captured in its entirety at sunrise, and the animals were processed throughout that same day. Several baboons were anaesthetised at a time and taken to a processing area by vehicle. Pulse, respiration rate and temperature were monitored during anaesthesia. Processing was completed within 30-45 minutes per animal and four animals were processed simultaneously. Lactating females and adult males were processed early in the day, and only minimal samples were taken from infants, to minimise stress. The youngest infants were not anaesthetised. All the captured animals were released together at the capture site, and provided with corn kernels after their recovery from the anaesthetic, the following morning.

During processing, a full physical examination of each baboon was carried out, with any injuries or symptoms of illness documented. Each baboon was weighed, and a dental examination and morphometric measurements were taken to estimate age and condition. Individuals were checked for external parasites, and faecal samples were taken where possible for parasitological and hormonal analyses. Blood samples were also taken for biochemistry and haematology analyses. Each of these data contributed to the long-term datasets of the Tsaobis Baboon Project and an investigation into mate choice, health, and MHC genes (Huchard 2008).

Tissue biopsies were taken from the ears. This sampling fulfilled two aims: first to take a clean tissue sample from which genetic analyses could be performed, and second to allow individual identification of baboon in the field by direct observation, by varying the location (or combinations of locations) at which the notch was made. These notches simulated the natural tears that baboons often acquire over the course of their lives.

DNA extraction, amplification and sequencing for the two study groups captured in 2005-6 were conducted by Harry Marshall, Charlotte Staples, Elise Huchard and Leslie Knapp at the Institute of Zoology (ZSL) and at the Anthropology Department, Cambridge University. These samples were then combined with samples collected and analysed in previous years from another four groups, for the purposes of calculating pairwise genetic relatedness in the population as whole (Table 2.3). Genomic DNA was extracted from tissue using a QIAamp kit according to manufacturer's (QIAGEN) instructions, and 17 human primers were selected that were known to work in other nonhuman primates and exhibited reasonable heterozygosity (Table 2.4).

Figure 2.7
Individual cages were locked in triads to provide a steady structure (on which the baboons could climb) and spread-out over the capture site, with approximately 5m between triads of cages. Photo courtesy of Elise Huchard.

Table 2.3
Sample sizes used to calculate genetic relatedness among individuals, broken down by group size. Groups L and J are the subjects being investigated in this thesis.

Group	Year trapped	Group size	*n* trapped
F	2000	17	17
G	2000	27	26
H	2001	73	54
I	2001	19	18
J	2006	57	55
L	2006	32	32

Table 2.4.
Microsatellite primers used, and their properties.

No.	Primer	Allele size	Number of alleles
1	d6s271	173-192	4
2	d3s1768	187-211	6
3	d1s533	191-203	3
4	d16s402	139-162	3
5	d13s375	163-189	4
6	d4s243	156-176	5
7	d7s503	149-159	3
8	d13s317	243-259	5
9	d18s537	191-207	5
10	d13s159	166-189	4
11	d5s1457	112-138	5
12	d3s1766	193-231	6
13	d1s548	181-213	6
14	d1s550	136-158	5
15	d14s306	151-187	9
16	d4s2408	314-334	5
17	d4s1627	256-276	3

After amplification, samples were sequenced in an ABI 3100 Genetic Analyzer and the sizes of the alleles in each were determined by detection of the fluorescent tag on the end of the DNA strand. Alleles were then presented as peaks on electropherograms in GeneMapper software. Once all the appropriate settings were entered into the program the allele sizes were automatically assigned. This procedure was repeated until each homozygous individual was typed at least three times, and each heterozygote individual was typed at least once.

Using these allele sizes for each individual from the above analyses, I then calculated six different estimates of pairwise relatedness, *r*, between all sampled individuals in the population (n=21,946), using Coancestry software (Wang 2006) version 1.0. The different estimators calculated were those of Lynch (1999); Ritland (1996); Queller and Goodnight (1989); Lynch and Ritland (1999); Wang (dyadic estimator) (2004); and Wang (triadic estimator) (2007). All estimators were strongly correlated (Table 2.5). Therefore, throughout the rest of this thesis, when testing for an effect of relatedness I use only three of these estimators. The first two are among the most commonly cited estimators: Queller & Goodnight, and Lynch and Ritland (see Csillery et al., 2006). The third is the more recently developed Wang's triadic estimator, which provides the best overall performance in estimating relatedness (as measured by the root mean squared error) when compared to the other six estimators (Wang, 2007). Where the results of any statistical analysis involving relatedness are cited in this thesis, they are given for the Wang (2007) estimator, although all such statistical tests were repeated with the other two estimators described and the same results obtained in every case.

The pattern of relatedness in the small and large study groups according to Wang's (2007) estimator are shown in Figure 2.8. These patterns show that, as typical for most baboon groups, many individuals in the group are unrelated but most show some degree of kinship, with a small number showing a very high degree of relatedness (e.g. see Silk et al. 2006a; 2006b). This provides a good range of variation with which to explore the effects of kinship on information use (producer-scrounger dynamics) and leader-follower behaviour across individuals in the two study groups in subsequent chapters (Chapters 3 and 7 respectively).

Table 2.5.
Spearman's rank correlations between different estimates of pairwise relatedness across all possible dyads (n=21946). All correlations were significant at P<0.0001.

	Wang (2007)	Lynch & Ritland	Queller & Goodnight	Wang (2004)	Lynch	Ritland
Lynch & Ritland	0.799					
Queller & Goodnight	0.747	0.821				
Wang (2004)	0.696	0.730	0.864			
Lynch	0.690	0.714	0.883	0.979		
Ritland	0.705	0.908	0.787	0.664	0.672	
Wang (2007)	0.986	0.829	0.762	0.714	0.705	0.736

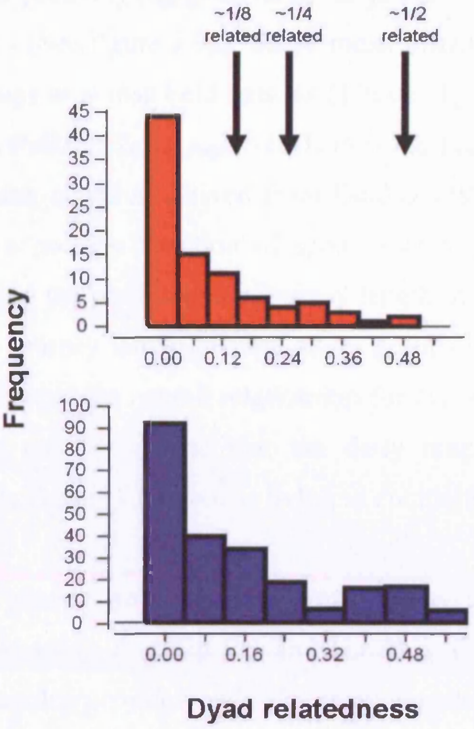


Figure 2.8. Frequency histograms for pairwise relatedness among all adult baboons in the large (blue) and small (red) study groups. Data for the Wang (2007) estimator is presented.

(3) Home range & daily travel distances

Full-day follows of the baboon groups were accompanied by GPS data collection. Readings of the group position were taken using a handheld GPS (Garmin Etrex®). Coordinates were taken from the centre of the group, and the accuracy of these measurements was always <10m (as measured in real-time on the GPS unit). The first reading was taken at the baboon group's morning sleeping site, on the arrival of the observers just before dawn, and the second once the group left the sleeping site. Following the baboons' departure, GPS recordings were taken at 30-minte intervals throughout the day. The session would end at the evening sleeping site where the baboons settled down to sleep, where a final point would be taken after sunset when the observers left the group. This allowed the daily travel distance to be calculated as the sum of the distances between GPS points.

The mean daily travel distances during the 2005 field season was 6.0 km for both groups (n_{large}=116 days, range 3.7 - 10.1 km; n_{small}=134 days, range 1.7 - 9.8 km). During the 2006 field season mean daily travel distance was 5.7 km and

6.2 km for the large and small group respectively (n_{large}=65 days, range 3.2 - 10.7 km; n_{small}=46 days range 1.9 - 9.7 km) (See figure 2.9a). These mean distances did not differ significantly among groups or across field seasons (T-tests: $T_{groups-2005}$= -0.01, P=0.99; $T_{groups-2006}$= -1.98, P=0.06; $T_{season-large}$= -1.41, P=0.16; $T_{season-small}$= -0.99, P=0.33). Using a regression equation derived from Dunbar (1992) that predicts day journey length as a positive function of group size and a negative function of rainfall, I calculated the predicted day journey length of the two study groups. The predicted day journey length of both study groups was close to the real average distance, and fitted the overall relationship for baboons well (Figure 2.9b and 2.9c). These results indicate that the daily ranging behaviour of these two study groups are typical for baboons living in comparable groups and environments.

The home range (minimum convex polygon home range) was also calculated on a month-by-month basis using ArcMap 9.2 and Hawth's Tools extension package (http://www.spatialecology.com/htools/). The ranging patterns of each group are shown in Figure 2.10. It is noticeable that the range use of each of the groups showed much variation by month and across seasons. These patterns most likely reflect monthly variation in the spatial distribution of food resources, which are believed to play a primary role in determining baboon home range area (Altmann and Altmann, 1970; Barton et al., 1996). It is also possible that these patterns may partially reflect the influence of a series of feeding experiments that I carried out to explore leadership and despotism (Chapter 7), although comparable patterns of variation outside the experimental months suggests that the distribution of natural food resources most likely played the primary role.

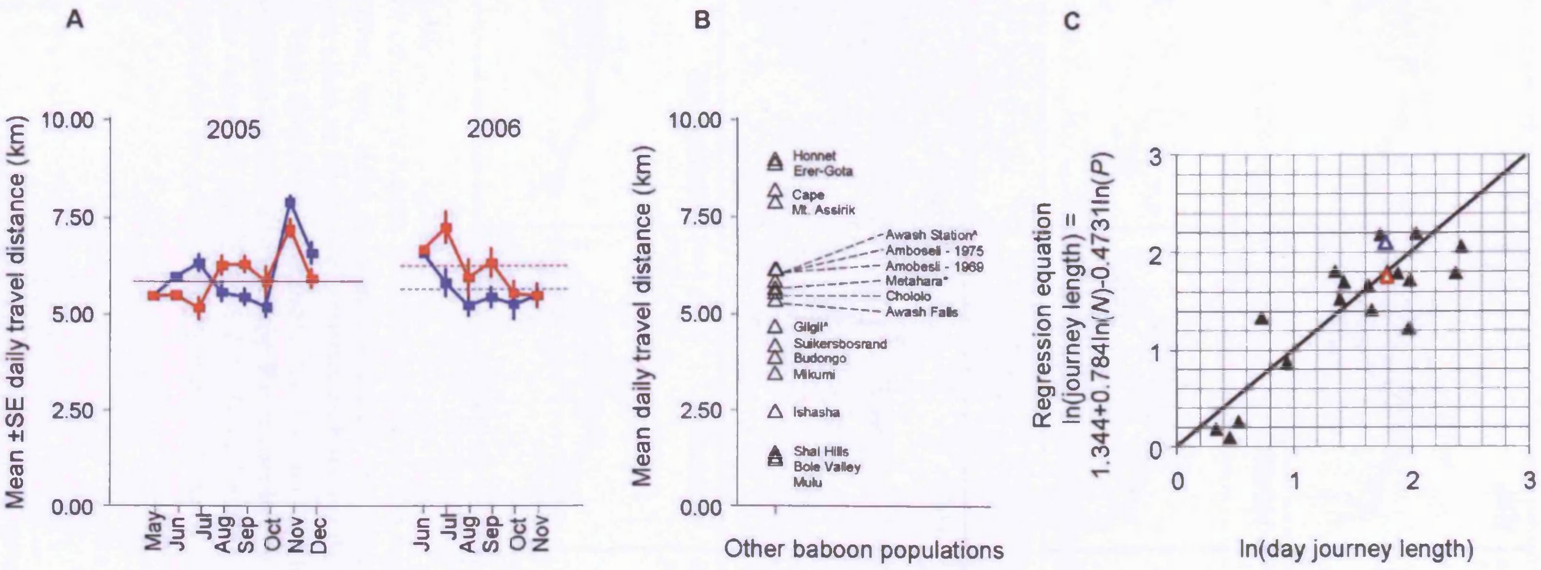


Figure 2.9.
(A). Mean daily travel distances by month for each field season. Group L (small group) is shown in red, and group J (large group) is shown in blue. (B). Mean daily travel distances of other baboon populations, following data presented by Dunbar (1992). (C). Predicted day journey length as a function of group size and rainfall, and observed day journey length in populations shown in B, with the two study groups at Tsaobis added to the dataset (red and blue triangles). In the regression equation on the Y-axis, N = group size, P = mean annual rainfall (after Dunbar, 1992).

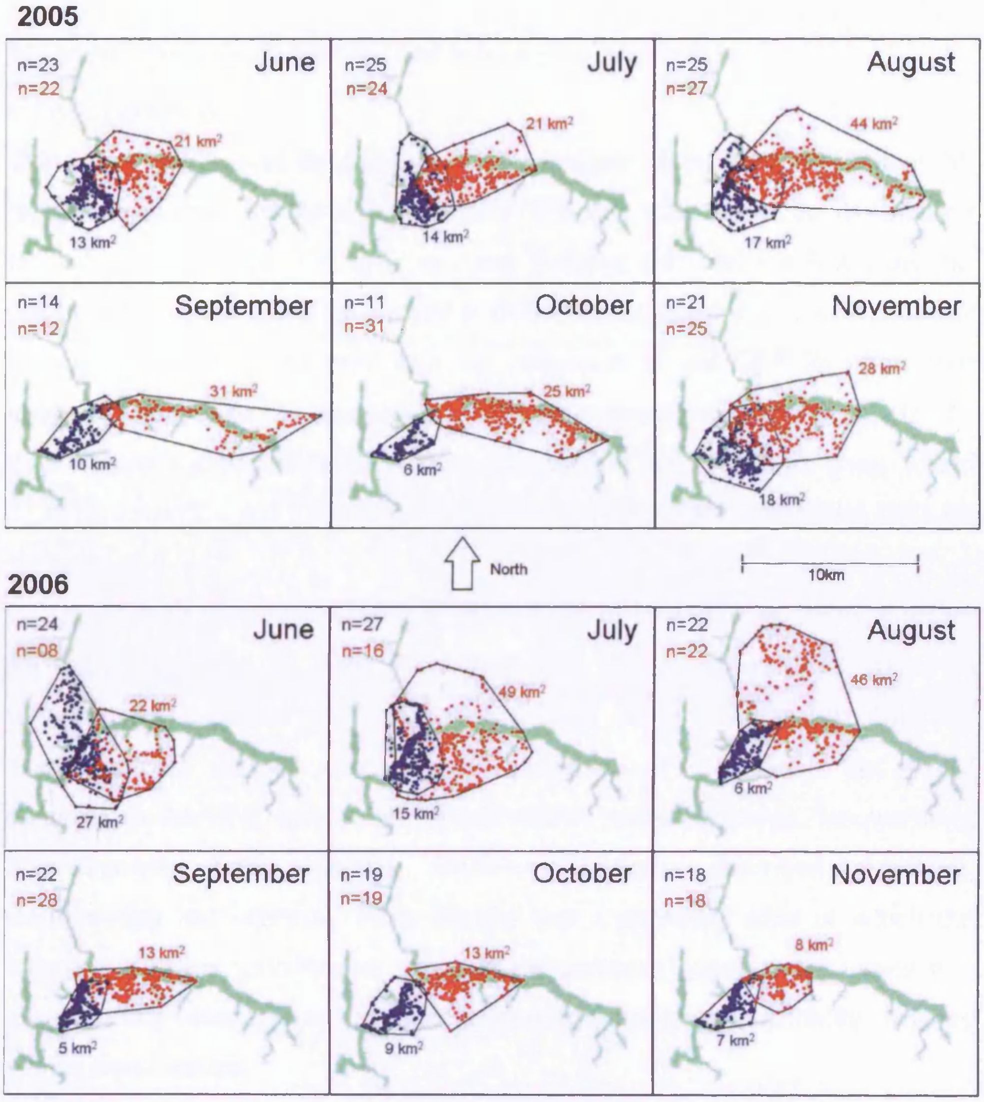


Figure 2.10.
Minimum convex polygons of home ranges for the large (blue) and small (red) groups, over two field seasons, separated by month. Dots represent GPS coordinates taken at 30-minute intervals within days throughout each month. The number of days that the home ranges in each panel are based upon is indicated in the top left-hand corner. The Swakop River and its main tributaries are depicted in green for reference (see Figure 2.2). Data for May and December 2005 and 2006 are available but are n<5 days per group in each case, so are not shown.

(4) Activity budgets, habitat use and baboon food preferences

(a) Activity budgets

The activity budgets of the baboons were determined from scan sampling at 30-min intervals collected throughout the day. The first scan was made 30 min after the baboon group had left their morning sleeping site, and the last scan was conducted once the group had settled at their evening sleeping site shortly before sunset. These data coincided with the collection of the GPS locations (see above). A total of 6535 scans across both baboon groups were obtained from 517 days of observations. 3826 scans were conducted in 2005 (1476 for group J, and 2350 for group L), and 2709 scans in 2006 (1636 scans for group J, and 1073 for group L).

At each scan, the number of individuals in view was recorded, together with the proportion of these individuals that were (i) travelling; (ii) travel foraging; (iii) stationary foraging; (iv) resting; (v) grooming; (vi) drinking. *Travelling* was defined as the rapid locomotion of individuals, and *travel foraging* as the slow locomotion of individuals while searching, manipulating and ingesting food material. *Stationary foraging* described searching, manipulating and ingesting food. *Resting* was a sedentary state in which the baboons were not travelling or foraging and included sleeping. *Grooming* was allogrooming between social partners. *Drinking* described the drinking of water from a water source.

An overview of these patterns of activity (Figure 2.11) for both groups reveal these to be typical of general activity patterns reported in other baboon groups (cf. data presented in Bronikowski and Altmann, 1996; Dunbar, 1992). In addition, previous research has suggested that time budgets should become more stressed in larger groups: individuals in such groups spend more time foraging as a result of higher feeding competition (Beauchamp, 1998; Janson and Goldsmith, 1995; Wrangham et al., 1993), and thus have less time for resting and/or grooming (Berman et al., 2008; Dunbar, 1992; Lehmann et al., 2007b). Reduced grooming in the larger group was seen here (Figure 2.11), although the difference is perhaps smaller than might have been expected given the relatively large differences in group sizes (Dunbar, 1992). These activity data are subsequently used to investigate patterns of behavioural synchrony and their consequences in Chapters 5 and 6.

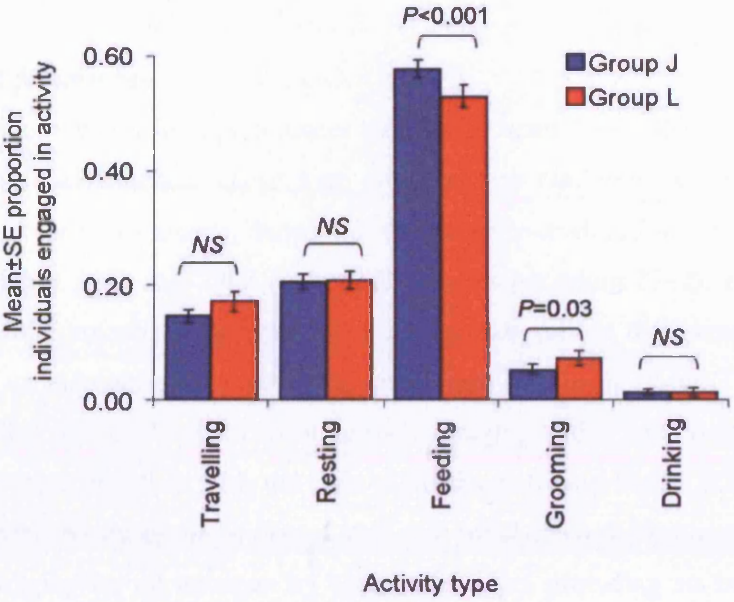


Figure 2.11.
Summary of activity budget data for each group pooled over the two field seasons. n=3423 scans for the small group (L) and 3122 scans for the large group (J). 'Feeding' category is made up of both 'travel' and 'stationary' foraging for the purposes of this analysis. Mean proportion of individuals is calculated from 30-minute group scan data (see main text). Significant differences as calculated by 2-tailed Mann Whitney tests are indicated.

(b) Habitat use

During group scans (see above) the predominant habitat type within which the baboons were ranging was also recorded, as either 'open desert', or 'riparian woodland' habitat (see Figure 2.3). Typical vegetation found on the open desert habitat includes perennial grasses and herbs, e.g. *Aristida* spp. and *Petalidium variable*, with shrubs and dwarf trees, e.g. *Catophractes alexandri*, *Acacia erubescens* and especially *Commiphora virgata*. In the woodland habitat, vegetation is supported by groundwater and dominated by *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica*. Vegetation within each habitat type was therefore categorized as (i) open (mostly devoid of vegetation), (ii) grasses and herbs, (iii) shrubs, and (iv) trees. The influence of habitat with regard to information use is investigated in Chapter 3. The role of habitat upon coordinated behaviour is investigated both with respect to group synchrony (Chapter 5) and its effects on interspecific interactions (Chapter 6).

(c) Food preferences

Analyses of baboon food preferences were based upon data collected during 972 one-hour focal watches. These were conducted on randomly selected foraging adults from the two groups, during full-day dawn-to-dusk follows, between June to December 2005 and 2006 (mean±SE watches per adult=27±2). Each time a focal animal entered a food patch for >5 seconds (rather than simply passing through it) and consumed food it was considered a foraging event. The duration of time that the focal animal spent actively foraging within each food patch was then recorded, together with the type of food patch (see Figure 2.12 for main food types). Based on these data, I was able breakdown the proportion of time spent foraging by all baboons by food patch type, providing an indication of temporal changes in food preferences over both field seasons (Figure 2.13). The tree *Prosopis glandulosa*, and the shrub *Salvadora persica*, are the main dietary components, although there is considerable variation in their importance in the diet across both months and years. These are two of the most abundant species in the Swakop woodlands, where the *P. glandulosa* often form monodominant stands and the *S. persica* large thickets. Herbs, grasses and insects are only important earlier in the year, indicating the importance of rainfall in the production of these foods: as the field season progresses and the environment becomes drier, these foods disappear. These descriptive data on diet will be referred to in relation to information use (Chapter 3) and interspecific associations (Chapter 6).

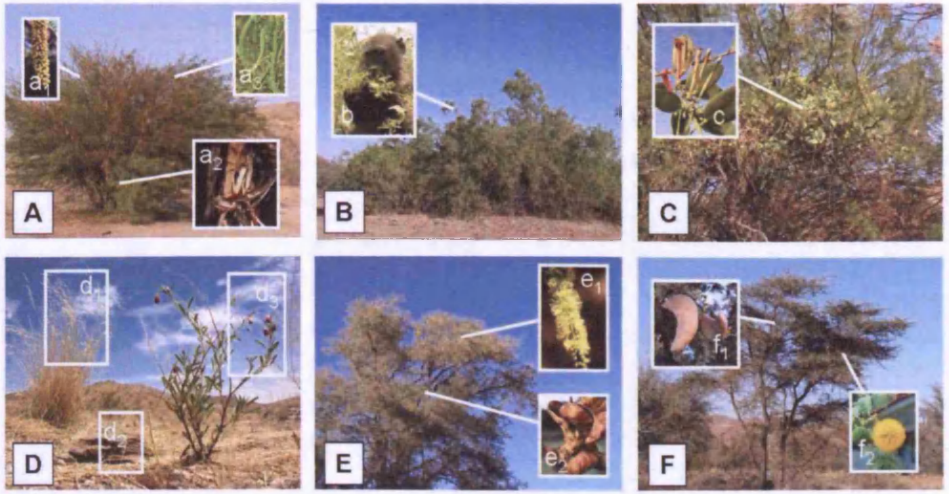


Figure 2.12.
Major baboon food types. (A) *Prosopis glandulosa*; (B) *Salvadora persica*; (C) *Tapinanthus oleifolius* which is a hemi-parasite that grows within the canopy of A, B, E and F; (D) *Aristida* grass spp, shrubs, and invertebrates; (E) *Faidherbia albida*; (F) *Acacia tortilis* and *Acacia erioloba*. Inset (lower case letters) pictures show major food items for each food type. (a_1) flowers; (a_2) bark; (a_3) pods and seeds (canopy and ground); (b) berries; (c) flowers and berries (canopy and ground); (d_1) grasses roots and shoots; (d_2) invertebrates (under rocks); (d_3) flowers and seeds; (e_1) flowers (canopy); (e_2) pods and seeds (canopy and ground); (f_1) pods and seeds (canopy and ground); (f_2) flowers (canopy).

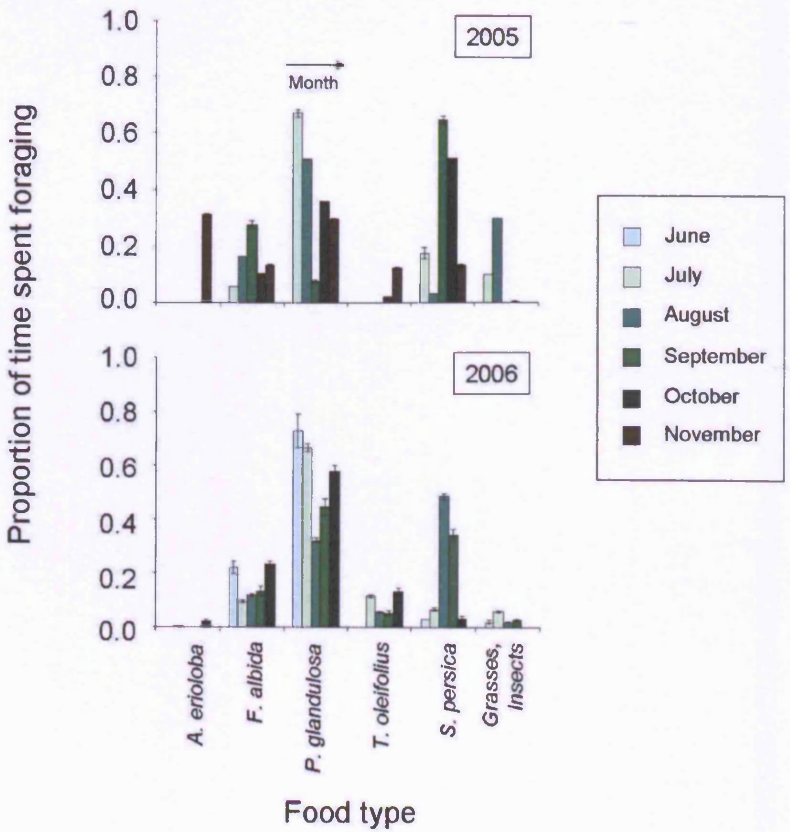


Figure 2.13.
Baboon food preferences (pooled across all individuals in both study groups) by month and field season, presented as the proportion of total observed foraging time during individual focal watches (for foraging events lasting >5 seconds). Error bars indicate standard errors across individuals. Insufficient focals were obtained in June 2005 and November 2006, so these months are absent from the figure. See Figure 2.12 for description of foods.

Summary

This chapter has described the study site, subjects and key descriptive data: social relationships (grooming, dominance, kinship), ranging patterns, activity and habitat use, and basic foraging ecology. Overall, these findings indicate that the baboon groups in the population show patterns of behaviour and ecology similar to populations elsewhere in Africa. Specifically, the baboons live in a range of group sizes, which range (and forage) over considerable distances each day. Additionally, despite differences in group size, groups are characterised by similar (and complex) social and genetic relationships among individuals. The information presented in this chapter will be referred to when required in the chapters that follow.

Chapter 3 – Know thy neighbour? The producer-scrounger game applied to primate social foraging

A manuscript based upon this chapter is under review as:

King, A. J., Issac, N. J. B. & Cowlishaw, G. (Under Review) Ecology, group structure, and dyadic interactions shape producer-scrounger dynamics in baboons. *Behavioral Ecology*.

Abstract

Producer-scrounger games are models used to explain the tactics of socially foraging animals where individuals can either search for their food (produce) or join the food discoveries of others (scrounge). However, empirical testing of such social foraging models have generally been restricted to indoor aviary experiments. Here, I examine social foraging decisions of naturally foraging wild chacma baboons (*Papio ursinus*). Thirty six adult baboons from two groups were observed during full-follows: data from nearly 10,000 foraging events were analysed using cross-classified, generalised linear mixed models. First, as assumed by producer-scrounger games, I show that baboons alter their foraging tactics in accordance with food distribution and spatial position. Second, I show that relative differences in social dominance between foraging neighbours indicate a phenotype-limited producer-scrounger game, and scrounging is more frequent among individuals of strong social affiliation. However, I find no effect of kinship or group size. Finally, I find strong sex differences: female baboons scrounge more from male neighbours when pregnant, and less when in oestrus, whilst male baboons scrounge indiscriminately with respect to female reproductive status. These results suggest that in addition to broad-scale ecological influences, a myriad of social and reproductive factors can shape producer-scrounger dynamics for wild animals living in complex social groups.

Introduction

Group living can provide a variety of benefits to individual group members (Krause and Ruxton, 2002). One of these benefits is the advantage that social information derived from the behaviour of conspecifics confers to individuals (Dall et al., 2005; Fraser et al., 2006; King and Cowlishaw, 2007- Chapter 4). For groups of individuals in a patch-foraging scenario (Charnov, 1976) certain individuals may try to avoid the cost of searching for food by utilising information provided by group-mates, to make an indirect assessment of food patch locations and qualities (Valone and Templeton, 2002). Two different theoretical frameworks have been proposed.

For some social foragers, when one group member finds food, all the remaining individuals join their discovery. In this type of system, which is referred to as the 'information sharing' model (Beauchamp & Giraldeau 1996), all individuals search for food independently while at the same time monitoring the behaviour of other group members, all group members have similar joining frequencies, and joining increases with group size (Ruxton et al., 1995). Yet one can imagine a range of circumstances where adaptive changes in the joining behaviour of group foragers would be likely to yield higher individual foraging rewards. This has led to a game-theoretic view of social foraging: 'the producer-scrounger' model, in which individuals can choose to search for food (produce), or wait for another individual to find food and join them at their food discovery (scrounge) (Ranta et al., 1996; Ranta et al., 1993; Vickery et al., 1991). Producer-scrounger games assume incompatibility between producing and scrounging strategies. This does not mean that an individual must *always* play producer or *always* play scrounger (Giraldeau and Caraco, 2000). Instead, individuals can alternate between the producer and scrounger alternatives, provided that when an individual is producing (i.e. searching for food) it cannot simultaneously be scrounging (i.e. monitoring other group members' success). This is consistent with other theoretical models that typically treat foraging and scanning as mutually incompatible behaviours (Lima, 1987; McNamara and Houston, 1992; Pulliam et al., 1982), and empirical observations that show vigilance behaviour substantially reduces the feeding rates of individuals (Beauchamp and Livoreil, 1997; Saino, 1994), although see Cowlishaw et al. (2004).

Whether a forager adopts a producer or scrounger strategy at any point in time is likely to reflect a variety of different environmental and social factors. Early producer-scrounger models revealed that the evolutionarily stable proportion of scroungers depends on the fraction of each food patch available to producers, known as the 'finder's advantage': the number of items obtained by the finder before the arrival of other individuals (Vickery et al., 1991). The finder's advantage is small where a large volume of food occurs in a few large patches, and larger where a small volume of food occurs in small but numerous food patches (Giraldeau and Caraco, 2000; Giraldeau and Livoreil, 1998). Scrounging should therefore be more common where food items are clumped in a few rich patches; where producers aren't able to consume all available food items before the arrival of scroungers (Giraldeau and Beauchamp, 1999). It follows that where food items are clumped in a few rich patches, an increase in group size will also lead to more frequent scrounging behaviour, simply as a result of decreased opportunity to produce (Coolen, 2002). The spatial position an individual occupies can be important for foraging tactics too (Barta et al., 1997; Di Bitetti and Janson, 2001; Hirsch, 2007; Mathot and Giraldeau, 2008). Opportunities to produce will more often present themselves to an individual in peripheral positions, since this reduces competition by fellow producers (and increases the time required taken by scroungers to arrive). In contrast, opportunities to scrounge will be more common for individuals in close proximity to group-mates, especially those placed at the back or centre of a foraging progression, where they are able to survey multiple scrounging opportunities (and reduce the time required to reach them).

More recently, it has been suggested that social factors can also play a role in determining individual producer-scrounger behaviour, i.e. a phenotype-limited game (Barta and Giraldeau, 1998; Liker and Barta, 2002). Where there is a large difference in the competitive ability of individuals, one implication is that better competitors, i.e. dominant animals, will mainly play scrounger whereas subordinates will mostly play producer, at least where food sources can be monopolised. Likewise, producers may be more tolerant of group-mates of close social affiliation and/or genetic kinship joining them at food patches (sensu Hamilton, 1964; Trivers, 1971). These patterns may be further moderated by reproductive strategies, e.g. scrounging behaviour between non-related social allies can reflect food-sharing interactions of male-female sexual partners in some bird species (Beauchamp, 2000b; Bugnyar and Kotrschal, 2002). Such effects may be substantial and widespread in natural populations of social foragers, especially given the importance of social interactions on wider patterns of behaviour (Krause et al., 2007). However, empirical support for the role of social factors is poor. Investigations of dominance as a predictor of scrounger behaviour have produced conflicting results (Beauchamp, 2006; Di Bitetti and Janson, 2001; Lendvai et al., 2006; McCormack et al., 2007), and the few studies completed on the effect of social affiliation and kinship are yet to present conclusive findings for either factor influencing producer-scrounger foraging tactics (Beauchamp, 2000a; Ha et al., 2003; McCormack et al., 2007).

In this third chapter, I explore the application of producer-scrounger models to socially foraging wild baboons (*Papio ursinus*) in central Namibia. I expect 'adaptive plasticity' where the ratio of producers and scroungers is expected to change at any given time as a consequence of foragers altering their allocation through the assessment of local conditions (Giraldeau and Caraco, 2000).

I begin by investigating three characteristic patterns in producer-scrounger systems (see above): individuals will be more likely to scrounge in habitats in which they encounter larger food patches, when foraging in a larger group, and when closer to the centre of a group. I then go on to investigate the importance of three social factors: dominance rank, social affiliation, and kinship. I investigate these factors at the basic level at which they operate—within dyads (a dyadic relationship refers to the interaction between two group-mates). For dominance relationships, I predict that individuals will scrounge more from neighbours of lower dominance rank than themselves (Liker and Barta, 2002). For social affiliation, I predict that individuals will scrounge more from neighbours with whom they have a strong social relationship and/or from whom they have negotiated tolerance at the feeding site (Barrett et al., 1999; Silk, 2007c). For kinship, I predict that individuals scrounge more from close kin (Belisle and Chapais, 2001; Silk, 2002).

Finally, baboon social relationships can further differ along two important axes. First, within and between sexes: females are philopatric and develop long-term bonds with other females (Silk et al., 2006a; Silk et al., 2006b; Smith et al.,

2003) whereas males disperse and may transfer repeatedly between social groups (Alberts and Altmann, 1995). Consequently, it might be expected that social relationships and kinship will be more important in female-female dyads than in mixed-sex dyads (I do not consider male-male dyads in this analysis since males are rarely foraging neighbours). The second axis of variation in baboon social relationships is related to reproductive strategies. Males not only mate guard (form sexual consortships with) females during their oestrus period (Bercovitch, 1991; Weingrill et al., 2003), but may also develop strong 'friendships' with the lactating mothers of their infants in order to protect their offspring from infanticide (Palombit et al., 2001; Palombit et al., 1997). The resulting foraging patterns shown by females in mixed-sex dyads will likely be different in each case. Specifically, oestrous females are likely to produce more (since the mate-guarding male tends to follow the female rather than lead her), while lactating females are likely to scrounge more (as they follow their male 'friends').

Methods

Study Site and Subjects

Fieldwork was carried out at Tsaobis Leopard Park, Namibia (22°23'S 15°45'W) on 36 adult members of two habituated groups of chacma baboons. There were n=22, and n=14 adults from groups containing 57 and 32 individuals respectively (see Chapter 2). To recap, baboons in this semi-desert region forage in discrete food patches found in two distinct habitats: riparian woodland and open desert (Cowlishaw, 1997b; Cowlishaw and Davies, 1997) (See Chapter 2; Figure 2.3). The riparian woodland habitat occurs in groves along the banks of a dry riverbed and consists mainly of *Prosopis glandulosa*, *Salvadora persica* and *Faidherbia albida*. These trees and shrubs form large and discrete food patches that can contain multiple foraging individuals. The open desert habitat, in contrast, is characterised by herbs and scattered dwarf shrubs and trees (mainly *Commiphora virgata*). Here, food patches are comprised of these small dispersed plants together with invertebrates that the baboons acquire by turning over rocks: these food patches are rarely large enough for more than one individual. The riparian woodland and open desert habitats are therefore subsequently referred to as large-patch and small-patch habitats, respectively (see Figure 3.1 for a summary of habitat types). Food items within patches in both habitats include seed pods, flowers, berries, and invertebrates (see Chapter 2; Figure 2.12). These are typically small and relatively inconspicuous, and require dedicated search time in the patch.

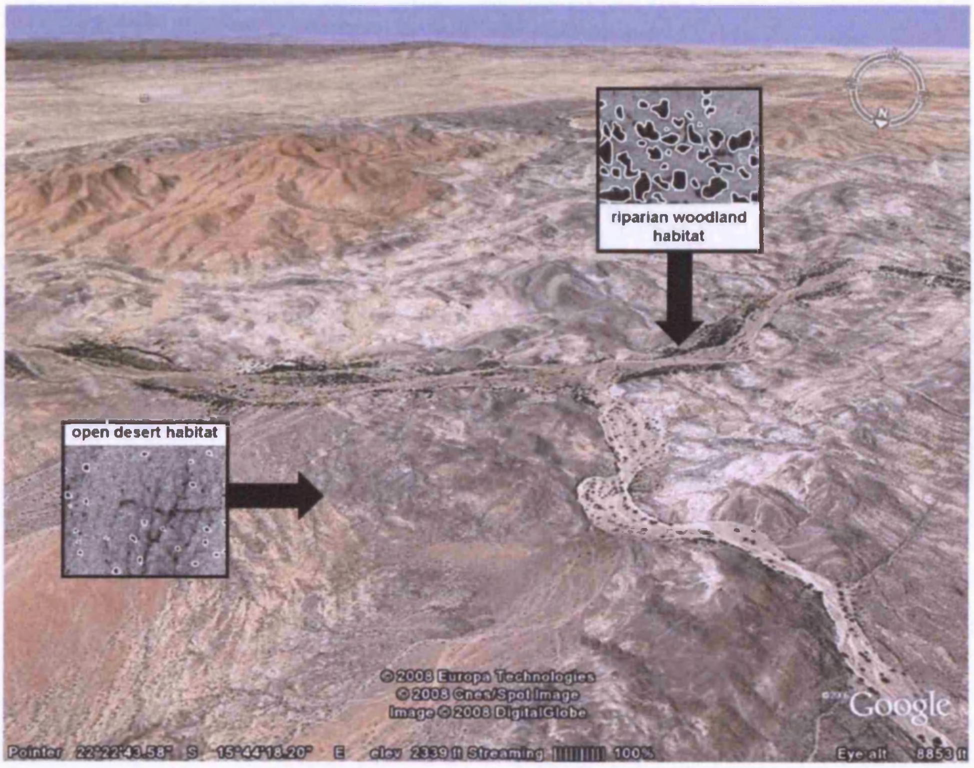


Figure 3.1.
Study region and examples of baboon foraging habitats and patches. "Small-patch habitat" was open desert where food items were dispersed in many small patches, i.e. grasses, herbs and shrubs, and invertebrates under rocks. "Large-patch habitat" was riparian woodland where food items were clumped in larger food patches, i.e. large shrubs and trees. Discrete food patches are indicated by a white outline in boxes showing enlarged areas of each of the habitat types. Enlarged areas are approximately 100m^2. The background image is available freely from Google Earth. The enlarged boxes are taken from an aerial photograph of the study region.

Observational Data

A total of 972 one-hour focal watches were conducted on randomly selected foraging adults from the two groups, during full-day dawn-to-dusk follows, between June to December 2005 and 2006 (mean±SE watches per adult = 27±2).

Each time a focal entered a new food patch for >5 seconds and consumed food it was considered a foraging event. Food patches were defined as discrete foraging patches. A mean±SE of 266±32 foraging events were recorded per individual, and a mean±SE of 10±1.5 foraging events per individual per focal watch, producing a total of 9,605 foraging events. These were defined as 'scrounging' events if a focal baboon joined a food patch in which another foraging individual(s) was already present, and as 'producing' events if the focal animal chose to search for food in an unoccupied patch.

Foraging events were recorded as occurring in either large-patch habitat or small-patch habitat (Figure 3.1). Focal position within the group was recorded as either 'back', 'middle', 'front' (all of which are 'central' positions), or 'periphery'. In the field this was estimated according to the number and distribution of individuals around the focal animal. If position could not be established (due to poor visibility, n=833) it was recorded as 'unknown'. Focal female reproductive state was recorded at the start of each focal watch in four categories: oestrous cycling (fertile versus non-fertile phases), pregnant, and lactating. The fertile versus non-fertile phase of each female was identified by the state of her ano-genital skin which, as in many catarrhine primate species, gradually swells during each oestrous cycle, reaching its maximal size around the time of ovulation (fertile phase), before rapidly returning to its non-swollen state (non-fertile phase). (See Zinner et al., 2004).

Dominance, social affiliation (strength and symmetry of grooming indices), and kinship relationships between all focal individuals and their nearest foraging neighbour at each foraging event were calculated (see Chapter 2 for details of dominance and grooming data). For scrounger events, the nearest foraging neighbour would be in the same patch, while for producer events the nearest foraging neighbour would be in another patch (since, by definition, if the nearest foraging neighbour was in the same patch then it became a scrounging event). Infrequently, all neighbours were engaged in non-foraging behaviours (locomotion, resting, grooming) or no neighbours were in sight of the focal individual whilst foraging, i.e. there was no opportunity to scrounge. These cases were removed from the dataset prior to analysis.

Statistical Analyses

Simple bivariate relationships were tested using standard two-tailed parametric tests (or non-parametric tests where the data could not be normalised). To assess the variables influencing individual producer-scrounger tactics during foraging events, I used Generalised Linear Mixed Models (GLMMs) (Goldstein, 2003). I used producer-scrounger behaviour as a binary response term, with binomial errors and a logit link function. Data were collected by observing the foraging events of a single focal individual, with a specific neighbour, during a focal watch. I therefore used cross-classified GLMMs, implemented in MLwiN (Rasbash et al., 2004) and fitted 'individual identity', 'neighbour identity' and 'focal number' as random effects, to control for the non-independence of repeated foraging events, and the repeated interactions with specific neighbours, within and across focal watches. I conducted a total of four models.

The first model tested the effect of ecological factors on the probability of an individual scrounging for all possible dyad combinations (n=9,110 foraging events). In this 'ecological model', I fitted the following as categorical fixed effects: habitat type (small patch, large patch), spatial position (back, middle, front, peripheral), and group identity (small, large). I then conducted a further three models to investigate producer-scrounger foraging patterns for specific dyad types, namely (i) female-female (n=4,393), (ii) female-male (n=2,593), and (iii) male-female (n=2,124) foraging dyads. (Male-male foraging dyads were not considered in any analyses as they were rarely neighbours n=295). In these dyads, the first individual is the animal that makes the foraging decision (i.e. the focal animal) while the second is the nearest group-mate in the food patch it joins (scrounger event) or could have potentially joined (producer event). For each model I fitted the fixed ecological factors already described. I then fitted the forager's relative dominance rank, social affiliation (strength and symmetry of grooming), and genetic relatedness to its neighbour as continuous fixed effects. I also entered female reproductive state (cycling non-swollen, cycling swollen, pregnant, and lactating), and the occurrence of male mate guarding (consort, nonconsort) as fixed categorical effects to explore the influence of reproductive patterns on producer-scrounger foraging dynamics among females and males.

Final models were run for 5×10^5 iterations using a Markov-chain Monte Carlo algorithm. Raftery-Lewis $\hat{N}$ values were then checked. These are diagnostics based upon the behaviour of the 2.5% and 97.5% quantiles of any effects under consideration, and can be used to estimate the length of the Markov chain required (Goldstein, 2003). All model $\hat{N}$ values were less than 50,000 and so were proven to be sufficient. I then checked that the parameter estimates (fixed and random effects) had stabilised, i.e. their standard errors reached a constant value. Significance of terms was tested using the Wald statistic, evaluated against the Chi-square distribution (Goldstein, 2003).

Results

Baboons attended the food discoveries of group mates in 0.37±0.06 (mean proportion ± SE) of foraging events. I found no overall difference in the levels of scrounging between males and females: 0.34±0.05 versus 0.36±0.03 (t-test for unequal variances: $t = -0.34$, $df = 12$, $P = 0.74$). I also found no significant correlation between dominance rank and the average proportion of scrounger events across individuals (Pearson's $r_s = -0.033$, $n = 36$, $P = 0.85$). There was however, variation among individuals in their use of either tactic (Figure 3.2). Patch residence times also reflected food patch sizes with baboons foraging for 2.4±0.2 minutes per patch in small-patch desert habitat compared to 9.3±0.4 minutes per patch in large-patch woodland habitat. Average patch time across all foraging events for producers was also shorter than that for scroungers (Figure 3.3).

To verify that the baboons are following a producer-scrounger game, it is useful to ascertain whether the observed baboon foraging patterns fit the basic pattern of the theory. In particular, one characteristic pattern of producer-scrounger games is that producers tend to leave patches before scroungers, since although both foragers satiate at the same rate the producer satiates more quickly due to the benefits of the finder's advantage (Giraldeau and Caraco, 2000; Rita et al., 1997). In the baboon system, this is precisely the pattern we see (Figure 3.3).

One potential confounding factor is the size of the patch, which differs substantially between habitats, since if producers tend to visit smaller patches then the patches they are foraging in will deplete more quickly, also leading to lower residence times. However, even within habitats, we see the same pattern (Figure 3.3). While it cannot be ruled out that within-habitat variation in patch size might still contribute to this pattern, the available evidence is consistent with the baboons following a producer-scrounger game, as I would expect given the nature of the foraging system. A more thorough understanding of the adoption of producer-scrounger tactics requires multivariate analyses that consider the effect of multiple factors simultaneously. I therefore proceed with a series of GLMM analyses to investigate how foragers alter their allocation to either the producer or scrounger tactic through assessment of local conditions.

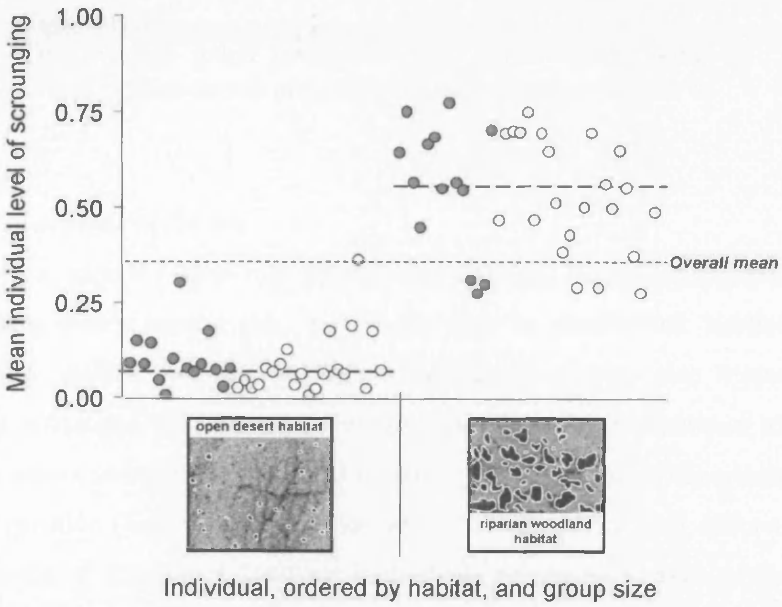


Figure 3.2.
Mean individual level of scrounging for baboons in the small group n=14 adults (grey filled points), and the large group, n=22 adults (white filled points) when in small-patch habitat (open desert) and large-patch habitat (riparian woodland). The mean average level of scrounging for individuals in each habitat type is shown by dotted lines, and the mean overall level of scrounging is also indicated.

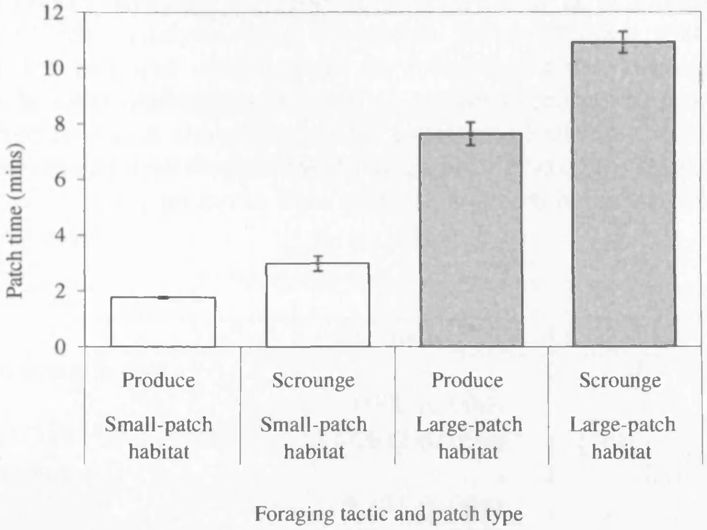


Figure 3.3.
The average patch residence time across all foraging events pooled across all individuals from both groups.

The effect of ecological factors

The ecological model (Table 3.1) showed that baboons scrounged significantly more in large-patch habitat (i.e. woodland) than in small-patch habitat (i.e. desert). The spatial position an individual occupied was also important: individuals scrounged significantly more when positioned at the centre or back of a foraging group, compared to a frontal position, and least of all when placed in a peripheral position (Figure 3.4). I did not however find a significant difference in the prevalence of scrounging between individuals belonging to each of the two (large versus small) groups.

Table 3.1.
Ecological factors affecting the probability of scrounging in foraging baboons (n=9,110). GLMM analysis with a binomial error structure and logit link, controlling for repeated observations on individual focal animals and their neighbours between and across observation sessions (entered as cross-classified random effects). Table shows parameter estimates (Estimate), standard errors (SE) and associated test statistic (Wald statistic). ***<0.001, **<0.01, *<0.05. Values for non-significant terms were obtained from fitting terms individually to the minimal model.

Model term	Estimate (SE)	d.f.	Wald
Habitat food-patch size		1	703.76***
Small	0.000 (0.000)		
Large	2.622 (0.099)		
Spatial position		3	58.16***
Back	0.131 (0.094)		
Middle	0.000 (0.000)		
Front	-0.413 (0.074)		
Peripheral	-1.108 (0.210)		
Group identity		1	0.24
Small	0.000 (0.000)		
Large	0.139 (0.284)		
Focal number (random term)	1.751 (0.284)		
Individual identity (random term)	0.565 (0.188)		
Neighbour identity (random term)	0.159 (0.059)		
Constant	-2.529 (0.383)		

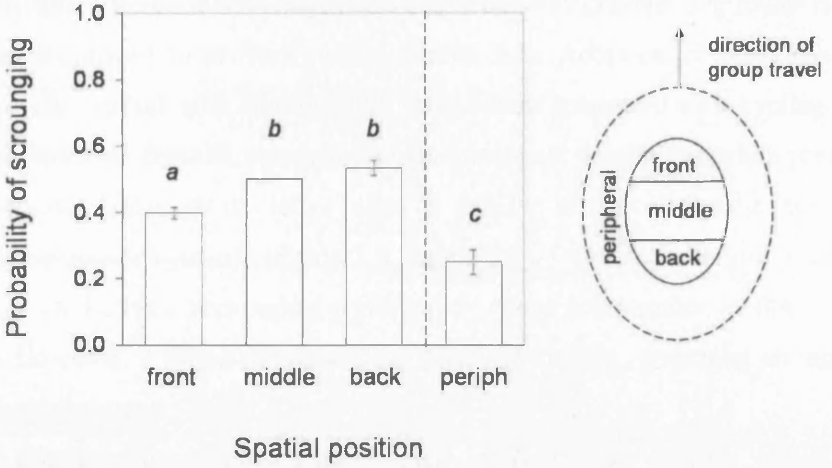


Figure 3.4.
The fitted values for the effect of spatial position (relative to middle position) upon the probability of scrounging in foraging baboons. Values are obtained from the parameters given in Table 3.1, controlling for the effect of all other significant terms and for the influence of repeated measures of individuals, neighbours and observation sessions. Letters indicate significant pairwise differences between spatial categories at $P<0.05$, i.e. categories with different letters are statistically different. A diagrammatic representation of spatial positioning is also shown.

The effects of social and reproductive factors

I then explored the influence of social factors and reproductive patterns of individuals presented with an opportunity to scrounge from a same- or different-sex neighbour, i.e. models for female-female dyads, male-female dyads, and female-male dyads. The qualitative effects of ecological factors were consistent in all models.

The female-female model showed that females scrounged more from those group-mates with whom they shared a strong social relationship (Table 3.2; Figure 3.5a), as well as from individuals that were lower ranked than themselves, and this relationship was more marked when in small-patch habitat (interaction effect: Table 3.2; Figure 3.5b). I found no significant effect of kinship or grooming symmetry in that dyad on the probability of scrounging (Table 3.2).

The female-male model showed that females scrounged more where the relative-rank difference with their male neighbour was greatest (i.e. lower-ranked females scrounged most from males) (Table 3.3). Adoption of scrounging by females also varied with reproductive state: when compared to a cycling non-swollen baseline, females scrounged more from male neighbours when pregnant and lactating (although the latter failed to achieve statistical significance), and less during swollen periods (Table 3.3; Figure 3.6). I also found a group identity effect, with females scrounging significantly more from males in the smaller group. However, I found no significant effect of kinship, grooming strength or grooming symmetry (Table 3.3).

Finally, the male-female model showed that neither social nor reproductive factors affected male adoption of the scrounger tactic (Table 3.3). Instead, for male-female dyads, only ecological factors were significant, in the directions already described. Thus, male foraging tactics appear to be independent of social and reproductive relationships to neighbours. Once ecological factors have been considered, a male baboon scrounges indiscriminately with respect to its female neighbour.

Table 3.2.
Factors affecting the probability of scrounging within female-female dyads (n=4,393). GLMM analysis with a binomial error structure and logit link, controlling for repeated observations on individual focal animals and their neighbours between and across observation sessions (entered as cross-classified random effects). Table shows parameter estimates (Estimate), standard errors (SE) and associated test statistic (Wald statistic). ***<0.001, **<0.01, *<0.05. †Refer to methods for units of measurement for social effects. ^Results shown are for Wang's (2007) pairwise estimator; other estimators of relatedness used were also non-significant. Values for non-significant terms were obtained from fitting terms individually to the minimal model, and non-significant two-way interactions are not shown for simplicity.

Model term	Estimate (SE)	d.f.	Wald
Ecological factors			
Habitat food-patch size		1	292.81***
Small	0.000 (0.000)		
Large	2.832 (0.165)		
Spatial position		3	16.06**
Back	0.256 (0.147)		
Middle	0.000 (0.000)		
Front	-0.307 (0.123)		
Peripheral	-1.115 (0.493)		
Group identity		1	0.30
Small	0.000 (0.000)		
Large	0.271 (0.498)		
Social Factors†			
Grooming strength index	0.581 (0.271)	1	4.75*
Grooming symmetry index	0.204 (0.154)	1	1.75
Relative-rank difference	0.539 (0.425)	1	1.61
Pairwise relatedness^	0.095 (0.410)	1	0.06
Habitat*Relative-rank difference		1	4.52*
Small patch*relative-rank difference	0.973 (0.458)		
Large patch*relative-rank difference	0.000 (0.000)		
Focal number (random term)	2.370 (0.471)		
Individual identity (random term)	0.850 (0.341)		
Neighbour identity (random term)	0.209 (0.116)		
Constant	-2.735 (0.347)		

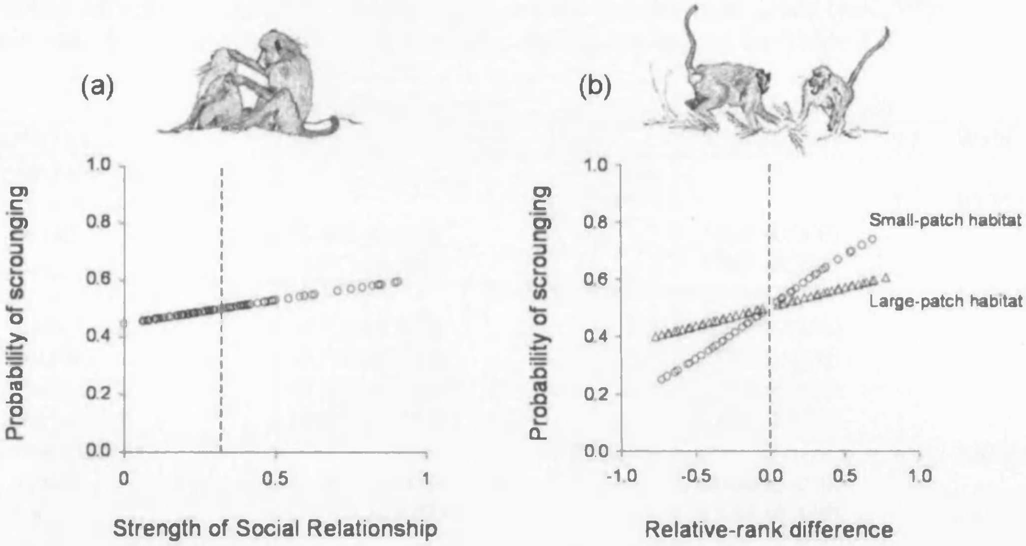


Figure 3.5.
The fitted values for (a) strength of social relationship and (b) the interaction effect of relative-rank difference*habitat, upon the probability of scrounging within female baboon foraging dyads. Effects shown are relative to a dyad of zero relative-rank difference, and the mean strength social relationship (indicated by dashed lines). Values are obtained from the parameters given in Table 3.2, controlling for the effect of all other significant terms and for the influence of repeated measures of individuals, neighbours and observation sessions.

Table 3.3.
Factors effecting probability of scrounging within female-male dyads (n=2,593), and male-female dyads (n=2,124). For more details, see legend for Table 3.2.

	Female-male dyads			*Male-female dyads*		
Model term	Estimate (SE)	d.f.	Wald	Estimate (SE)	d.f.	Wald
Ecological factors						
Habitat food-patch size		1	284.18***		1	30.31***
Small	0.000 (0.000)			0.000 (0.000)		
Large	3.947 (0.234)			1.547 (0.281)		
Spatial position		3	13.53**		3	16.33***
Back	0.328 (0.322)			-0.298 (0.258)		
Middle	0.000 (0.000)			0.000 (0.000)		
Front	-0.655 (0.216)			-0.495 (0.200)		
Peripheral	-0.559 (0.453)			-2.087 (0.598)		
Group identity		1	5.08*		1	2.45
Small	0.000 (0.000)			0.000 (0.000)		
Large	-1.517 (0.673)			0.656 (0.419)		
Social Factors†						
Grooming strength index	0.495 (0.276)	1	3.21	0.100 (0.270)	1	0.02
Grooming symmetry index	-0.138 (0.259)	1	0.28	0.276 (0.519)	1	1.25
Relative-rank difference	2.064 (0.787)	1	6.87**	-0.566 (0.433)	1	1.63
Pairwise relatedness^	-1.624 (0.974)	1	2.78	-1.473 (0.806)	1	3.34
Reproductive Factors						
Female state		3	10.53*		3	0.92
Non-swollen	0.000 (0.000)			0.000 (0.000)		
Swollen (oestrus)	-1.084 (0.634)			-0.311 (0.478)		
Pregnant	0.849 (0.317)			-0.083 (0.276)		
Lactating	0.551 (0.295)			0.219 (0.262)		
Focal number (random term)	3.061 (0.169)			0.055 (0.417)		
Individual identity (random term)	1.306 (0.572)			2.626 (0.604)		
Neighbour identity (random term)	0.250 (0.324)			0.682 (0.180)		
Constant	-1.808 (0.766)			-1.320 (0.422)		

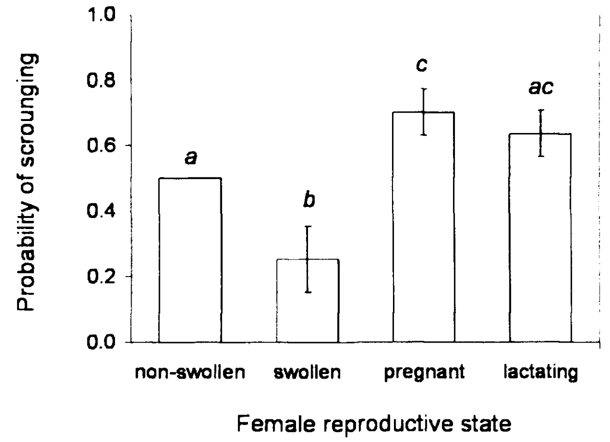


Figure 3.6.
The fitted values for the effect of female reproductive state (relative to non-swollen) upon the probability of scrounging from a male neighbour. Values are obtained from the parameters given in Table 3.3, controlling for the effect of all other significant terms and for the influence of repeated measures of individuals, neighbours and observation sessions. Letters indicate significant pairwise differences between reproductive categories at $P<0.05$, i.e. categories with different letters are statistically different.

Discussion

Despite the potential for producer-scrounger models to explain many of the intricacies of social foraging tactics in group-living animals, the subject has not received much attention in the field, and most studies have largely been confined to the realm of indoor aviary experiments. Many primate species engage in a considerable amount of social foraging, offering a valuable opportunity to test the predictions of producer-scrounger models. This study provides the most complete application to date of the producer-scrounger game to animals foraging under natural conditions and in stable social groups. In this study, I found good general support for the producer-scrounger framework, although there were also some notable cases where predictions were not met (see Table 3.4 for a summary). Here I consider those results that supported predictions (and their reliability), and what might explain the failure to support other predictions.

Table 3.4.
Predictions of producer-scrounger models tested, and the findings.

	Predictions of Producer-Scrounger Models[1]	**Support?**	
Ecological	Individuals will be more likely to scrounge in large-patch habitat	*Yes*	All individuals
	Individuals will be more likely to scrounge in a larger foraging group	*No*	All individuals
	Individuals will be more likely to scrounge when closer to the centre of a group	*Yes*	All individuals
Social	Individuals will scrounge more from neighbours of lower dominance rank than themselves	*Yes*	Females, in small-patch habitat
	Individuals will scrounge more from neighbours with whom they have a strong social relationship and/or from whom they have negotiated tolerance at the feeding site	*Yes*	Females only (strength of grooming relationship)
	Individuals scrounge more from close kin	*No*	All individuals
Reproductive	Social relationships and kinship will be more important in female-female dyads than in mixed-sex dyads	*Yes*	Males scrounge from females indiscriminately
	Elevated levels of producing by oestrous females, and of scrounging by lactating females, in mixed-sex dyads	*Yes/No*	Oestrous females produce more, but pregnant females scrounge more, from males

[1] See Chapter introduction for background and references.

The effects of ecological factors

Increased scrounger behaviour in response to larger patch sizes (due to a decrease in the finder's advantage) is a central prediction of producer-scrounger games. Experimental manipulation of the finder's advantage has been successfully carried out in a number of bird species (Coolen, 2002; Coolen et al., 2001; Giraldeau and Livoreil, 1998) and also for capuchin monkeys *Cebus apella* (Di Bitetti and Janson, 2001), but has yet to be tested under non-experimental conditions for wild foraging, non-avian species. I found that when baboons forage in small-patch habitat, they almost always act as producers. In comparison, an individual foraging in large-patch habitat is 14 times more likely to scrounge. The fact that producers also spent significantly less time at patches than scroungers in each habitat type is consistent with the producer commencing food harvesting in the patch earlier (than a scrounger) and managing to monopolise a fraction of the prey items (finder's advantage) before the scroungers come to take their benefit (Rita et al., 1997).

Nevertheless, two additional factors that could not be measured here may also be contributing to the difference in allocation of scrounger tactics in the two habitats. First, in the large-patch habitat (woodland) there are fewer patches to choose from, and opportunities to produce may be restricted since patches are likely already occupied. Second, predation risk is known to be higher in this habitat (Cowlishaw, 1997a; Cowlishaw, 1997b) which may encourage the use of the scrounger tactic (Barta and Giraldeau, 2000; Barta et al., 2004; Koops and Giraldeau, 1996; Mathot and Giraldeau, 2008). Indeed the presence of existing forager(s) may improve an individuals information regarding not only foraging opportunity but also level of predation risk (King and Cowlishaw, 2007).

Spatial sorting has long been recognised in animal groups (Bumann et al., 1997; Hall and Fedigan, 1997; Hirsch, 2007), and I found that spatial position was an important determinant of producer-scrounger behaviour in baboons. Genetic algorithm simulations by Barta et al. (1997) have shown that scroungers are more likely to be found in central positions, whereas producers should be more common on the group's periphery. These predictions have recently been found to hold for natural foraging populations of birds (Flynn and Giraldeau, 2001; Monus and Barta, 2008), and this is exactly the pattern observed here. As pointed out by Monus and Barta, this result can be a consequence of two alternate processes, which are difficult to distinguish between: (1) individuals actively seeking scrounger opportunities occupy central positions while producers aspire towards the periphery or (2) individuals close to the centre simply have more opportunities to join foraging group-mates. In baboons, a combination of both processes may be the most likely situation.

Surprisingly, I did not find an overall difference in the probability of scrounging in the larger group in comparison to the smaller group (cf. Coolen, 2002). Since the producer-scrounger game predicts a higher frequency of scroungers when group size is greater, all other things being equal, this pattern is inconsistent with producer-scrounger theory. Given the field conditions and associated difficulty of controlling for many potentially confounding factors, this result does not provide a strong rejection of the game's applicability. However, it may indicate that something not assumed by the producer-scrounger models may be occurring and warrant further investigation. An example of one such factor could be forager density. For several previous studies that consider group size, scrounging is positively correlated with the density of individuals in a foraging group (Barta et al., 2004; Monus and Barta, 2008). For the baboon groups under investigation, despite differences in group size, the density of foragers was comparable across both groups. This was a consequence of the larger of the two groups simply spreading out over a wider foraging area: the foraging area for the larger group was 1.53 times that of the smaller group (mean±SE: 6,018 ± $6m^2$ compared to $3{,}922\pm2m^2$ respectively; unequal *t*-test: t = 2.6, df = 479, *P* = 0.004). Interestingly, this difference is almost exactly equivalent to the difference in the number of adults in each group: 22/14 = 1.57. This suggests that to conclusively test the effect of group size upon the overall proportion of scrounging in baboon groups a more detailed analysis that considers a variety of group sizes is required.

The effects of social and reproductive factors

I also considered the effect of multiple social and reproductive factors on foraging tactics among same sex (female-female) and different sex (male-female, female-male) dyads. I first discuss social effects for same-sex dyads.

For a wide range of species, including baboons, more dominant foragers have priority of access at feeding sites (Barton et al., 1996; Brodin et al., 2001; Fero et al., 2007). Consequently, phenotype-limited producer-scrounger models predict that dominants will more often scrounge from lower ranked group-mates. I show exactly this pattern—female baboons increased their adoption of the scrounger tactic when presented with an opportunity to scrounge from a lower-ranked female neighbour where food sources could be monopolised. Yet other empirical studies report mixed results (Barta and Giraldeau, 1998; Barta and Giraldeau, 2000; Beauchamp, 2006; Bicca-Marques and Garber, 2005; Di Bitetti and Janson, 2001; Liker and Barta, 2002; McCormack et al., 2007). So what might explain such inconsistencies? Food distribution likely plays a mediating role. The interaction effect suggests that scrounging from subordinates may be more profitable where patches are small and thus food items monopolisable by the dominant. But methodology likely plays a role too. I examined the influence of dominance as a property of a dyad, rather than absolute dominance, and also controlled for other ecological and social effects. In the case of the latter, associations between such effects may have potentially important implications if not statistically or experimentally controlled, e.g. if spatial position is arbitrated by dominance. The results of previous studies might therefore reflect differences in food patch size configurations, and/or methodological differences.

The other two social factors investigated were social affiliation (grooming) and kinship. In both cases, strong affiliation/kinship was expected to promote scrounging among females, although I did not anticipate identical patterns since the two are only weakly (non-significantly) correlated in the sample.

First, the results indicate that social affiliation is an important determinant of scrounging behaviour among females. A full interpretation of this result requires a consideration of the index of social affiliation I used: grooming. Grooming is the standard measure of social relationships and social bonding in primates (Kudo and Dunbar, 2001; Schino, 2007; Silk, 2007b), and is further known to be associated with parasite removal (Boccia et al., 1989; Zamma, 2002), the release of endorphins (Kaverne et al., 1989; Schino et al., 1988), and reduction of stress in the groomer and/or groomee (Schutt et al., 2007). However, it has also been recently proposed that grooming might be used as a commodity that is traded between individuals in return for more grooming or other services (i.e. reciprocal altruism), which might include tolerance at a feeding site and therefore acceptance of scrounger behaviour (Barrett et al., 1999; Schino, 2007; Seyfarth and Cheney, 1984). In this case, I would have expected that the grooming symmetry in a dyad would predict scrounging behaviour most strongly (i.e. the focal grooms its neighbour in order to 'purchase' tolerance of scrounging). Although I did not find evidence in support of such an effect, my test of this prediction remains inconclusive. This is primarily because I measured grooming symmetry with a single value across the study period, whereas grooming symmetry may vary over time and the key period of grooming transaction for any scrounging event may rather be in the hours or days that precede it. Nevertheless, as far as I have been able to test this hypothesis, I have not been able to support it. In contrast, the overall strength of grooming relationship a female baboon holds with her neighbour was a good predictor of scrounging. This result suggests that individuals who spend a lot of time grooming one another, whether related or not, will be more likely to tolerate scrounging from one another and thus receive a foraging benefit (i.e. conditional mutualism).

Second, I found no effect of kinship on scrounging behaviour among females. Although unexpected, this corroborates the findings of two recent bird studies, where kinship similarly failed to affect producer or scrounger tactic use (Ha et al., 2003; McCormack et al., 2007). An earlier study in this baboon population also supports my finding that social affiliation is more important than kinship: Devas (2005) showed that individual food intake rates increased when foraging neighbours were close affiliates, but not when such neighbours were close kin. Finally, the results of other studies examining co-feeding at food patches across a number of species have shown kinship only to be important at parent-offspring levels of relatedness (Belisle and Chapais, 2001; Nystrand, 2006; Rossiter et al., 2002; Sklepkovych, 1997). Given that this study focussed on relationships between pairs of adults, who on average are less closely related than parent-offspring pairs, it thus remains the case that kinship might still be important for producer-scrounger decisions in baboon dyads comprised of parents and offspring. Meanwhile, these findings add to a growing body of research that indicates cooperation between individuals in animal groups can occur between kin and non-kin alike (e.g. Langergraber et al., 2007).

The analysis of producer-scrounger foraging patterns within different sex dyads also produced interesting results. Females scrounged significantly more from males when there was a large difference in rank (i.e. lowest ranked females), and in the smaller group. The group-size effect might be interpreted simply as an artefact of the male: female ratio in the two groups. For a single random chance encounter, females in the larger group would encounter males with a probability of 0.18, compared to 0.28 in the smaller group, and so have more opportunity to scrounge from males. In contrast, the low-ranked female effect appears more difficult to explain. However, I expect that this again comes down to opportunity. The lowest-ranked females are likely not tolerated by higher-ranked females, and so cannot join them at food patches. Therefore scrounging from males instead may offer these females a greater chance of success and also reduce the likelihood of escalated conflict.

Finally, reproductive patterns also had a strong influence on patterns of producing and scrounging in the female-male model. In the first case, females produced more when in oestrus, as predicted given that mate-guarding males tend to follow rather than lead the female. In the second case, females scrounged more when pregnant (and lactating, although this was not statistically significant). This pattern was not expected, but may be explained by the fact that both pregnant and lactating females have higher energy demands due to their reproductive state (Altmann, 1980; Dunbar and Dunbar, 1988), since previous models of producer-scrounger behaviour have predicted that hungrier animals should scrounge more (see Lendvai et al., 2004).

Concluding comments

To date, there has been little opportunity to integrate observations of social foraging interactions of wild, socially feeding animals, with data on ecological, social and reproductive factors. I have demonstrated that broad-scale ecological factors influence baboon foraging behaviour in a way consistent with producer-scrounger models. Moreover, these findings add a further level of understanding to how social and reproductive forces, interact with, or operate in spite of, such ecological factors on producer-scrounger dynamics. I have shown an effect of both dominance and social affiliation between individuals, and have highlighted the importance of reproductive patterns on foraging behaviour for individuals living in a complex social system. It is hoped that further work will explore the generality of these findings for other populations and species.

Chapter 4 – When to use social information: the advantage of large group size in individual decision-making

The manuscript presented in this chapter is published as:

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Abstract

Correct decision making is crucial for animals to maximize foraging success and minimize predation risk. Group-living animals can make such decisions by using their own personal information or by pooling information of other group members (i.e. social information). Here, I investigate how individuals might best balance their use of personal and social information. I use a simple modelling approach in which individual decisions based upon social information are more likely to be correct when more individuals are involved and their personal information is more accurate. The model predicts that when the personal information of group members is poor (accurate less than half the time), individuals should avoid pooling information. In contrast, when personal information is reliable (accurate at least half the time), individuals should use personal information less often and social information more often, and this effect should grow stronger in larger groups. One implication of this pattern is that social information allows less well-informed members of large groups to reach a correct decision with the same probability as more well-informed members of small groups. Thus, animals in larger groups may be able to minimize the costs of collecting personal information without impairing their ability to make correct decisions.

Introduction

When moving through its habitat, a group-living animal directly interacts with its environment to gather both 'personal information' from environmental cues and 'social information' from the behaviour of conspecifics (Dall et al., 2005; Grocott, 2003). Other group members will present social information to an individual in a variety of ways (Bradbury and Vehrencamp, 1998; McGregor, 2005) that can be broadly categorized as evolved 'signals' and social 'cues' (Dall et al., 2005; Danchin et al., 2004). Signals refer to intentional communication while cues refer to information produced incidentally by individuals (Danchin et al., 2004; Valone, 1989; Valone and Templeton, 2002), e.g. the foraging behaviour of others reveals the location of food (see Chapter 3) while flight behaviour indicates impending danger. Individuals monitoring the behaviour of other group members may be able to make faster, more accurate assessments of their environment through the information that signals and cues provide (Valone and Templeton, 2002). Similarly, theoretical work that focuses on group decision making suggests that decisions based on information pooled from many group members may be more accurate than decisions based on the information of a single individual (Simons, 2004) and correct group decisions might even occur solely on the basis of cues (Couzin et al., 2005).

Nevertheless, animals in groups will not use social information indiscriminately. Rather, individuals will use socially acquired and personal information according to the respective reliability of these alternative information sources (Bergen et al., 2004; Dall et al., 2005). The balance between personal and social information use is thus likely to reflect individuals adjusting their decision making to exploit the most reliable information available (Bergen et al., 2004; Nordell and Valone, 1998). The relative quality of social versus personal information and the number of individuals sharing information (i.e. group size) are likely to be crucial determinants in this process (e.g. Bergen et al., 2004; Fraser et al., 2006). However, a general understanding of how these factors interact to influence information use remains to be established.

In this chapter, I use a simple model to investigate how individuals might balance their use of personal information against social information when making decisions. Drawing on Condorcet's eighteenth-century jury theorem, I first investigate how the quality of social information, i.e. personal information pooled across n group members, varies with both the number of individuals and the quality of the personal information involved. I then ask how individuals might best balance their use of personal and social information for groups of different sizes.

Methods

Condorcet's binomial jury theorem (following List, 2004) is used to explore how the quality of personal information compares to the quality of social information available to an individual. I take the quality of personal information (I_p) to be the probability that the personally acquired information possessed by an individual is correct. The quality of social information (I_s), the probability that the majority of the group is correct, is then calculated as follows:

$$I_s = \sum_{k>n/2}^{n} \binom{n}{k} I_p^k (1 - I_p)^{n-k},$$

where n is the number of individuals in the group and k individuals comprise the majority (e.g. in a group of five, the majority will comprise three or more individuals). All the analyses are for odd groups sizes only, $1<n<51$, to avoid ties (where the same number of individuals are correct and incorrect). This model considers a simplified case where (i) information is discrete (e.g. a predator is present or absent, a food patch is rich or poor), (ii) group membership is homogeneous (i.e. all group members have the same quality of personal information), and (iii) personal and social information are equally available (i.e. there are no differential costs to using either type of information).

Results

First, I examined how the quality of social information varies with both the number of individuals and the quality of the personal information involved (Figure 4.1). I found that when the quality of personal information is high (I_p>0.5), individuals that pool this information should make more correct decisions than those that do not. In contrast, when the quality of personal information is poor (I_p<0.5), decisions based on pooled information are less likely to be correct than those based on personal information alone. The magnitude of each of these effects is greater in larger groups (Figure 4.1).

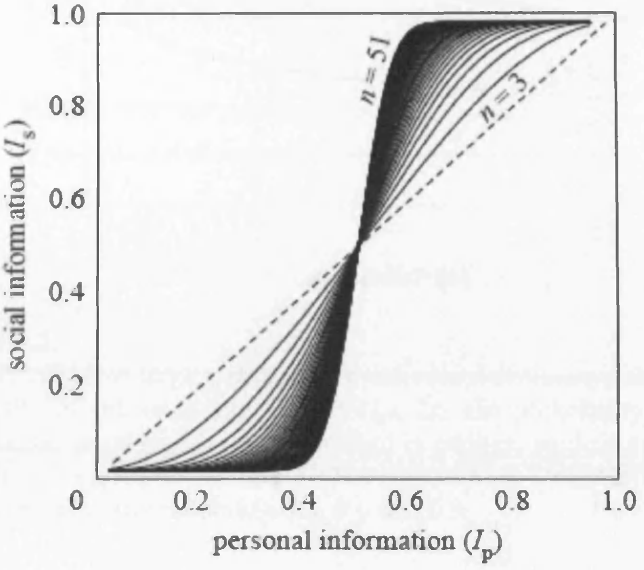


Figure 4.1.
Relative quality of social versus personal information. Plot of quality of social information (I_s), i.e. the probability that the majority of the group is correct, against the quality of personal information (I_p), i.e. the probability that the information possessed by an individual is correct. Lines plotted are for odd group sizes (n) up to 51. To the left-hand side of the dashed line through the origin (n=1) are represented all scenarios where an individual should use social information; to the right-hand side of the line, an individual would do better to rely on its own personally acquired information.

I then asked how individuals might best balance their use of personal and social information for groups of different size. I found that as groups grow larger, the quality of personal information required to maintain high-quality social information is reduced (Figure 4.2). Thus, individuals in larger groups ($n>21$) can make decisions on the basis of social information with a higher likelihood of being correct (I_s=0.9) when personal information is relatively low (I_p=0.64), whereas individuals in smaller groups (n=3) would need higher-quality personal information (I_p=0.80) to achieve the same level of social information accuracy.

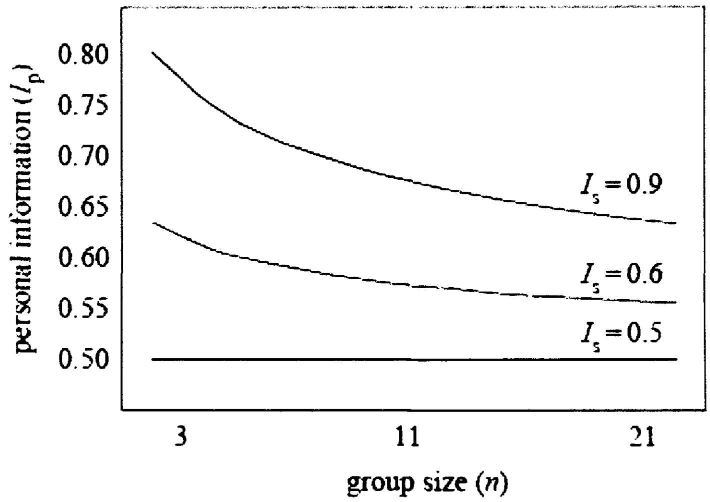


Figure 4.2.
The advantage of large group size in individual decision making. Plot of quality of personal information (I_p), i.e. the probability that the information possessed by an individual is correct, against group size (n). Lines are plotted for odd n ($3<n<21$), where social information (I_s) is correct with probability 0.5, 0.6 and 0.9.

Discussion

It is already well established that group living can provide benefits to individual group members (Krause and Ruxton, 2002). Information sharing is one of these benefits: animals in groups can base their decisions not only on their own information but also that of others (e.g. Kerth et al., 2006, Chapter 3). This is beneficial because individuals which observe group mates can obtain more accurate information and thus make better-informed decisions on the basis of the most reliable information available (Bergen et al., 2004; Fraser et al., 2006).

Here, I have adopted Condorcet's jury theorem to explore how group-living animals might balance their use of personal and social information. I have found that individuals are more likely to make correct decisions when they pool the personal information of others, provided that such personal information is of good quality (correct at least half of the time). Counter-intuitively, given earlier work on information use by animals (Ward and Zahavi, 1973), I have also found that when personal information is of poor quality (correct less than half the time), it is better for individuals to avoid using pooled information. Perhaps, most importantly, I have also found a clear group-size effect in the reliability of personal and social information. When personal information is poor, the likelihood that social information is correct progressively deteriorates as groups grow larger. However, when personal information is of good quality, social information allows less well-informed members of large groups to reach a correct decision with the same probability as more well-informed members of small groups.

This approach has only considered the case where all the group members have the same quality of personal information and both personal and social information are already available. These conditions will not always be met, and further modelling studies might usefully explore the effects of variation in personal information across individuals (Couzin et al., 2005; Franks et al., 2002; Reebs, 2000) and the differential costs that might be involved in the acquisition and processing of personal and social information (Dall et al., 2005). It would also be of interest to consider those cases where information is graded rather than discrete (Dall et al., 2005; Valone and Templeton, 2002), such that a range of information values (rather than the dichotomous correct–incorrect alternatives used here) could be explored. Nevertheless, this study provides a simple conceptual model to understand how individuals in groups of different size might balance their use of social information with personal information.

This model may also offer a framework for improving our understanding of the benefits of living in groups. For individuals living or interacting in groups, using social information may offer yet another advantage to group living, and can promote the evolution of sociality (Beauchamp et al., 1997; Buckley, 1997a; Buckley, 1997b; Safi and Kerth, 2007). The group size–predator detection effect (Elgar, 1989; Roberts, 1996) provides a classic example. Animals in larger groups are commonly observed to scan less frequently for predators while maintaining their overall detection rate, allowing them more time for feeding (for a recent example, see Fernandez et al., 2003). Reduced vigilance in larger groups may result from the dilution of predation risk (Roberts, 1996) or an increase in feeding competition (Beauchamp and Ruxton, 2003), but this model provides an explanation for how the overall detection rate can be maintained when individual vigilance has been reduced and provides further understanding of why individuals might be willing to lower their vigilance in the first place. By pooling information, animals in larger groups can make decisions with the same accuracy as those in smaller groups even when their personal information is less accurate.

Chapter 5 – The role of individual state and the environment on behavioural synchrony in baboon groups

Abstract

Coordinated behaviour across individual group members is essential if a group is to remain spatially coherent. In this chapter, I investigate what factors can promote or constrain the achievement of behavioural synchrony (measured as diversity in activities among group-members) in a complex social system: chacma baboons (*Papio ursinus*). Two wild groups were studied in the field by instantaneous scan sampling during full-day follows, generating 6535 scans over 517 days. Observed behavioural synchrony showed greater variability than that expected by a statistical null model in which each baboon acted independently of another. Using a generalised linear mixed model to explore this variability, I found that the probability of a group being synchronised increased with the number of pregnant females, but decreased with the number of sexually-swollen females. Synchrony also declined throughout the day. I interpreted these two results in terms of variations in the activity budgets of both sexes, and changing levels of satiation among individual group members, respectively. Synchrony was also highest in closed woodland habitat, and lowest in open desert habitat. This is interpreted as a consequence of two factors that may not be independent: food patch configuration and predation risk. Finally, I found a non-linear relationship with increasing group cohesion, which may suggest that where the opportunity for transfer of information is limited, behavioural synchrony can be constrained. Overall, these findings indicate support for activity budgets, habitat constraints and group properties all having an effect on patterns of behavioural synchrony in baboon groups.

Introduction

Synchronised behaviour occurs when large numbers of individuals perform activities together in unison, and is often ubiquitous with animal aggregation (Sumpter, 2006). Famous examples involve the simultaneous flashing of fireflies (e.g. Copeland and Moiseff) or the close synchrony of births in some animal groups (e.g. Gregg et al., 2001; Porter and Wilkinson, 2001; Rutberg, 1984). In fireflies, synchronised flashing is performed entirely by males and is associated with mating behaviour, which is likely to serve to attract females at a localised level (Ermentrout, 1991; Otte and Smiley, 1977). In the case of reproductive cycles, birth synchrony can act as a predator-swamping strategy, reducing the predation of vulnerable offspring and increasing the probability of neonate survivorship (Boinski, 1987; Rutberg, 1984). But behavioural synchrony can be more spontaneous and occur on an almost minute-to-minute basis. For example, a highly-aligned group of animals moving through their environment can be said to have momentarily synchronised their direction of movement (Sumpter, 2006). But why do the behaviours of many individuals become synchronised in these different ways? Variations in a group's behavioural synchrony most likely reflect changes in the costs and benefits of realising activity synchrony (Rands et al., 2003).

The benefits of synchrony may be substantial. Behavioural synchrony may be necessary for individuals to maximise the benefits of group-living. Take the classic examples of sociality increasing foraging benefits and reducing predation risk. Individuals attempting to find food at the same time can increase their opportunity for information transfer (i.e. acquiring social information) about the locations and qualities of food resources, e.g. by monitoring the foraging success of others (Fernandez-Juricic et al., 2007; King and Cowlishaw, 2007-Chapter 4; Valone, 2007). Likewise, Rodriguez-Girones, & Vasquez (2002) argue that that coordinating anti-predator scans among group members can be more efficient than independent scanning (even if individuals must spend a large share of their time coordinating their behaviour) provided that detection information is rapidly shared among group members (Bednekoff and Lima, 1998). Otherwise, independent scanning may reduce the probability of predator detection due to long gaps where no individuals are vigilant (Ward, 1985).

But behavioural synchrony may be costly to achieve. First, differences in the optimal activity schedules of animals of different age, sex, or reproductive state can impact on the ability of groups to achieve synchrony. This 'activity-budget hypothesis' is suggested as an important factor mediating intersexual social segregation and is thought to explain asynchrony in activity between the sexes in ungulate species (Conradt and Roper, 2000; Ruckstuhl and Kokko, 2002; Shannon et al., 2008). But this hypothesis is not limited to age-sex classes. For example, other physiological-morphological characteristics can impact on nutritional demands (e.g. reproductive state: Barrett et al., 2006; Key and Ross, 1999; Miller et al., 2006) resulting in differences in the duration of foraging bouts and movement rates among individuals, making it costly to remain associated and in synchrony (Rands et al., 2003; Rands et al., 2008; Shannon et al., 2008). Indeed, evolutionary game-theory models (e.g. Conradt and Roper, 2007) and more mechanistic models (e.g. Kuramoto, 1984) tackling this topic predict that where between-individual variation in the timing of activities becomes too large then synchrony will break down. Second, differences in food patch configurations or predation risks associated with different habitat types may affect a group's ability to synchronise their activities (the 'habitat-constraints hypothesis'). For instance, in the case of food patch configuration, groups feeding on scattered food resources may find it difficult to preserve group synchrony, since not all group members will be able to forage together at specific locations (Kazahari and Agetsuma, 2008; Nonaka and Holme, 2007; Vahl et al., 2007). Whilst groups moving through high-predation risk habitats (Cowlishaw, 1997a; Cowlishaw, 1997b) may need to be more highly synchronised in order to manage this risk (refer back to Chapter 1 for a discussion of this point). Finally, group members may become visually isolated, or move out of auditory range as a consequence of inter-neighbour distance independent of any habitat effects. Here, behavioural synchrony may break down as a result of reduced opportunity for the use of socially transmitted information via signals or cues (the 'group-structure hypothesis') (see Braune et al., 2005; Cortopassi and Bradbury, 2006; Fletcher, 2008). Consequently, activity-, habitat- and group-related processes may explain variability in behavioural synchrony within animal groups.

In this chapter, I investigate behavioural synchrony in a complex social system: wild chacma baboons (*Papio ursinus*) in central Namibia. I begin by testing whether observed variation in behavioural synchrony within wild baboon groups is greater than expected by a statistical null model where each baboon's behaviour is independent of the rest of the group. I then ask to what degree this observed variability in behavioural synchrony can be explained by individual activity budgets (hypothesis H1), habitat constraints (H2) and/or group structure (H3). These hypotheses are not mutually exclusive, and I outline my predictions for each below.

In the case of individual activity budgets, female baboons experience changes in energy requirements according to their reproductive state (cycling, pregnant, and lactating: (Domb and Pagel, 2001; Lemasson et al., 2008) and vary their time spent feeding accordingly (e.g. Altmann and Samuels, 1992; Dunbar et al., 2002). An increased number of females in each reproductive state is therefore predicted to increase behavioural synchrony, as a consequence of more homogeneous energy requirements among females (prediction 1.1). Variation in energetic state among group members is also likely to be lowest first thing in the morning (e.g. Macleod et al., 2005) when all individuals are hungry irrespective of identity. In contrast, energetic state, and hunger levels, will be more variable as the day progresses, as a result of phenotype-limited foraging success and satiation requirements, caused by difference in age (e.g. Heise and Moore, 2003; Limmer and Becker, 2007), size (e.g. Michelena et al., 2006), or dominance (e.g. Kazahari and Agetsuma, 2008; McCormack et al., 2007, Chapter 3) (prediction 1.2).

Baboon habitat in this semi-desert region falls within two broad categories: rocky desert habitats and riparian woodland groves along a dry ephemeral river (see Chapter 2). These differ along two important axes: food patch configuration (Chapter 3) and predation risk (Cowlishaw, 1997a). I expect that behavioural synchrony will be higher in the woodland habitat compared to the desert habitat as a consequence of both these factors. In the case of food patch configuration, where patches are larger and closer together (riparian woodlands) individuals are expected to spend more time feeding in patches and less time either travelling or travel-feeding (picking at small food items during locomotion) between patches. In contrast, in the desert (where patches are smaller and more dispersed), individuals need to distribute their time more evenly across feeding, travel feeding, and travelling, leading to lower levels of synchrony (prediction 2.1). According to the standard formulation of the habitat-constraints hypothesis, the woodland habitat is more homogeneous than the open desert, and so should be associated with higher synchrony. Concerning predation risk, Cowlishaw (1997a) showed that baboons in this population may adopt a time-minimizing strategy, foraging intensively in areas of high predation risk (i.e. distant from refuges) to leave the area as rapidly as possible. Since baboons are at greater risk of predation in riparian woodland (Cowlishaw, 1997b), groups might be more highly synchronised in their behaviours to minimise the time spent in these high-risk habitats (prediction 2.2).

Lastly I expect synchrony to alter according to group properties. I predict that where groups spread out over a larger area, behavioural synchrony will decrease as a likely consequence of reduced opportunity for maintaining communication among individuals (Dostalkova and Spinka, 2007; Fernandez-Juricic et al., 2007; Valone, 2007) (prediction 3.1). To test this prediction I explore the effects of group cohesion, calculated as a function of the area occupied by group members and the number of individuals in view. As larger groups are also likely to spread out over wider areas, especially during foraging to reduce levels of intra-group food competition (e.g. Agetsuma, 1995), I predict that the larger study group will show lower behavioural synchrony than the smaller study group (prediction 3.2).

Methods

Fieldwork was carried out at Tsaobis Leopard Park, Namibia (22°23'S 15°45'W) on two groups of wild chacma baboons (one large, one small) over two field seasons in 2005 and 2006 (see Chapter 2 for further details).

Observational Data

At the beginning of each day the reproductive state of each female group member was recorded as one of four categories: (i) the non-fertile phase of the oestrous cycle, (ii) sexually swollen (the fertile phase of the cycle), (iii) pregnant, and (iv) lactating. The non-fertile and sexually-swollen phase of each female was identified by the state of her ano-genital skin; pregnant females were identified by prolonged non-swollen periods; lactating females were identified as those suckling infants (refer to Chapter 2 for more details on identification of female reproductive state). The proportions of females in each reproductive state could therefore be calculated for each observation day.

Scan sampling at 30-min intervals was also conducted throughout the day, with the first scan beginning 30 minutes after the baboon group had left their morning sleeping site, and the last scan conducted once the group had settled at their evening sleeping site shortly before sunset. A total of 6535 scans across both baboon groups were obtained from 517 days of observations over two field seasons. 3826 scans were conducted in 2005 (n_{large} = 1476, n_{small} = 2350), and 2709 scans in 2006 (n_{large} = 1636, n_{small} = 1073). At each scan, the number of individuals in view was recorded, and the predominant vegetation in which they were ranging was noted as (i) riparian woodland; (ii) desert scrub and dwarf trees, (iii) perennial grasses; (iv) open ground (i.e. bare sand and/or rock mostly absent of vegetation). Of the individuals in view, their distance in meters from front to back, *a* (last and first individual with respect to the general direction of group travel), and side to side, *b* (farthest individuals either side of the group's centre) was estimated. Initially, distances were recorded using a Buschnell® rangefinder with 1m accuracy at distances between 50 and 200 meters. Once observers could consistently estimate these distances by eye with an error of less than ~10%, the range-finder was used only intermittently. The estimated elliptical area of the group was then calculated as Π*a*b. From this the average area occupied by a single baboon, or group cohesion as a function of the number of baboons in view and the area they occupied, was determined. The activity of each individual in view was assigned as either (i) travelling; (ii) travel foraging; (iii) stationary foraging; (iv) resting; (v) grooming; and (vi) drinking. *Travelling* was defined as the rapid locomotion of individuals, *travel foraging* as the slow locomotion of individuals while searching, manipulating and ingesting food material. *Stationary foraging* described searching, manipulating and ingesting food. *Resting* was a sedentary state in which they were not travelling or foraging and included sleeping. *Grooming* was allogrooming between social partners. *Drinking* described drinking from a water source.

Calculating Synchrony

Since I am concerned with understanding what affects general behavioural synchrony in baboons, I assess synchrony across a number of broad activity categories (above), and use relatively long sampling intervals of 30-minutes, whilst controlling statistically for the number of individuals in view (see Analyses of Observational Data, below). Specific techniques for quantifying behavioural synchronisation have been devised by Engel & Lamprecht (1997) and used to show synchronisation of behaviour in ungulates. Such techniques have been used to investigate differences in behavioural synchronisation for particular activities between particular individuals or subgroups, e.g. males and females (e.g. Dunbar and Shi, 2008), juveniles and adults (e.g. Ruckstuhl, 1999). However, such a measure will not work here, where the question of interest is not the degree of concurrence between a focal animal and its neighbour for a particular activity, but for the group's behavioural synchrony across all individuals and activities. There are other possible approaches: more recent theoretical techniques have devised simple statistics as a means of assessing the proportion of a population that is synchronised at a moment in time (e.g. Rands et al., 2008). However, Rands and colleagues advised caution against its usefulness in empirical studies – particularly because synchrony was near unity in most of the models that they examined. To quantify the degree of behavioural synchrony across whole baboon groups based on all the activities which they performed, I therefore used a very simple index that measures diversity in categorical data: the Simpson's Diversity Index (e.g. Krebs, 1989; Peet, 1974).

The first step was to calculate the proportion of group members, p, which belong to the i-th activity category at each time point, t. This provides a proportion of the group engaged in each activity type. The behavioural synchrony (Bs) exhibited by group members at each scan, t, was then calculated as:

$$Bs = \sum_{i=6}^{S} \frac{n_i(n_i - 1)}{N(N-1)}$$

Where n_i is the number of individuals engaged in a specific activity (i), and N is the total number of individuals in view, for $i = 6$ activity categories. Values near zero therefore correspond to times where groups are heterogeneous with respect to behaviour and are thus considered asynchronous, whereas values near one represent times when groups are homogenous with respect to behaviour and are thus synchronous. This statistic has a simple intuitive interpretation: it represents the probability that if two individuals were randomly chosen in the group at time point t, they would be performing the same behaviour.

Statistical Null Model

To investigate whether variability in behavioural synchrony in wild baboon groups is greater than would be expected by chance, I compared the observed patterns of synchrony with those obtained from a null model in which each baboon's behaviour was simulated independently of the rest of the group. Each baboon was assigned a probability of performing an activity, based upon the average proportion of time the baboons spent engaged in (i) travelling; (ii) travel foraging; (iii) stationary foraging; (iv) resting; (v) grooming; and (vi) drinking, derived from scan data for each group. I then simulated each individual's activity 3423 times for n=32 baboons, and 3112 times for n=57 baboons, which was equivalent to number of scan observations conducted for these two group sizes. Using these simulated datasets I then calculated *Bs* for each simulation for both the small group and the large group, generating a distribution of synchrony scores for each group if all the baboons acted independently of one another. These simulated distributions thus served as a 'null model' to compare against the observed distributions of synchrony. These simulations were carried out in R version 2.7.0 (2008). The differences between the observed and simulated distributions were compared with a Levene's test (Johnson and Wichern, 1992).

Analyses of Observational Data

To assess the variables influencing behavioural synchrony within baboon groups, I used a Generalised Linear Mixed Model (GLMM) with binomial errors and a logit link function (Rasbash et al., 2004). Scan data were collected repeatedly within and across days, and so 'scan number', and 'observation day' were fitted as random effects, to control for non-independence of observations, i.e. where synchrony at time t will influence the probability of synchrony at *t* +1 or -1. I fitted habitat type (woodland, shrub, grass, open) and group identity (large, small) as categorical fixed effects. I fitted the proportion of females in the same reproductive state (four variables, one for each state), diversity of female reproductive state (calculated in the same manner as *Bs*), group cohesion, and also number of individuals in view during the scan, as continuous variables. Entering the number of individuals in view as a continuous variable is required to test and control for its potential effect on group synchrony (e.g. synchrony might appear higher when fewer animals are in view, because a smaller number of animals may exhibit a narrower range of activities). Group cohesion was Log_{10} transformed to normalise data, and all continuous variables were entered with their mean as the reference point, e.g. mean group cohesion was set to zero for comparison.

All fixed effects were entered and dropped sequentially until only those that explained significant variation remained: the minimal model. Each dropped term was then put back into the model to obtain their level of non-significance, and check that significant terms had not been wrongly excluded. In all cases the same minimal model was derived by removing terms from the maximal model and adding terms to the simplest model. Correlations between continuous fixed effects were found to be statistically independent (Pearson's correlations: $P>0.05$ in all cases), and were initially entered into the models together. The diversity of female reproductive state was entered into the model without the other variables of female state of which it is a composite. Biologically relevant two-way interactions and non-linear effects were also tested, and are presented where found to be significant. Significance was tested using the Wald statistic, evaluated against the Chi-square distribution.

Results

Behavioural synchrony compared to a null model

I found that variability in behavioural synchrony was significantly larger than that predicted by the statistical null model where individual baboons behave independently of one another in both groups (Figure 5.1; Levene's $\text{Test}_{\text{small}}$ = 4722, P<0.001, n=3422; Levene's $\text{Test}_{\text{large}}$ = 8626, P<0.001, n=3122).

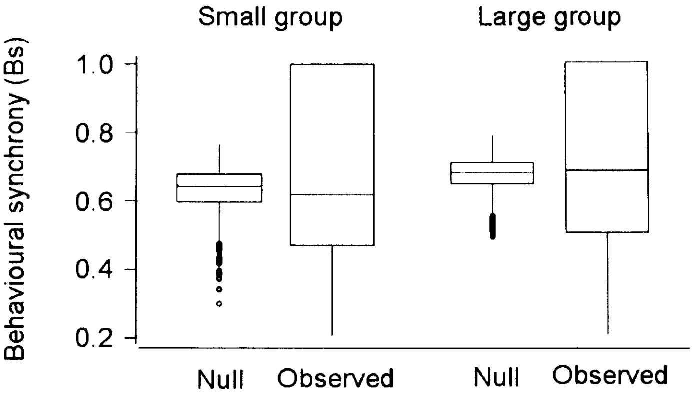


Figure 5.1
Boxplots providing a graphical summary of variability in behavioural synchrony for each baboon group, comparing a null model (in which all baboons act independently of one another) with the observed data. The rectangular box represents the middle 50% (inter-quartile range) of the data, and the lines extending to either side indicate the general extent of the data. The median values are marked inside each box. Outliers are indicated by open circles.

What predicts variability in behavioural synchrony?

First, I investigated and controlled for the proportion of individuals in view. As expected, I found that the probability of behavioural synchrony was greatest when smaller proportions of the group were in view. However, this effect seemed to be apparent only at relatively low numbers (i.e. <25% of group visible), and the differences in synchrony observed between intermediate and higher proportions of individuals in view were negligible (Figure 5.2).

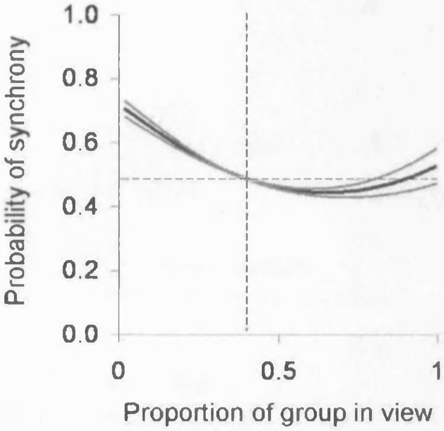


Figure 5.2.
The effects of the number of baboons in view at any one scan upon the probability of group synchrony, as predicted from a GLMM controlling for repeated scan observations within and across days, and with all other significant effects set to their reference categories/average value. The effect shown is relative to an average proportion of group members in view (approximately n=12 and 24 individuals in the small and large group, respectively), indicated by the dotted axis through the figure centre. Predicted standard errors are indicated by grey lines.

An increased number of females in the same reproductive state were predicted to increase behavioural synchrony (prediction 1.1). This prediction was supported only in part. I found that the proportion of females in a pregnant state increased synchrony, but the proportion of sexually-swollen females' decreased synchrony (Table 5.1, Figure 5.3a). No effect was found for other female reproductive states (lactating or non-fertile phase cycling females), and entering an index of 'synchrony of female reproductive state', as a measure of overall convergence in female state, also had no effect (Table 5.1). It is therefore clear that the numbers of pregnant and sexually swollen females act in opposite and opposing directions with respect to group activity synchrony. Behavioural synchrony also decreased as a function of time of day, in support of prediction 1.2 (Table 5.1, Figure 5.3b).

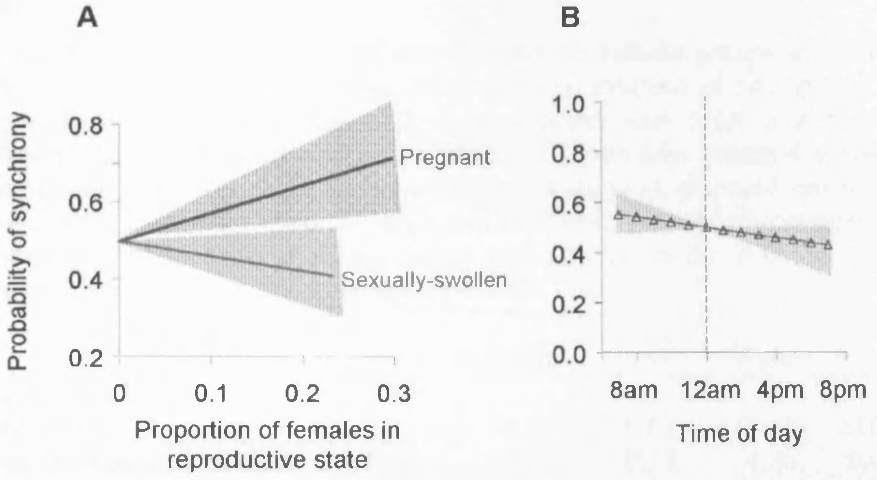


Figure 5.3.
The effects of (A) the proportions of pregnant and sexually-swollen females, and (B) time of day, upon the probability of group synchrony, as predicted from a GLMM controlling for repeated scan observations within and across days, and with all other significant effects set to their reference categories/average value. The time-of-day effect is shown relative to mid-day, indicated by the dotted line. Shaded areas represent standard errors of predictions.

Table 5.1

Factors affecting the synchrony of activities within baboon groups as predicted from a GLMM analysis based upon 6535 scan observations of two groups. The models were run with a binomial error structure and logit link function, controlling for repeated observations within and across days (entered as random effects). The table shows parameter estimates (Estimate), standard errors (SE), associated test statistic (Wald statistic), and *P* values. Values for non-significant terms were obtained from fitting terms individually to the minimal model. Interactions were tested, but were not significant.

	Estimate	SE	Wald	*P*
Minimal model				
Hour of day	-0.04	0.01	25.41	<0.001
Proportion females sexually-swollen	-1.14	0.52	4.86	0.027
Proportion females pregnant	2.00	0.69	8.42	0.003
Habitat			48.25	<0.001
Desert 'open'	0.00	0.00		
Desert 'grass'	0.21	0.08		
Desert 'shrub'	0.36	0.11		
Woodland 'tree'	0.55	0.08		
Density of individuals	-0.92	0.25	14.13	<0.001
Density of individuals^2	0.13	0.06	4.70	0.035
Proportion individuals in view	-3.65	0.55	44.31	<0.001
Proportion individuals in view^2	2.88	0.61	22.45	<0.001
Non-significant terms				
Group size			0.17	0.680
Small	0.00	0.00		
Large	0.08	0.08		
Proportion females lactating	-1.61	1.50	0.01	0.916
Proportion females non-fertile phase	0.16	1.49	0.01	0.913
Overall synchrony in female state	-0.12	0.38	0.10	0.749
Constant	3.03	0.30		
Day (random effect)	0.00	0.00		
Scan within day (random effect)	0.04	0.02		

In the case of habitat, the baboon groups showed clear and significant differences in their synchrony among different vegetation types in line with predictions 2.1 and 2.2. When ranging in woodland habitat, synchrony was highest, and when ranging in open desert habitat synchrony was lowest. Groups showed an intermediate level of synchrony when ranging in grass or desert shrub habitats (Table 5.1, Figure 5.4).

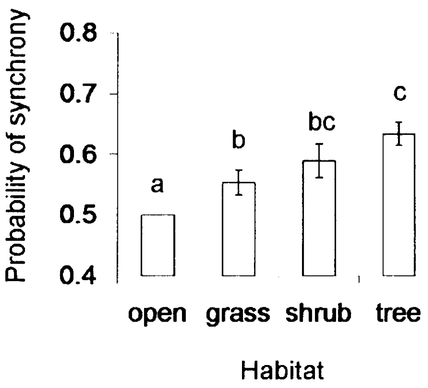


Figure 5.4.
The mean effect±SE of habitat categories upon synchrony in activities, as predicted from a GLMM controlling for repeated scan observations within and across days, and with all other significant effects set to their reference categories/average value. Significant differences between habitat types are indicated by different letters; where means do not differ, they share the same letter.

In the case of group structure, I found that where group cohesion was higher (high cohesion indicates individuals were spread over a smaller area), group behavioural synchrony also increased, in support of prediction 3.1. However, this was not a linear effect (Table 5.1). Nevertheless, where group cohesion was higher than average, there was an approximately linear increase in synchrony with cohesion (Figure 5.5). No overall difference was found between the large and small groups with respect to synchrony, failing to support prediction 3.2 (Table 5.1).

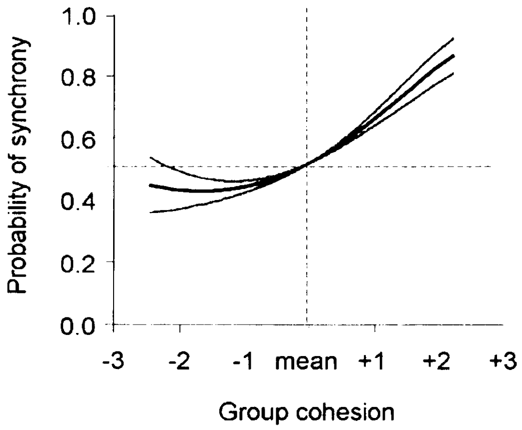


Figure 5.5.
The effect of group cohesion on group synchrony as predicted from a GLMM controlling for repeated scan observations within and across days, and with all other significant effects set to their reference categories/average value. The effect shown is relative to average group cohesion (approximately an area of $80m^2$ per baboon), indicated by the dotted lines through the figure centre. Standard errors are indicated by grey lines.

Discussion

Two animals can either behave in the same way or not. The random expectation for the same behaviour to occur simultaneously in both is simply the product of the relative behavioural frequencies and durations in the two partners (e.g. Lamprecht, 1985). But if there are more than two individuals in a group, it is more difficult to define behavioural synchrony (Engel and Lamprecht, 1997): an animal may, at any point, behave in synchrony with some of its group-mates, but asynchronously with others. One approach to this problem has been to assess the degree of synchrony of a specific individual with respect to its group-mates (Engel and Lamprecht, 1997). A complimentary approach, which I have developed in this study, has been to investigate overall behavioural synchrony across all group members.

In this study, a comparison between the observed patterns of synchrony with a null model indicated that the baboon groups were both more and less synchronous than would be expected by chance. (The average synchrony does not differ, since the null model simulations are based on the mean pattern in the observed data). To the best of my knowledge, this is the first time that observed patterns of synchrony have been compared to a null model. Thus, it is difficult to assess the extent to which this pattern might be typical of other group-living species. Nevertheless, the observed distribution of synchrony indicates that some factors are driving the baboons to be asynchronous in their activities, while others are having an even stronger effect on driving the baboons to be more synchronous (compare the upper and lower tails of the distributions). On this basis, I then tested three hypotheses relating to the activity-, habitat- and group-related processes that might be responsible for these patterns of synchrony.

Activity budget hypothesis.

Two of my results provide support for the activity-budgets hypothesis (H1). However, my findings were not entirely consistent with my initial predictions. First, I have shown that behavioural synchrony increases with the proportion of pregnant females, but decreases with the proportion of sexually-swollen females. The former pattern was predicted on the basis that females in the same reproductive state share similar energetic requirements and are thus more likely to synchronise their activities (prediction 1.1). However the proportion of females in other reproductive states (and also overall concurrence in state) should have also had a positive influence on synchrony if this was the case – which they did not. How can this inconsistency, and the significant negative effect of the number of sexually-swollen females, be resolved? An alternative explanation would be that it is not simply female energetic requirements but also the influence of female reproductive patterns on male behaviour that is critical (Cowlishaw, 1999).

Female reproductive state influences male behaviour in various ways. Male behaviour is most affected when females are sexually swollen as a consequence of mate guarding behaviour (see Bercovitch, 1991; Crockford et al., 2007; Weingrill et al., 2003). Lactating females also attract male protection services, where males provide protection of suckling infants from other males, and the risk of infanticide (see Barrett and Henzi, 2003; Lemasson et al., 2008).

Pregnant females and cycling non-swollen females however, do not much alter male behaviour since both mating opportunity and infants are absent.

Thus, by considering (1) the increasing energy demands of pregnant and lactating females (which should serve to increase synchrony, as more females spend more time foraging), and (2) the effect of female reproductive stage on males, the effect of female reproductive state can be explained. First, when females are swollen, there is a strong drive towards asynchrony (through male effects) but no drive towards synchrony (since there is little increase in energy demands), thus the net effect is one of increased asynchrony. Second, when females are pregnant, there is no drive towards asynchrony (there are no male effects) but there is a strong drive towards synchrony (because of increased energy demands), so the net effect is one of increased synchrony.

Crucially, by considering both increasing energy demands of females, and the consequential effect on male behaviour, this also explains the absence of an effect for increasing non-swollen and lactating females. In the first case – cycling non-swollen females – there is no drive towards asynchrony (through male effects) or synchrony (through energy effects), so there is no effect overall. By a similar logic, in the case of lactating females, there is a drive towards both asynchrony (through male infant-protection services) and synchrony (through higher energy demands) which seem to act to cancel one another out, again leading to no effect overall. These interpretations are also consistent with male baboons having a particularly strong influence in maintenance of group spacing (Cowlishaw, 1998) and group movement patterns (Kummer, 1968; Stueckle and Zinner, 2008, Chapter 7).

In support of the second prediction of the activity-budgets hypothesis, I found that behavioural synchrony is highest in the morning and decreases throughout the day. This suggests that early in the day, when all individuals are hungry, i.e. relatively homogeneous with respect to energetic state (e.g. Macleod et al., 2005), synchrony in behaviour is more likely to occur. In contrast, later in the day, individuals will become satiated at different rates, as a consequence of both stochastic processes and phenotypic variation, and engage in other activities accordingly. Stochastic processes refer to the role that chance plays in the number and quality of food patches an individual encounters over the course of a day. Phenotypic variation refers to a variety of possible factors that may influence satiation rates. One of these is body size variation: younger animals have lower food requirements, due to their smaller size, and thus will stop foraging before older (larger) animals. Dominance is likely to be important too. For example, in a socially-foraging bird, the green woodhoopoe, *Phoeniculus purpureus*, dominant individuals exclude subordinates from prime feeding areas, which results in subordinates leaving groups to forage alone (Radford and Du Plessis, 2003) – i.e. synchrony and ultimately groups break down (Conradt and Roper, 2000). Dominant baboons also monopolise food patches (Chapter 3; Chapter 7), but – in contrast to woodhoopoes – these groups only rarely fission. If monopolisation by dominant baboons reduces the foraging performance of subordinates, they might need to prolong their foraging time later in the day, thus resulting in lower behavioural synchrony at the group level.

Habitat constraints hypothesis

Concerning the habitat-constraints hypothesis, I found that behavioural synchronisation was highest in riparian woodland habitat and lowest in the open desert habitat, as predicted by both food patch configuration and predation risk (predictions 2.1 and 2.2). In addition, there is another reason why animals foraging together on large patches in the riparian woodland might synchronise their activities: social information can improve the accuracy of patch quality assessments (Clark and Mangel, 1984), thus improving the efficiency of individual foraging decisions (King and Cowlishaw, 2007- Chapter 4). Such a pattern would not be seen in the open desert habitats, where food patches are too small to share and individuals act more as producers than scroungers (Chapter 3). However, disentangling the effects of foraging (either with respect to patch configuration or social information) and predation risk on the relationship between group synchrony in this study is difficult. One possible approach is to consider the interaction effects. If predation was important, we might expect the smaller group to be more synchronous in high-risk woodland habitat than the large group. However, there was not a significant interaction between group and habitat. This suggests that foraging (patch configuration or social information) may be the most important activity driving this pattern. Further work using a spatially-explicit analysis of synchrony with respect to distance from refuge (an index of safety from predators) would help to separate further these relative effects on behavioural synchrony.

Group structure hypothesis

I have also shown that the spatial properties of baboon groups (hypothesis H3) have an effect on behavioural synchrony. Acquiring social information might be mediated by neighbour distance (Fernandez-Juricic et al., 2007; Fernandez-Juricic and Kacelnik, 2004), and my finding that behavioural synchrony is highest were groups are more cohesive (prediction 3.1) supports this argument. I suggest that where synchrony is beneficial, it will be more readily attained where group members can more easily monitor group-mates. This is supported by the fact that at low levels of group cohesion (i.e. negative values in figure 5.5) there is very little difference in the levels of behavioural synchrony, and only once cohesion is near or above average does synchrony increase. Lower synchrony at poor cohesion is supported by findings in other taxa. For instance, once the range of inter-individual distances observed in natural fish shoals increases beyond four body lengths, information transfer becomes limited (Pitcher and Parrish, 1993). However, this result may also be an artefact of the constraints certain behaviours place on cohesion. Take the example of grooming behaviour. When groups are resting, they tend to cluster together and also to groom one another (which in itself requires at least two individuals to be in close proximity), which would generate an apparent relationship between cohesion and synchrony. To investigate the potential for such confounding effects, further investigations into behavioural synchrony at a finer scale are required.

I did not, however, find support for my prediction that larger groups have more difficulty in attaining behavioural synchrony, and therefore will show lower overall levels of synchrony than the small group (prediction 3.2). No significant interactions (e.g. with habitat) were found either, which might have indicated that the larger group may be less synchronous as a result of intra-group feeding competition. In Chapter 3 I show that inter-individual distances are comparable in both groups, and this may explain why synchrony is maintained at equal levels despite variation in group size. However, with only two groups in this sample, further study across a variety of group sizes is required to investigate fully the potential group-size effects on behavioural synchrony.

Future directions

Taken together, the findings of this study indicate support for activity budgets, habitat constraints and group properties all having an effect on patterns of behavioural synchrony in baboon groups. This is consistent with patterns found by previous research that has focused on ungulate species. However, the precise costs and benefits of varying levels of behavioural synchrony remain to be elucidated. Such elucidation may require carefully designed experiments under controlled conditions (e.g. see Ruckstuhl (1999). Yet further field research is also still required. For example, whilst I have clearly shown variability in female reproductive state can influence behavioural synchrony, the significance of consequential changes in male activity patterns was not anticipated. This finding highlights the need for studies to examine synchrony over reproductive and non-reproductive periods (e.g. see Turner et al., 2005).

Refinements of the statistical null model are also possible. In my comparison of the expected and observed synchrony, my estimates of expected synchrony were based on a simplified null model. For instance, the null model assumes that the activity of any individual is independent of what it was doing in the previous scan. Also, the model was constructed as if all individuals were always in view, which in reality was not the case. Thus, a more sophisticated null model could be developed, in which individual activities could be assigned a probability of occurring that is appropriately modified by the activity just performed, and in which only a variable sub-sample of the group is assessed at each simulated scan. Nevertheless, while these refinements might provide a more accurate assessment of the pattern of variation in synchrony, they would have no consequence on the subsequent tests of the hypotheses under study, since such confounding factors were controlled for statistically throughout the analysis.

Perhaps most importantly, further investigations into the behavioural mechanisms that enable synchrony to occur are also required. Whilst multivariate approaches – like that applied here – can reveal much about the factors which might constrain or promote synchrony in groups, the mechanisms which mediate behavioural synchrony are still unknown. There are a number of possibilities. Synchrony among individuals may be triggered by an external event or by spatial coincidence, where the proximity of individuals results in them experiencing equivalent environmental conditions, which in turn stimulates similar behaviours independently of their neighbours (Engel and Lamprecht, 1997). Alternatively, synchrony may be dependent on social processes. A key concept that has recently emerged is self-organisation theory (e.g. Sumpter et al. 2008). This theory suggests that much of the coordination in the timing of activities evident in animal groups is the result of relatively simple interaction patterns among group members, since multiple individuals following simple movement rules can produce extremely synchronous behaviour (Cavagna et al., 2008a; Cavagna et al., 2008b).

The fundamental feedback mechanisms of self-organisation theory are appealing, because they suggest that much of the synchrony exhibited by animal groups may be explained without invoking complex decision-making abilities at the level of the individual (Couzin, 2007). However, these models are largely restricted to certain mechanistic aspects of social behaviour, where interactions are relatively simple and where patterns of synchronous group behaviour are dependent only upon local interactions among spatial neighbours. Moreover, these self-organising processes, work best where individuals all share the same goal, e.g. eusocial insects choosing a new nest site (Britton et al., 2002; Lindauer, 1957; Visscher, 2007), or navigating birds migrating to a specific location (Guilford and Chappell, 1996; Simons, 2004). Where groups experience conflicting individual interests (e.g. Conradt and Roper, 2000), and where group members can usually communicate directly with all other members (e.g. Boinski, 1993; Stewart and Harcourt, 1994), as found here, other mechanisms are possible. Decisions concerning the behavioural activities of many group members may be made in a democratic manner, where the average behaviour of individuals is adopted, or by a single animal or minority of animals in a more despotic manner, where the behaviour of that individual or minority dictates the behaviour of the others (Conradt and Roper, 2003; Conradt and Roper, 2007). A test between these alternate mechanisms of group decision-making is provided in Chapter 7.

Chapter 6 – Foraging opportunities drive interspecific associations between rock kestrels and desert baboons

The manuscript presented in this chapter is in press as:

King, A. J. & Cowlishaw (2009) Foraging opportunities drive interspecific associations between rock kestrels and desert baboons. *Journal of Zoology*. (See appendix).

Abstract

Interspecific associations can arise for varied reasons including reduced predation risk and improved foraging success. In the case of bird-primate associations, birds typically appear to follow primate groups to harvest insects flushed by primates' movements. However, whilst previous studies have linked temporal changes in bird-primate associations to environmental conditions, few have assessed the additional effects of bird activity patterns and primate group behaviour and none have disentangled their potentially interdependent effects. Here I test the hypothesis that foraging opportunities can drive interspecific associations in a previously un-described bird-primate association between rock kestrels (*Falco rupicolus*) and chacma baboons (*Papio ursinus*) in central Namibia. Data were collected from two baboon groups and associated kestrels using instantaneous scan sampling during full-day follows over a seven-month field period, and analysed using generalised linear mixed models. I found that kestrel associations with baboons vary with season, show diurnal cycles, and are more frequent when the baboons are in open desert habitat, engaged in travel foraging, and in a large group. These patterns are statistically independent and consistent with the hypothesis that the kestrel-baboon association is driven by the foraging opportunities acquired by the kestrels. As the baboons do not appear to gain any benefits nor incur any costs from the association, I conclude that the kestrels are likely to be commensal with the baboons.

Introduction

Associations between the members of two different species can vary in their duration and frequency, and are thought to form because of the benefits provided to individual members of one or both associating species (Stensland et al., 2003). These associations can be described in one of three ways depending upon how the benefits are distributed: (i) mutualism, where members of both species benefit, (ii) parasitism, where members of one species benefits at the expense of the other, and (iii) commensalism, where members of one species benefit and the other is unaffected by the association. Benefits include many of the same reasons that single-species groups form, such as improved predator detection and avoidance (McGraw and Bshary, 2002; Morse, 1977; Teelen, 2007) or increased foraging efficiency (Bearzi, 2006; Buchanan-Smith, 1999; Peres, 1992).

Where associating species do not share the same predators, foraging benefits may be the most important driver of interspecific associations. Studies that have reported improved individual foraging efficiency as a result of interspecific association are plentiful within and across a variety of animal taxa. (Beisiegel, 2007; Buchanan-Smith, 1999; Ruggiero and Eves, 1998), and often involve commensal relationships (Dickman, 1992; Herring and Herring, 2007; Schaefer and Fagan, 2006). In the case of bird-primate commensal relationships, bird species such as kites (Egler, 1991; Fontaine, 1980; Heymann, 1992), and woodcreepers and cuckoos (Boinski and Scott, 1988; Hankerson et al., 2006; Kuniy et al., 2003), are all reported to associate with primate groups. Such insectivorous birds are thought to benefit from the disturbance created by the primates' movement through vegetation, allowing the birds to harvest flushed prey, whilst the primates receive no evident benefit (Boinski and Scott, 1988; Egler, 1991). Such studies are largely confined to the neotropics (although see Ruggiero and Eves, 1998; Seavy et al., 2001), and routinely describe trends in the temporal frequency of associations throughout the day and across seasons (e.g. Boinski and Scott, 1988; Ferrari, 1990). These patterns are thought to reflect environmental changes in insect availability (Hankerson et al., 2006; Rodrigues et al., 1994). However, relatively few studies have controlled for the effect of bird behaviour, e.g. diurnal foraging cycles, or examined the influences of primate group behaviour upon such bird-primate associations (cf. Boinski and

Scott, 1988). Moreover, none have disentangled the potentially interdependent effects of these factors.

In this chapter I examine an association between rock kestrels (*Falco rupicolus*) and chacma baboons (*Papio ursinus*) on the edge of the Namib Desert, Namibia. During the associations, kestrels were seen to prey on the Orthopteran insects (grasshoppers, locusts and crickets) that fly into the air following their disturbance by the baboons, and I test the hypothesis that this association arises from the foraging opportunities derived by the kestrels. I do this by first investigating the predicted effects of environmental conditions and kestrel activity. Second, I then test for the predicted effects of specific primate group behaviours on the availability of kestrel prey items, and thus potential for associations. The predictions for each of these effects are described in turn.

For environmental conditions, we know that Orthopteran species density increases in association with rainfall in arid regions (Belovsky and Slade, 1995; Noy-Meir, 1973). If kestrel-baboon associations reflect seasonal changes in insect availability, I would predict a seasonal pattern of kestrel-baboon association that reflects rainfall (prediction P1). Associations are also likely to change in accordance with kestrel activity patterns. Kestrels can show remarkable constancy from day to day in the temporal distribution of specific behaviours and of spatial movements that are a consequence of both prey activity patterns and environmental variables (Barnard, 1986; Rijnsdorp et al., 1981). I therefore predicted associations to occur most frequently post-dawn and pre-sunset (P2) when kestrels traditionally forage (Rijnsdorp et al., 1981; Van Zyl et al., 1994).

Finally, in the case of primate group behaviour, the collective activities of the baboon groups may influence the likelihood of kestrel-baboon associations in three ways. First, habitat type (in which the baboons are observed foraging) may affect kestrel associations as a consequence of variation in Orthoptera prey densities (e.g. Babah and Sword, 2004) and differences in the opportunity for aerial prey detection and capture by the kestrels (e.g. Thiollay and Clobert, 1990). I therefore predict that kestrel-baboon associations will be most likely when baboons are in those habitats where both the density and detectability/catchability of Orthoptera prey species are highest, i.e. open, grassland habitat rather than closed, woodland habitat (P3). Second, specific collective activities of baboons may be more likely to disturb Orthopteran species, generating foraging opportunities for kestrels and thus promoting associations. I therefore test the prediction that kestrel-baboon associations will be more likely when the baboons are collectively more active (travelling and travel foraging) than when they are sedentary (resting, stationary foraging), since that is when they are actively disturbing rocks and vegetation (P4). Third, I test the prediction that kestrels associate more when the baboons are in a large group rather than a small group, given that more individuals will cause more disturbances of Orthopteran species over a larger area (P5).

Methods

Study Site and Subjects

The study subjects were wild rock kestrels present in the area and the two baboon groups already described in Chapter 2. The study site has already been described (Chapter 2), but I will restate information pertinent for this chapter here. The landscape is dominated by mountains and ravines which are fringed by steep rocky foothills and gravel and alluvial plains, through which the ephemeral Swakop River passes. Annual rainfall is light and seasonal: mean ± SE = 215 ± 17 mm, n = 36 years, with rains falling primarily in the late austral summer (January–March) (Figure 6.1). However, these rains support a relatively diverse desert plant community (Cowlishaw & Davies 1997). Typical vegetation found on the hills and plains includes perennial grasses and herbs, e.g. *Aristida* spp. and *Petalidium variable*, with shrubs and dwarf trees, e.g. *Catophractes alexandri*, *Acacia erubescens* and especially *Commiphora virgata*. During the austral summer, baboons often forage on the vegetation and small invertebrate prey found in these open, rocky desert habitats (hereafter referred to as 'open desert'). During the winter, as these foods die back following the rains, the baboons forage increasingly on the flowers, fruits and pods of the large shrubs and trees that grow in patches of riparian woodland along the Swakop River (hereafter referred to as ‘closed woodland’). These woodlands are supported by groundwater and dominated by *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica*.

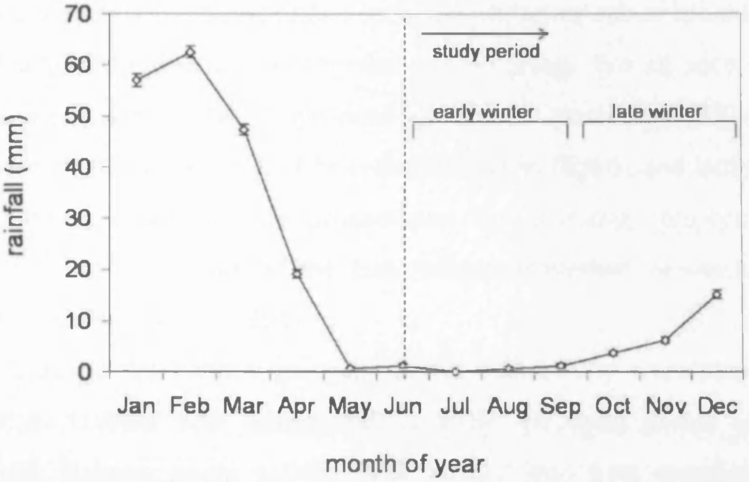


Figure 6.1.
Mean±SE monthly rainfall in the study region (Karibib) between 1961-1997. Study period is from June-December 2005.

Data Collection

The two baboon groups were followed on foot from dawn to dusk from June to December 2005, (121 days for group L; 75 days for group J). Detailed behavioural and ecological data were collected on the baboons and the occurrence of kestrel-baboon associations. However, individual kestrels were not identifiable, and their behaviour and activities outside of observed associations were not known.

Data were collected by scan sampling at 30-minute intervals throughout the day, with the first scan beginning 30 minutes after the baboon group had left their morning sleeping site. A total of 3,951 scans across both baboon groups were obtained. Baboon groups travelled large distances each day (range 1.8 – 9.8km, average±SE = 5.9±0.06, n = 180 days), and each group occupied adjacent home-ranges that overlapped (see Chapter 3). Kestrel densities at the site are unknown, but elsewhere in their range can be found at up to 24.3 pairs per 100km^2 (Eastern Cape, South Africa: Van Zyl, 1999). Given the more arid nature of the Tsaobis environment, it is likely that kestrel densities are substantially lower at this locality.

Data on the presence or absence of kestrel-baboon associations were recorded at each scan. Associations occurred whenever one or more kestrels were present within the area covered by the baboon group. For all such observations kestrels were seen to be 'flight-hunting' and/or 'perching' (Rijnsdorp et al., 1981), which involved bouts of hovering and short flights, and sitting in trees or shrubs with a view of the ground and the baboons, respectively. These behaviours are known to be the most effective method of catching prey by kestrels (Rijnsdorp et al., 1981).

Data on the baboon group's habitat and activity were also collected at each scan. Habitat was categorised as either (i) open desert or (ii) closed woodland. Baboon group activity was divided into four speed-related binary response variables (i.e. $\leq 50\%$ group members engaged in behaviour vs. $> 50\%$ engaged in behaviour): (i) travelling, (ii) travel foraging, (iii) stationary foraging and (iv) resting. *Travelling* was defined as the rapid locomotion of individuals, and *travel foraging* as the slow locomotion of individuals while searching, manipulating, and ingesting food material. *Stationary foraging* describes searching, manipulating, and ingesting food material while remaining in one location. *Resting* describes the baboons' sedentary state in which they were not travelling or foraging and included grooming and sleeping.

Statistical Analyses

To assess the variables influencing the kestrel-baboon association, I used a Generalised Linear Mixed Model (GLMM) with binomial error structure and a logit link function implemented in MLwiN (Rasbash et al., 2004). I used association, non-association as a binary response term, and fitted 'scan number' and 'observation day' as a random effect to take account of repeated measures within and across days respectively (Browne et al., 2001). The following categorical variables were entered as fixed effects: habitat (open desert, closed woodland), activity (four variables, see above), group identity (large, small) and time of year (June-September, termed early winter, September-December termed late winter; see Figure 6.1). Time of day was fitted as a continuous variable (centred at 12:00 midday). All fixed effects were entered and dropped sequentially until only those that explained significant variation remained (minimal model, e.g. Sokal and Rohlf, 1995). Each dropped term was then put back into the model to obtain their level of non-significance, and check that significant terms had not been wrongly excluded. Biologically relevant two-way interactions were also tested, but did not contribute significantly to the explanatory power of the model and are not discussed further. The significance of effects was tested using the Wald statistic, evaluated against the Chi-square distribution.

Results

During baboon-group scans, 1-4 kestrels were observed associating with groups (median: 1 kestrel) for on average 3.5% of all scan observations during the study period (June-December 2005). During these associations the kestrels appeared to follow the baboons and monitor their activities, frequently catching Orthopteran prey 'on the wing' as they were disturbed by the baboons (see Figure 6.2).

The results of the GLMM are consistent with the hypothesis that the kestrel-baboon associations are driven by the foraging opportunities acquired by the kestrels. First, kestrel-baboon associations were shown to reflect seasonal changes in insect availability; being more common in the early austral winter compared to the late austral winter (Table 6.1; Figure 6.3a) as predicted (P1). Second, kestrel-baboon associations were more common in those periods when kestrels traditionally forage, with peaks in the early morning and late afternoon (Table 6.1; Figure 6.3b), as predicted (P2). Three aspects of baboon group behaviour were also shown to influence the likelihood of kestrel-baboon associations, in support of predictions P3, P4, and P5. In the case of habitat (P3), kestrels were significantly more likely to associate with baboons in open desert habitat compared to closed woodland habitat (Table 6.1; Figure 6.4a). Kestrel-baboon associations were also most frequent when the baboons were travel foraging (Table 6.1; Figure 6.4b), and for the large baboon group compared to the small group (Table 6.1; Figure 6.4c) (P4, P5 respectively). I found that variation in the numbers of baboons engaged in other activities (travelling, resting, and stationary foraging) had no significant effect upon probability of kestrel associations (Table 6.1), although the directions of these trends were in the anticipated directions, i.e. negative where the majority of baboons were resting, and positive when the majority were travelling or stationary foraging.

Hence, these results show that although kestrels were present in only 3.5% of all baboon-group scans, they were present in 22% of baboon-group scans observed during the first six hours of the day in the early austral winter period, when the baboons were travel foraging in open desert habitat (n = 238).

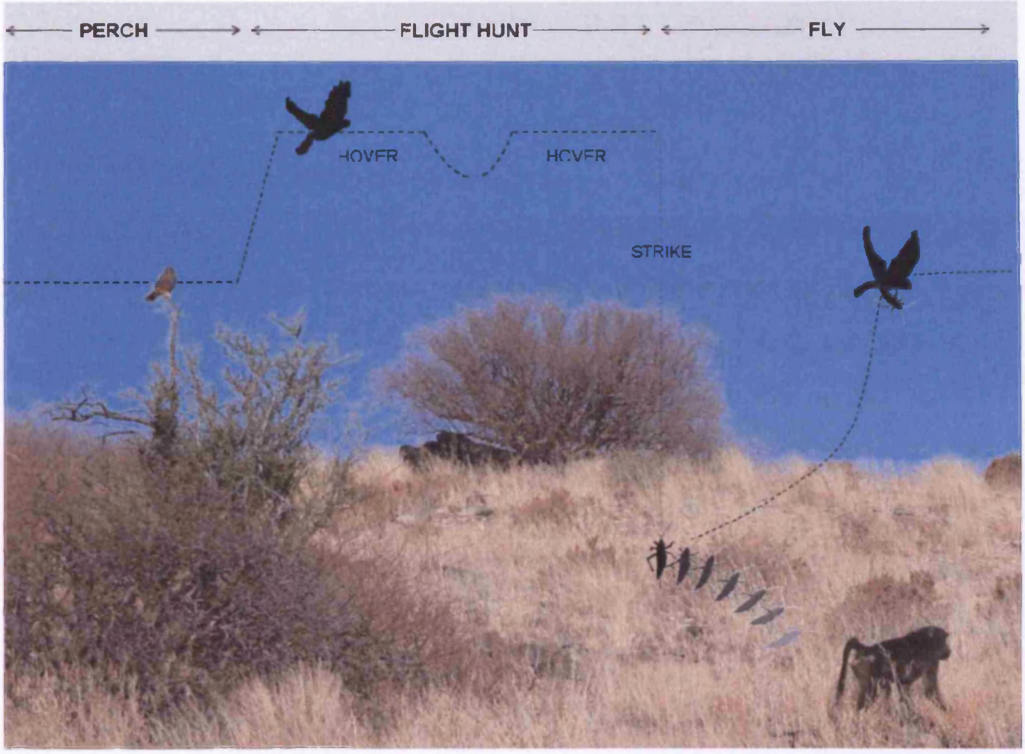


Figure 6.2.
Schematic representation of the foraging opportunities derived by kestrels from their association with baboon groups. Flight-hunting includes the short flights in between bouts of hovering. The perched kestrel (left hand side) and baboon (lower right hand side) are from the original photograph; all other elements are graphic representations through time. Scheme adapted from the behaviour categories and diagram published by Rijnsdorp et al. (1981).

Table 6.1.
Factors affecting the probability of kestrel-baboon associations, controlling for repeated scan observations within and across days (each entered as a random effects). Table shows parameter estimates (effect), standard errors (s.e.), statistical values (Wald statistic) and significance evaluated against a Chi-squared distribution (*P*) based on 3,951 scan observations of two baboon groups. Estimates for non-significant terms were obtained from adding terms individually to the minimal model.

Model term	Estimate (s.e.)	d.f.	Wald	*P*
Time of year		1	39.34	<0.001
Early winter	3.781 (0.603)			
Late winter	0.000 (0.000)			
Time of day		3	27.59	<0.001
Hour	-0.351 (0.077)			
Hour^2	0.029 (0.011)			
Hour^3	0.012 (0.003)			
Habitat		1	47.63	<0.001
Open desert	3.022 (0.438)			
Closed woodland	0.000 (0.000)			
Baboons travel foraging		1	18.18	<0.001
≤ 0.5 group	0.000 (0.000)			
> 0.5 group	2.602 (0.113)			
Baboon group identity		1	7.74	0.005
Small	0.000 (0.000)			
Large	0.681 (0.245)			
Scan observation (random term)	6.299 (0.629)			
Observation day (random term)	0.570 (0.245)			
Constant	-10.11 (0.773)			

Non-significant terms	Estimate (s.e.)	d.f.	Wald	*P*
Baboons stationary foraging		1	0.833	0.361
≤ 0.5 group	0.000 (0.000)			
> 0.5 group	0.297 (0.325)			
Baboons travelling		1	0.806	0.369
≤ 0.5 group	0.000 (0.000)			
> 0.5 group	0.316 (0.352)			
Baboons resting		1	0.701	0.402
≤ 0.5 group	0.000 (0.000)			
> 0.5 group	-0.807 (0.964)			

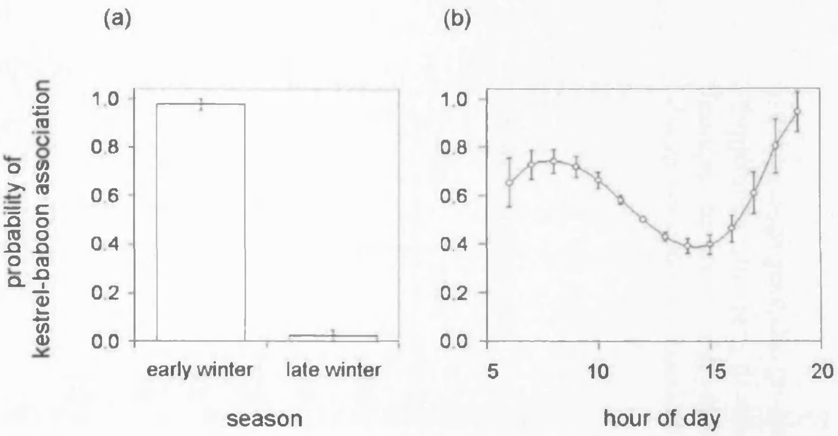


Figure 6.3.
The fitted values (±SE) for the effect of (a) season, and (b) time of day, on the probability of kestrel-baboon associations. Values are obtained from the model parameters given in Table 6.1, controlling for the effect of all other significant terms and for the influence of repeated observations within days.

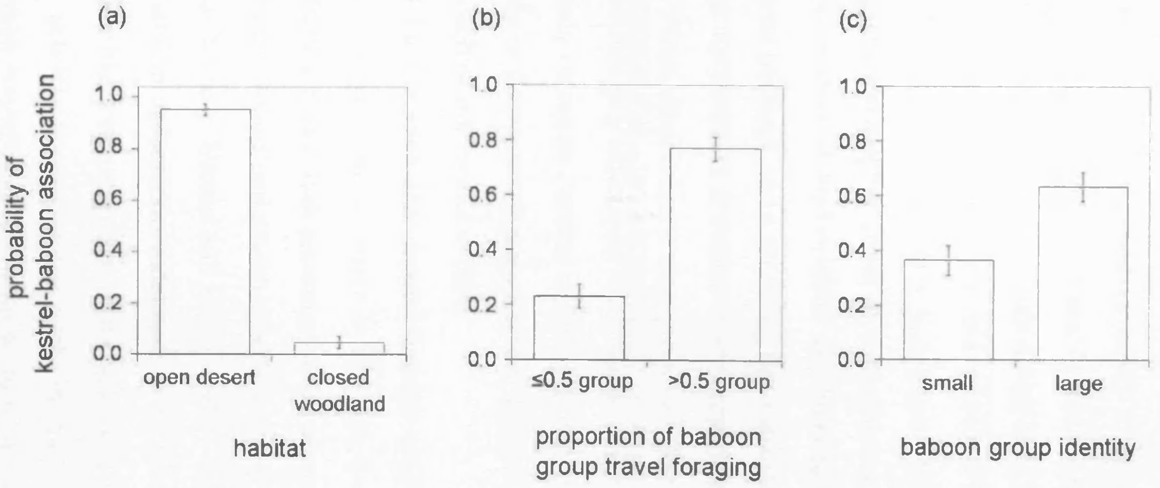


Figure 6.4.
The fitted values (±SE) for the effect of (a) habitat type, (b) proportion of baboon group travel foraging, and (c) baboon group identity, on the probability of kestrel-baboon associations. Values are obtained from the model parameters given in Table 6.1, controlling for the effect of all other significant terms and for the influence of repeated observations within days.

Discussion

Rock kestrel associations with chacma baboons are more common in the early austral winter, show diurnal cycles, and are more frequent when baboons are in open desert habitat, engaged in travel foraging, and in a large group. These patterns support the hypothesis that kestrels associate with baboons because they obtain foraging opportunities from doing so. The results are also consistent with my impressions that these are not chance events. Rather, when kestrels are present they appear to actively accompany the baboons, hovering above them and frequently swooping down to capture insects that have been flushed into the air. Other studies of bird-primate associations have similarly reported seasonal and diurnal patterns, and a tendency for associations to occur in conjunction with particular habitats and activities (e.g. Boinski and Scott, 1988; Zhang and Wang, 2000). These studies have also proposed that such associations arise from the improved foraging efficiency of the birds concerned, suggesting that this may be a relatively common pattern in bird-primate interactions. However, this is the first study to demonstrate the statistical independence of many of these effects. I discuss each of my results in turn.

I have shown that kestrel-baboon associations are more than 50 times more likely to occur in the early winter period of the study, compared to the late winter (Figure 6.3a). This pattern of association is consistent with the seasonality of breeding in locust and grasshopper species in response to rainfall in this sort of desert habitat (e.g. Hunter and Elder, 1999). I have also shown a diurnal cycle of kestrel-baboon association independent of baboon activity cycles. This diurnal pattern is a likely consequence of the activity cycles of kestrels, which are known to most actively forage in the early morning and late afternoon. I have also shown that variations in primate behaviour can clearly influence kestrel associations, in three different ways. First, the location of baboon groups is important. I have shown that despite baboons spending an approximately equal proportion of time in one of two habitats, open desert and closed woodland, kestrels were more than 20 times more likely to associate with baboons groups in open desert habitat (Figure 6.3a). This finding is consistent with the predicted increase in Orthoptera prey densities in this habitat type and/or improved detection and capture as a consequence of habitat structure. Second, I have shown that kestrel-baboon associations vary predictably with the collective behaviour of the group. Associations were more than two-and-a-half times more likely where at least 50% of a baboon group were engaged in travel foraging (Figure 6.4b). Since the periods when baboons were engaged in other behaviours (resting, stationary foraging, and travelling) had no significant effect, it appears that the active and continued disturbance of vegetation and substrates during travel-foraging is a critical element in the emergence of kestrel-baboon associations. Third, this is the first study to document a primate group-identity effect, which I interpret as a consequence of the respective sizes of the two baboon groups: a larger group size means more baboons to disturb Orthopteran prey. However, a larger range of group sizes is needed to illustrate a group size effect with certainty.

There are several areas where further research would be fruitful. One topic that would benefit from further investigation is the independent behaviour of the kestrels. For example, how does the foraging success of kestrels vary in the presence and absence of the baboons? The fact that pale chanting goshawks *Melierax canorus* have also been seen to associate with baboons under similar conditions (mid-morning in the early austral winter, while the baboons were travel foraging in open desert habitat), and show similar foraging behaviour (capturing on the wing the Orthopterans disturbed by the passage of the baboons) (AJK, GC personal observation), indicates that the potential for increased foraging opportunities may be substantial. Further refinements of my predictions are also possible. For example Van Zyl et al. (1994) suggested that kestrels may undertake relatively long-distance seasonal movements to track spatial variation in insect abundance. If the number of kestrels in the locality declined in the late austral winter as a result of such movements, it might contribute to the reduced frequency of kestrel-baboon associations recorded during this period. The breeding behaviour of kestrels at this study location are also unknown, although Namibian nest records indicate rock kestrels typically breed November-January elsewhere in Namibia (Southern African Ornithological Society, Van Zyl et al., 1994). Such information would allow us to test predictions about kestrel-baboon associations in the context of kestrel breeding biology. It would also be instructive to ask how kestrels locate their baboon groups. This may seem a relatively straightforward question, but the finding that kestrels more commonly associate with the larger of the two baboon groups might be partially explained by the fact that larger groups are more conspicuous. Bigger groups are not usually noisier, but when foraging do spread out over larger areas.

My findings suggest that foraging opportunities for kestrels lead them to associate with baboons. An increase in foraging efficiency for at least one species is a commonly cited reason for the evolution of associations between species (Hino, 1998; Rehg, 2006; Ruggiero and Eves, 1998). Nevertheless, there are other possibilities. The most important alternative explanation is defence against predators. The predator-defence hypothesis requires that the associating species share common predators, so that they can benefit from each other's anti-predator behaviour (Fichtel, 2004; Rainey et al., 2004; Zuberbuhler, 2000). However, in this case, baboons and kestrels are at risk from different types of predator: leopards and larger raptors, respectively (Cowlishaw, 1994; Petty et al., 2003). Although large raptors may prey on baboons in other areas of Africa, no predation has ever been observed in this population, and raptor attacks to date have been in the context of nest defence only (AJK, GC personal observation). (See also Cheney et al., 2004 for a recent discussion of raptor-baboon predation). Similarly, leopards do not predate kestrels (Hayward et al., 2006). Consequently, predator defence is unlikely to be a factor for either species.

Do the baboons receive any foraging benefits or costs from the kestrels? I was unable to discern any foraging benefits, and the costs may similarly be limited. When the baboons are travel foraging in the open desert habitat, they are not only feeding from grasses, herbs, and dwarf trees, but also turning over rocks and feeding on a variety of small invertebrate prey. These will opportunistically include Orthopteran species, which the baboons occasionally capture in mid-air as they take flight following their disturbance. However, such prey items make up only a small proportion of the baboon diet, and the kestrels only capture those Orthopterans that the baboons have already missed or ignored. Similarly, the baboons do not forage on other types of kestrel prey, such as lizards and mice. It is therefore unlikely that the kestrels pose a foraging cost to the baboons. In addition, there have been no observations of aggressive conflict between the kestrels and baboons, unlike that reported in another (very unusual) record of bird-primate interaction at Tsaobis involving black kites *Milvus migrans* competing with baboons for access to a fresh klipspringer *Oreotragus oreotragus* carcass (see Davies and Cowlishaw, 1996). Rather, the baboons consistently ignore the kestrels. Overall, the evidence suggests that the baboons experience no cost, and gain no ascertainable benefit from the accompanying kestrels.

In conclusion, my study suggests that rock kestrels associate with desert baboons in order to prey upon the Orthopteran species flushed by baboons. Future work examining differences in the prey capture rates of kestrels when foraging alone and in the presence of baboons will establish whether such associations lead to improved foraging performance. Baboons do not appear to gain any benefit or incur any costs from this association. The kestrel-baboon association therefore appears to be a commensal relationship. Subsequent studies of bird-primate associations might usefully consider the possibility that bird species not only rely on primates to flush potential prey, but vary their frequency of associations dependent on the collective activities (and consequent flushing achievements) of their commensals.

Chapter 7 – Dominance and affiliation mediate despotism in a social primate

A manuscript based on the findings of this chapter is published as:

King, A. J., Douglas, C. M. S., Huchard, E., Isaac, N. J. B. & Cowlishaw, G. (2008) Dominance and affiliation mediate despotism in a social primate. *Current Biology* 18, 1833-1838. (See appendix).

A popular science article based on the findings of this chapter is published as:

King, A. J. (2008) Dictators of the Desert. *BBC Wildlife*. 26, 50-55.
(See appendix).

Abstract

Group-living animals routinely have to reach a consensus decision and choose between mutually exclusive actions in order to coordinate their activities and benefit from sociality. Theoretical models predict 'democratic' rather than 'despotic' decisions to be widespread in social vertebrates, since they result in lower 'consensus costs' – the costs of an individual foregoing its optimal action to comply with the decision – for the group as a whole. Yet quantification of consensus costs is entirely lacking, and empirical observations provide strong support for occurrence of both democratic and despotic decisions in nature. I conducted a foraging experiment on a wild social primate (chacma baboons, *Papio ursinus*) in order to gain new insights into despotic group decision-making. The results show that group foraging decisions were consistently led by the individual who acquired the greatest benefits from those decisions, namely the dominant male. Subordinate group members followed the leader despite considerable consensus costs. Follower behaviour was mediated by social ties to the leader, and where these ties were weaker group fission was more likely to occur. These findings highlight the importance of leader incentives and social relationships in group decision-making processes and the emergence of despotism.

Introduction

The way in which group-living animals coordinate their actions is fundamental to our understanding of the evolutionary and ecological basis of sociality. The benefits of group-living are largely reliant on animals remaining cohesive, which often requires consensus choices from mutually exclusive actions (Conradt and Roper, 2007). Thus far, empirical work on consensus decision-making has primarily concentrated on the eusocial insects (Lindauer, 1957; Pratt et al., 2002; Pratt et al., 2005; Visscher, 2007), large insect swarms (Bazazi et al., 2008; Buhl et al., 2006), fish schools (Levin and Grillet, 1988), and bird flocks (Ballerini et al., 2008), where collective behaviour can emerge from simple rules of self-organisation (Couzin and Krause, 2003; Couzin et al., 2005; Sumpter, 2006). Much less is known about the underlying mechanisms for decision-making in social vertebrates, in which groups are socially complex and heterogeneous, and where individuals typically have long-term social relationships with one another (Conradt and Roper, 2005) (e.g. social birds, carnivores and primates). In these groups, individual group members often differ with respect to optimal activity budgets (Conradt and Roper, 2000), levels of information (Biro et al., 2006; Couzin et al., 2005) and ability to monopolise a resource (Koenig, 2002). Such differences lead to conflicts of interest that can impede the achievement of consensus decision making (Kerth et al., 2006).

In the face of such conflict, two different modes of decision-making might be adopted. First, consensus decisions can be reached democratically, whereby all group members contribute to the decision, independent of their individual identities or social status. At the other extreme, a decision can be despotic, taken by a single animal or a minority of 'leaders' with all other members ('followers') abiding by this decision (see Conradt and Roper, 2005). Theoretical models predict the former to be most common in nature (Conradt and Roper, 2003; Conradt and Roper, 2007), and this is supported by a number of empirical examples (e.g. Conradt and Roper, 2003; Prins, 1996; Stewart and Harcourt, 1994). However, despotic decisions are also widespread among group-living vertebrates (e.g. Byrne, 2000; Schaller, 1963; Squires and Daws, 1975; Stine et al., 1982; Sueur and Petit, 2008), not least in humans (Van Vugt, 2006).

The profusion of despotic decision-making in nature therefore presents a significant challenge to our understanding of sociality.

There are conceivably several different types of animal that might emerge as a leader. For instance, for group movements, the individuals with the greatest incentives (Erhart and Overdorff, 1998) or most pertinent information (Couzin et al., 2005) often lead groups, and are normally—but not always (Kummer, 1968)—at the front of group progressions. Yet the incentives or information required to create leaders does not necessarily generate following, and both processes are necessary for a despotic decision. New insights into group decision-making may therefore be acquired by not only understanding what incentives may be necessary for leaders to emerge but also why followers accept a leader's decisions, especially where this compromises their own activity (Conradt and Roper, 2005). In the latter case, one possibility is that long-term benefits derived from social or genetic ties with the leader outweigh the short-term costs associated with accepting the leader's current decision. This explanation is supported by recent research indicating that follower roles may be primarily associated with stable vertebrate social systems (Fischhoff et al., 2007; Sueur and Petit, 2008) where kin support one another during conflicts (Cheney and Seyfarth, 2007) and the cultivation and exploitation of social relationships with non-kin can also enhance fitness (Silk et al., 2003).

In this chapter, I use an experimental approach to explore the emergence of leader-follower behaviour in stable social vertebrate groups. Two baboon groups (one large, one small) were presented with an experimental food patch within their home range. This patch was of a size and shape predicted to create highly skewed foraging benefits amongst group members relative to naturally occurring food resources. Thus, patches were expected to create consistent incentives for a minority of dominant individuals to lead, and result in consensus costs for the majority of followers. I therefore interpreted visits to experimental food patches as being the result of despotic decisions, and visits to natural food patches as the result of democratic decisions. During these visits, the leader was defined as the animal that led the group into the patch (Dumont et al., 2005; Fischhoff et al., 2007), while others accompanying the leader were defined as followers. This approach allowed me to ask three specific questions: (1) whether the acquisition of foraging benefits by a minority of individuals creates incentives for them to lead; (2) whether group-mates are willing to follow leaders despite large consensus costs; and (3) whether such follower behaviour is mediated by social and/or genetic ties to the leader. Importantly, I addressed this by calculating estimates of the consensus costs and gains to individuals for alternate decision outcomes, allowing me to verify the role of leader incentives and follower costs in relation to despotism.

Methods

Study Site and Subjects

This chapter, like all previous chapters, focuses on adults only of two baboon groups in central Namibia (large group, n=22: 4 males, 18 females; small group, n=14: 4 males, 10 females). Baboon groups are an ideal model system in which to explore questions concerning leadership and group decision-making. Previous observations of baboon movement patterns suggest that their group decisions may be largely democratic in nature but also have the potential for active leadership (Byrne et al., 1989; Kummer, 1968; Norton, 1986; Stueckle and Zinner, 2008). Groups comprise a complex social system with linear dominance hierarchy and are heterogeneous in composition. The dominance hierarchy also results in large asymmetries in resource-holding potential (Koenig, 2002), and thus potentially high consensus costs from despotic foraging decisions. Furthermore, genetic and social ties among group members can influence individual behaviour (Cheney and Seyfarth, 2007) providing fitness benefits (Silk et al., 2003). See also Chapter 2.

Foraging Experiments

Each group was offered an experimental food patch placed at a single location within in its core home range (Figure 7.1). Patches were provided in two treatments, high contest competition (20 days) and low contest competition (20 days), both of which were of a size and shape to allow only a minority (<50%) of baboons access (although the high-contest patch excluded more individuals). The patch design was based on prior observation of the baboons' abilities to monopolise naturally occurring high-quality food patches. High-contest patches were $315m^2$ and $160m^2$ for large and small groups respectively, equivalent to an available area of approximately 12.5m^2/adult baboon. Low-contest patches were increased by a factor of two, to 630m^2 and 320m^2, equivalent to approximately 25m^2/baboon. For each patch condition the amount of food—dry maize kernels—presented remained constant within groups, so that the large group received more than the small group but the per capita amount remained at approximately 80g of maize per adult baboon in each case (each kernel was 0.39±0.01g). Low-contest patches followed high-contest patches with an intervening period of at least 10 days during which no experiments were conducted. Consecutive experimental days started once the group had encountered the patch by chance. One experiment was run for each group, the first with the large group (15.06.06 to 05.08.06) and the second with small group (24.08.06 to 15.10.06) during the same dry season (King and Cowlishaw, 2008, Chapters 2 and 6).

Two observers followed the baboon groups on foot for full days throughout the study period, recording the group's daily route taken and any approach to the experimental food patches (taking group coordinates using handheld Garmin Etrex® GPS units at 30-minute intervals: see Chapter 2). Upon approach and entry into the patch, these observers recorded individual arrival order, bite rates, and time spent in patch for all baboons (see below). To identify any fission events, and to corroborate arrival orders, a third observer was positioned at the food patches before sunrise each day.

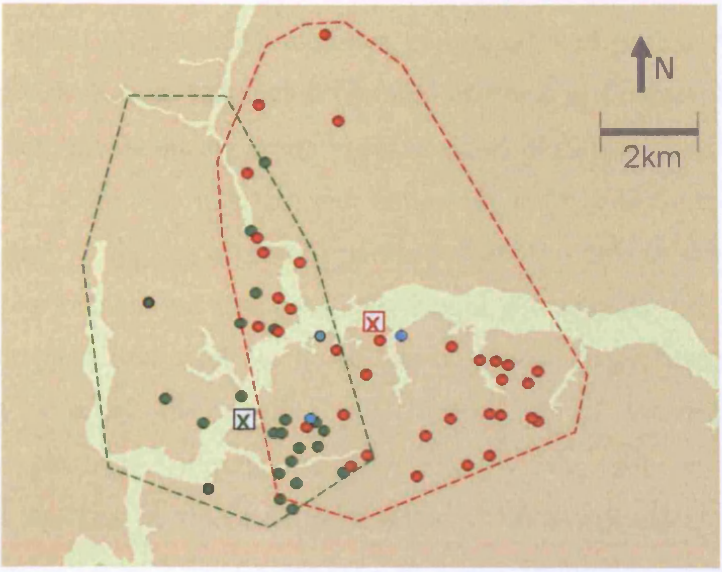


Figure 7.1.
Home range, sleeping sites, waterholes, and experimental patch locations. Minimum convex polygon home ranges for the 2006 study field season for the large (green) and small (red) study group are shown by dashed lines (See Chapter 2). Each group's respective sleeping site locations used are indicated by filled circles of the same colour. Waterholes are shown by blue filled circles. The small group used all three waterholes; the large group was seen to only use the most southerly waterholes. Experimental foraging patch locations are indicated by locations marked with an 'X'. Sites were chosen on the basis of comparable visibility, surrounding foraging opportunities, and proximity to key sleeping sites and water sources, whilst also being sure locations were far enough apart so that they would only likely be found by the intended group. Other baboon non-focal baboon groups range to the east and west along the Swakop river system and tributaries shown by light shaded regions.

Observational data

Dominance, social affiliation (strength of grooming), and genetic relationships for each individual were calculated (details provided in Chapter 2). Foraging benefits for individuals during group visits to experimental food patches, defined as the number of kernels ingested per visit, were calculated from the time an individual spent in the experimental patch (rather than outside the patch) and their mean bite rate during this time (one kernel is consumed per bite). These data were obtained from patch scans and bite-rate observations, respectively. The patch scans recorded the number and identity of all individuals on the experimental patch at 5-minute intervals. The bite-rate observations were 1-minute focal watches, in which all hand-to-mouth consumptions of corn kernels were recorded (Figure 7.2). As each focal watch finished, a new watch was initiated on another animal, until all individuals on the patch had been sampled. This process was then repeated until the patch was empty. In total, 957 scans were completed across both groups: n_{large}=553 (272, 281 scans for high-contest and low-contest patches, respectively), and n_{small}=404 (138, 267). Similarly, n_{large}=1036 (601, 435 for high-contest and low-contest patches, respectively) and n_{small}=331 (128, 203) bite-rate observations were completed. Individually, the mean±SE sample sizes were 64±1 scans and 34±1 bite-rate observations.

To measure the corresponding foraging benefits in natural food patches, one-hour focal watches on foraging adults were conducted during full-day follows, and were randomised throughout they day. Focals were only begun once groups had been foraging for more than 20 minutes, so as to exclude periods of inactivity when resting, at waterholes, or at sleeping sites. During focals, all time spent feeding in patches (rather than travelling between patches) was recorded by continuous monitoring. Bite-rate observations were also made on individuals opportunistically during focal watches where visibility permitted. This allowed me to calculate the average food bites consumed per unit of time feeding in natural patches for each individual. This in turn allowed me to compare the number of bites obtained while feeding in the experimental patch versus the number of bites obtained over a comparable time period feeding in natural patches: the consensus cost/gain. The natural foraging benefits corresponding to the high- and low-contest experimental patches were derived from a 20-day period preceding or following these patches, respectively. A mean±SE of 15±2 hours were recorded per individual, during which 25.5±1.5 bite-rate observations were recorded.

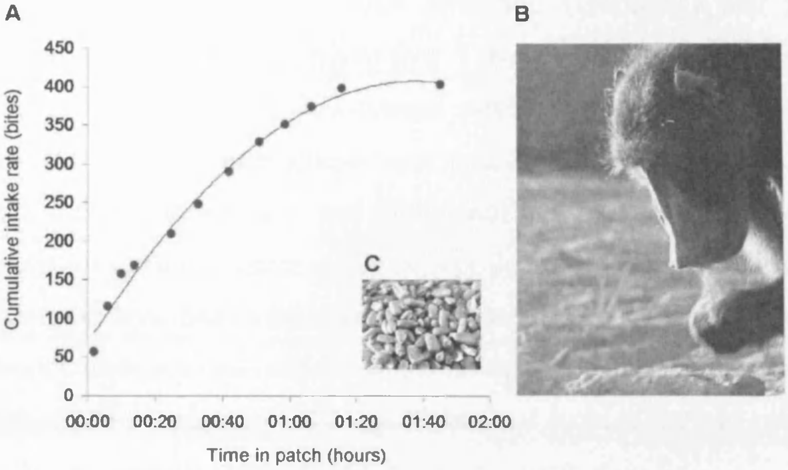


Figure 7.2.
Intake rate observations. (A). Example of bite rate observations of subordinate male during a single visit to the experimental patch presented in the high contest competition period. (B). Single bite of corn kernel. (C). Dried corn kernels used to bait the experimental patches. Intake rate remained approximately constant for 75% of the time individuals spent in experimental patches.

Statistical analyses

Simple bivariate relationships were tested using standard two-tailed parametric tests (or non-parametric tests where the data could not be normalised).

The distribution of foraging benefits among group members was tested against a null hypothesis of random foraging benefit within groups using a binomial (B) skew index developed by Nonacs (2003), as follows:

$$B=\sum_{i=1}^{N}\left(p_i-\frac{1}{N}\right)^2-\left(1-\frac{1}{N}\right)\Big/K,$$

where N is the total number of individuals (i.e. group size), and p_i is the individual foraging benefit as a proportion of the total group benefit (K) gained by the *i*th individual. See 'Observational data' (above) for details of how p_i, was calculated under natural and experimental foraging conditions.

Arrival orders were analysed using generalised linear mixed models (GLMMs). I conducted one model for each group, and explored the effects of individual dominance rank, plus social affiliation (grooming) and genetic relatedness to the individual who arrived first. I also tested for the overall effects of treatment (high-contest patch, low-contest patch) and sex (male, female) on arrival order. All two-way interactions were tested, but none were found to be significant. We incorporated 'day' and 'individual ID' as random effects in our models, to control for non-independence of repeated observations of individuals over experimental days. Backward elimination was used in selecting the minimal adequate model, and included only those factors that contributed significantly ($P < 0.05$) to the explanatory power. The significance of fixed terms was calculated as Wald statistics evaluated against the Chi-square distribution.

Results

I found that both baboon groups consistently visited the experimental food patch in preference to natural patches (Figure 7.3). Since only a minority of individuals could feed at these patches, this pattern suggests that despotic group decisions were the norm. The pattern of patch visits suggested that these decisions were made intentionally rather than opportunistically: at sunrise the groups usually travelled immediately and directly from their sleeping sites to the patch (mean±SE time of arrival: 08:21±5 mins), and groups subsequently spent a large proportion of their normal foraging time at the patch location, or at its periphery for those individuals who rarely entered the patch (mean±SE: 83±5 mins). This is comparable to over 30% of the baboon's normal daily foraging time (Chapter 2). The groups normally visited the location just once on any given day during the experimental period (median visits/day = 1), and only left the patch once it was completely empty. Additionally, examination of group daily travel routes showed that the groups passed through the experimental food patch locations significantly more often when food was present (χ^2_1=6.13, P=0.01; Figure 7.4).

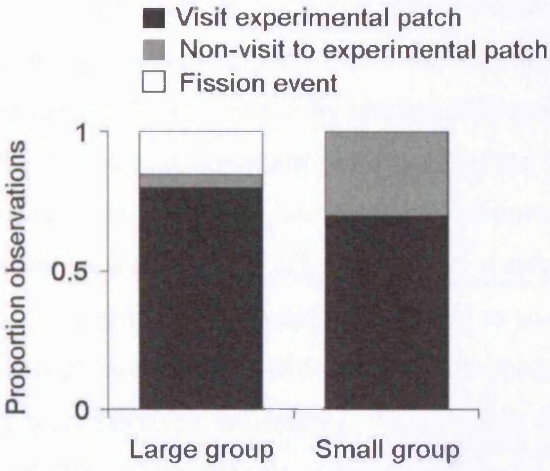


Figure 7.3.
Group decision outcomes. Group decisions which resulted in patch visits are shown in black, while non-visits are shown in grey. Group fissions, in which groups did not reach a consensus but rather split, are shown in white.

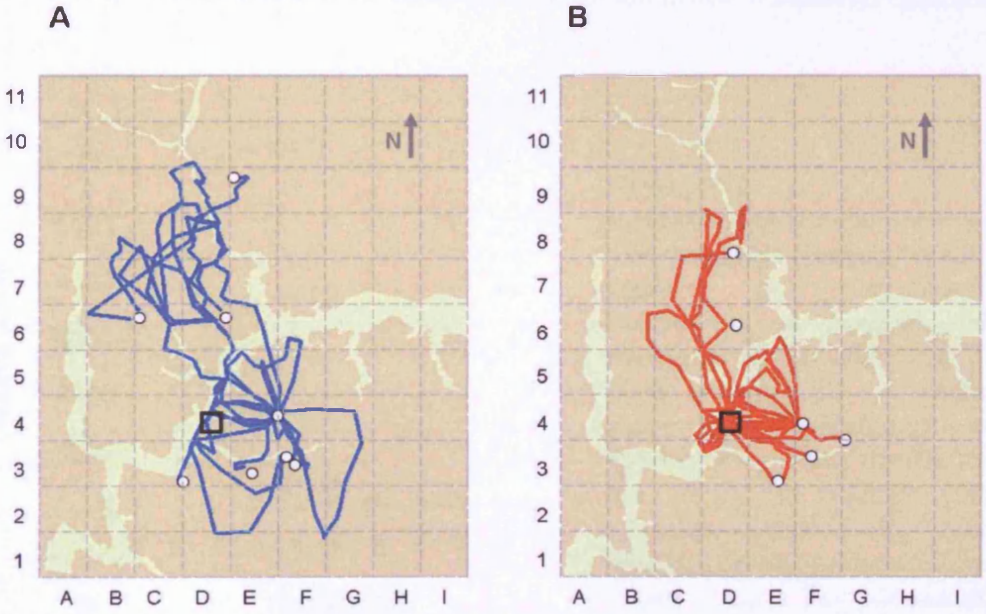


Figure 7.4.
Baboon group travel routes. An example of the daily travel routes for the large group when no food was presented, n=13 days (A), versus when food was presented experimentally as a 'high contest competition patch', n=16 days (B) at grid location D4 marked by a black square. Days when the group fissioned (n=3), or did not visit the experimental patch (n=1) in (B) have been excluded. Sleeping site locations, where the group started and ended each day are shown by white-filled circles. Light shaded areas represent the (dry) Swakop River and its tributaries. Grid cells represent 1km by 1km.

In both treatment types, the dominant male was usually the first to arrive at the food patch (Figure 7.5). Dominant males therefore acted as leaders more frequently than expected by chance (Binomial tests: *P*<0.001 for each group). I also found that dominant males gained the highest foraging benefits, except in the large group during low contest conditions where his attempts to monopolise a larger area and chase off competitors resulted in a reduced intake rate (Figure 7.5). Indeed, the dominant male tended to acquire the highest foraging benefits in the high contest-competition treatment where food was more easily monopolised (T-tests between treatments: $T_{large}=-2.25$, df=30, *P*=0.04; $T_{small}=-1.91$, df=25, *P*=0.098). Later arrivals at the experimental patches acquired progressively less food in both treatments (Figure 7.5). I also found that the influence of social rank on arrival extended beyond the leader, producing a linear increase in arrival order with rank (Table 7.1; Figure 7.6a).

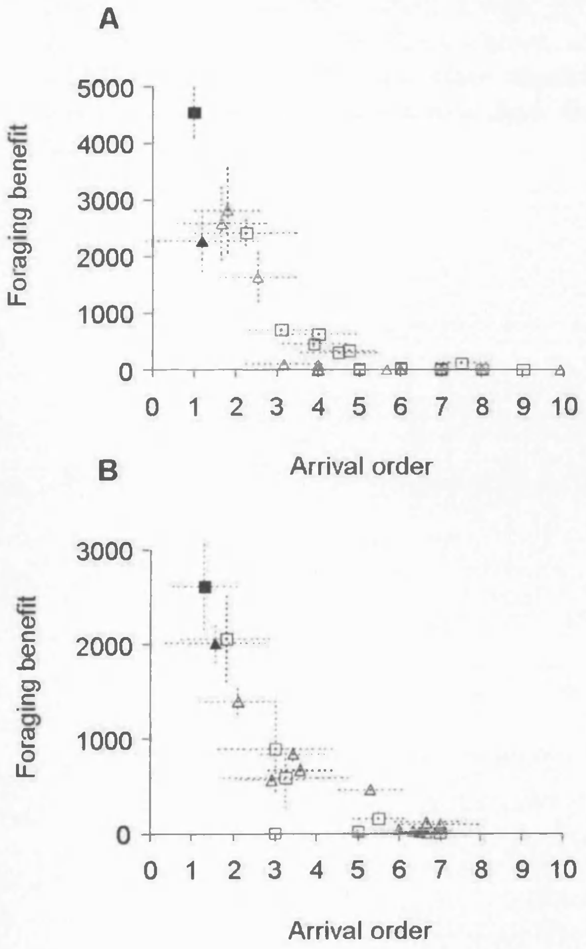


Figure 7.5.
Leader incentives and identity. The mean±SE foraging benefit attained in experimental patches as a function of mean±SE arrival order. (A) = large group; (B) = small group. Data for high and low contest-competition treatments are shown in squares and triangles, respectively, and standard errors are depicted by dotted lines. The dominant male is indicated by filled symbols.

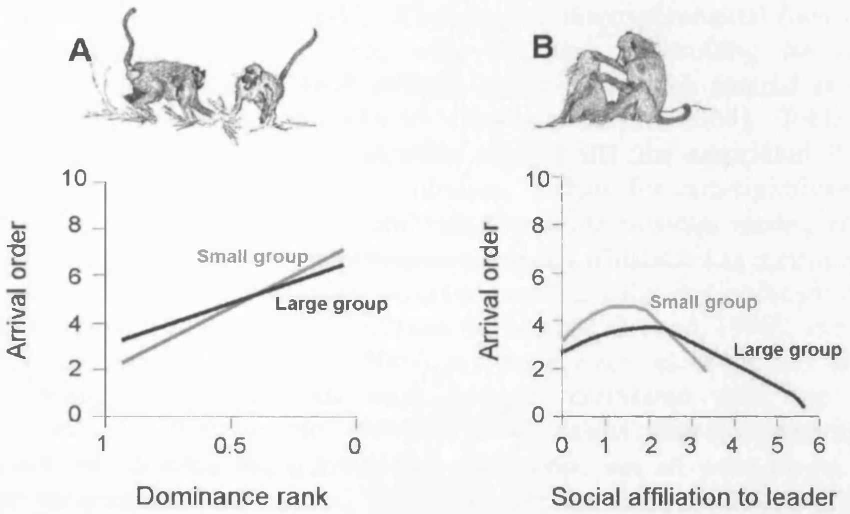


Figure 7.6.
The role of dominance rank and social affiliation. (A) High-ranked animals arrived earlier at experimental food patches than subordinates (GLMMs: small group, χ^2_1=32.9, P<0.001; large group, χ^2_1=2.9, P<0.001). (B) The effect of an individual's social affiliation to the leader on that individual's arrival order (GLMMs: small group, χ^2_1=37.4, P<0.001; large group, χ^2_1=33.8, P<0.001). The lines shown are the predicted effects from GLMMs controlling for all other significant effects and for repeated observations of individuals across days. See Table 7.1 for the full model results.

Table 7.1.

Factors affecting the arrival order of baboons to the experimental food patches. GLMM analysis with a normal error structure, controlling for repeated observations on individual focal animals across days (each entered as random effects) were conducted in MLwiN (Rasbash et al., 2004). Table shows parameter estimates (Estimate), standard errors (SE) and associated *P* values, evaluated against a chi-squared distribution. Values for non-significant terms were obtained from fitting terms individually to the minimal model, and there were no significant two-way interactions. Genetic affiliation was measured using three common estimators of pairwise relatedness: Queller & Goodnight (Queller and Goodnight, 1989), Lynch & Ritland (Lynch and Ritland, 1999), and Triadic identical by decent IBD (Wang, 2007). All three were calculated in Coancestry v1.0. (Wang, 2006), and all were strongly correlated with one another (Spearman's r_s >0.70; n=36, *P*<0.001 in all cases) (See Chapter 2). Each estimator was entered individually into the model, but all were found to have similar (non-significant) effects. The results for the Triadic IBD (Wang, 2007) estimator are presented here.

	Large group			*Small group*		
Effects	Estimate	SE	*P*	Estimate	SE	*P*
Dominance rank (scaled)	2.858	0.579	<0.001	3.488	0.608	<0.001
Social affiliation to leader (grooming index)	1.503	0.502	0.002	2.129	0.497	<0.001
Social affiliation to leader^2 (grooming index)	-0.319	0.088	<0.001	-0.753	0.153	<0.001
Genetic affiliation to leader (relatedness)	0.993	1.108	0.370	2.147	2.303	0.351
Treatment						
Low contest competition	0.000	0.000	-	0.000	0.000	-
High contest competition	-0.239	0.283	0.398	-0.342	0.241	0.157
Sex						
Male	0.000	0.000	-	0.000	0.000	-
Female	0.190	0.447	0.670	-0.825	0.503	0.101
Constant	3.553	0.236	-	2.844	0.370	-
Individual identity (random effect)	0.000	0.000	-	0.272	0.155	-
Day of experiment (random effect)	2.077	0.273	-	1.359	0.300	-

Calculation of consensus costs and gains of despotic decisions (calculated as the difference in consumption between natural and experimental conditions) revealed that a minority of group members obtained consensus gains, but the majority experienced substantial consensus costs when visiting the experimental patch (Figure 7.7). Moreover, these costs were more strongly skewed under conditions of high contest competition than low contest competition: the binomial skew index, B (Nonacs, 2003), increased by 27–76% between treatments in the large and small groups, respectively (Figure 7.7).

Given my finding that many followers experienced high consensus costs to following dominant-led group decisions, why follow? I found that individuals with stronger social affiliations to the leader followed more closely. However, this was not a linear effect, since some individuals were close followers despite low affiliation (Table 7.1; Figure 7.6b). These individuals were adult males who arrived closely behind the leader by virtue of their dominance rank rather than their social relationship. I found no effect of the genetic relationship an individual holds to the leader on follower behaviour (Table 7.1). I also tested for a more complex 'chain' effect, where an individual's follower behaviour is determined by the social or genetic relationship to the animal directly ahead of it, rather than to the leader. Thus, I compared the strength of social affiliation and genetic relatedness between sequential pairs (dyads) in the arrival order with that of an average pair in the group. I found no differences for social affiliation (Wilcoxon tests across all trials: $W_{large}=2967$, n=527, $P=0.68$; $W_{small}=1721$, n=226, $P=0.99$), nor for genetic relatedness in the large group (W=3860, n=527, $P=0.10$), while relatedness was lower than average in the small group (W=1381, n=226, $P=0.04$).

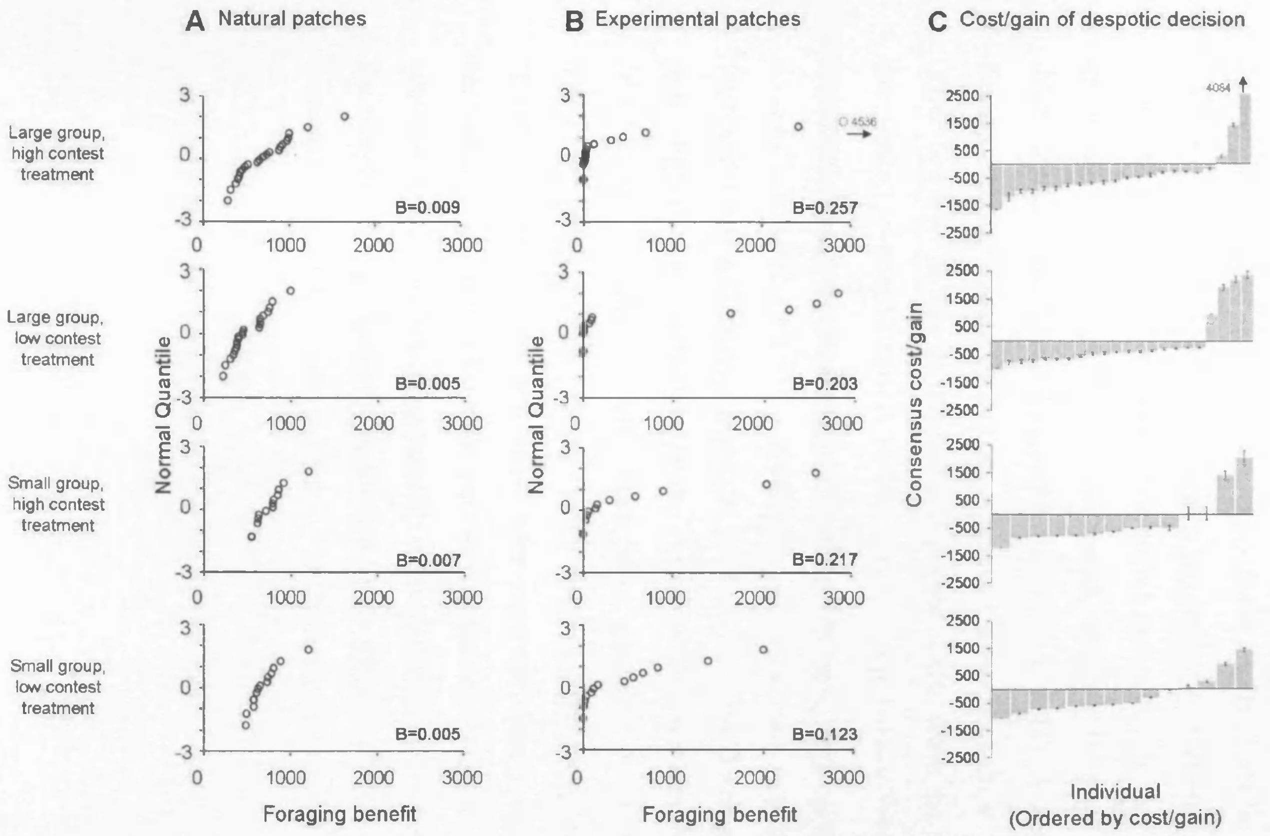
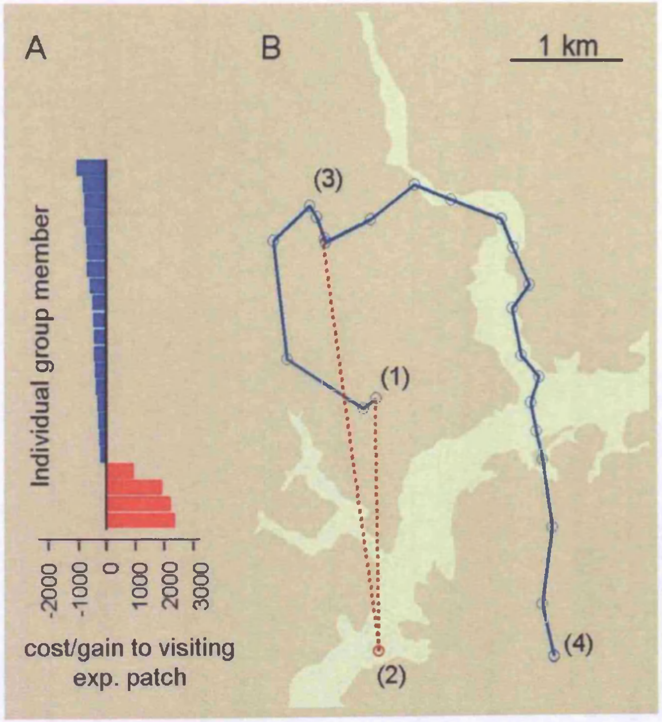


Figure 7.7.
Foraging benefits to alternate decisions, and consensus costs of despotism. (A) and (B) show normal quantile plots for the mean foraging benefits of natural and experimental patches for comparable time periods, obtained by individual baboons belonging to the large and small group under two contest-competition treatments. Normal quantile plots are used to indicate skew from normality: where the distribution is normal the points fall along a straight line. In addition, a binomial '*B*' skew index is given, where zero indicates a random distribution and higher values indicate increasing skew. (C) shows the mean daily consensus cost/gain ±SE for decisions to visit experimental patches over natural patches (i.e. foraging benefits in experimental patch minus foraging benefits in natural patch).

Occasionally, the groups did not collectively visit the experimental patch. Rather, the groups either fissioned into two subgroups of which only one visited the patch (n=6/80), or remained cohesive but failed to visit the patch entirely (n=14/80) (Figure 7.8). In both cases, there was no clear temporal pattern to suggest subordinates were learning to resist costly despotic decisions (Figure 7.9), nor was there any spatial pattern suggesting that group members were less inclined to visit on those days when travel costs were higher (t-tests comparing distances between sleeping site and patch where n>6 cases: fission, t_{large}=1.03 df=5, P=0.35; non-visits, t_{small}=0.86, df=11, P=0.41). I also considered that fission may be driven by higher consensus costs, but these were found not to differ between groups as would be expected if this were the case, given that all the fission events occurred in the large group (Mann-Whitney tests: 'high' treatment, n_{large}=16, n_{small}=11, W=266, *P*=0.83; 'low' treatment, n_{large}=16, n_{small}=17, W=248, *P*=0.73). I did find, however, certain patterns were associated with non-visits and group fission. In the first case, the dominant male was mate-guarding an oestrous female in the majority of non-visits by the small group (9/12 cases), whereas he was never mate-guarding on those days the group visited the patch (Fisher's Exact Test: *P*<0.001). No mate-guarding was recorded in the large group and non-visits were correspondingly rare (n=2/40). In the second case, fission events were only observed in the large troop, and occurred in accordance with the foraging benefits derived from the experimental patches, i.e. the minority subgroup was comparable to the number of animals acquiring a net consensus gain: mean ± SE = 3.8 ± 1.3 individuals (Figure 7.8).

Figure 7.8.

Example of a temporary fission event. During group fission, a small subgroup visited the experimental patch while the majority foraged elsewhere. (A) Shows the average consensus cost/gain of the decision to visit the experimental food patch for all group members during the treatment period (from Figure 4C in the main paper). (B) Shows the group's travel route for a fission event observed on 21/06/06 (row 2, day 7 in Figure S3). At point (1) all group members are at their sleeping site (06:00). A minority of four group members (red line and corresponding red coloured bars) fission from the main group and travel directly to the experimental food patch (2), arriving at 06:21 and departing at 07:31. The remainder of the group (blue line) leave the sleeping site in a different direction, and are rejoined by the red subgroup at 08:15. The full group remain cohesive for the remainder of the day arriving at a different sleeping site at 16:30 (4). Light shaded areas represent the (dry) Swakop River and its tributaries. The blue travel route is based on GPS locations taken every 30 minutes (open circles). The red travel route shows the straight line travel distance between observations of the sub-group, i.e. observed at the sleeping site (observer 1), experimental patch (observer 2), and when rejoining the main group (observer 1).



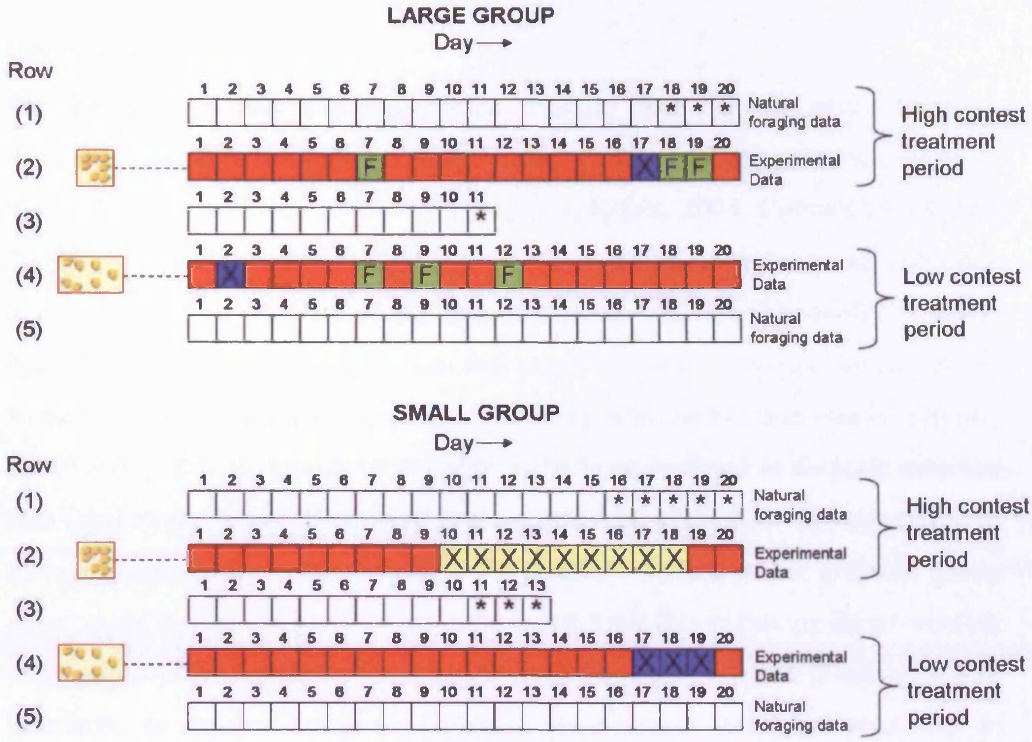


Figure 7.9.
Summary of decision outcomes by trial number. Rows 1-5 show up to 20 consecutive days over five consecutive periods for the small and large study groups. Boxes in rows (1), (3) and (5) are natural foraging days. Data on natural foraging were collected during rows (1) and (5). The '*' boxes in rows (1) and (3) represent days on which the experimental food patch was introduced to the baboon groups but it was not found. Rows (2) and (4) show days during which the baboon groups had the opportunity to visit the high-contest patch and low-contest patch, respectively, once it had been located on day 1. The colours and contents of boxes indicate decision outcomes on that day. Red boxes are group visits to the patch; blue 'X' boxes are days on which groups did not visit but naturally foraged; yellow 'X' boxes are days during which groups did not visit when the dominant male was in a consortship; and green 'F' boxes are days during which the groups did not reach a consensus and fissioned.

Discussion

The findings of this Chapter, which indicate that baboon group foraging decisions may arise through a despotic rather than democratic process, contradict the predictions of recent models (Conradt and Roper, 2003; Conradt and Roper, 2007). But for many social animals it might not be that rare for group decisions to be dictated by a minority of individuals who are known and consistent leaders. Indeed, "most observers of primates that range as cohesive groups are convinced some individuals have more influence on group movements than others" (Byrne, 2000) and vertebrate groups have traditionally been depicted as despotic societies (see Dyer et al., 2008). This result is also consistent with observational studies in other primate species. For instance, in geladas (*Theropithecus gelada*), group movements can be initiated by multiple individuals but decisions about whether the group follows are determined by the most dominant animals (Dunbar, 1983). Similarly, in another baboon population, most group members were seen to initiate group movements, but successful consensus decisions were only reached when adult males, and most often the dominant male, were involved (Stueckle and Zinner, 2008).

I have shown that for the two baboon groups under investigation, where high-status individuals have incentives to lead, a majority of subordinate individuals will accept their decisions, even where this compromises their own activity. This result is consistent for decision outcomes that differ in costs, and is coherent with high-ranking individuals having a particularly strong influence on the behaviour of other group members (Barton et al., 1996; Couzin, 2006; Smith et al., 2007). Indeed, follower behaviour appears to emerge as a combination of social rank and affiliation to the leader. In the first case, high-ranking animals most likely follow out of an interest in acquiring a share of the food in the patch, while in the second case lower-ranked animals appear to follow primarily as a consequence of social affiliation. I therefore suggest that the long-term benefits derived from social ties with the leader may outweigh the short-term costs associated with accepting the leader's current decision. Close association with these individuals may provide females and their dependent offspring with direct fitness benefits, such as increased infant survival (Palombit, 2003) and protection from predators (Cowlishaw, 1994). The absence of a kinship effect on follower behaviour might appear puzzling. However, in this case, the leader was most often the dominant male, who is an immigrant into the group and thus unrelated to other group members. It is plausible that in other systems where the dominant female (or another any individual that is related to other group members) has an incentive to lead, follower behaviour may well be mediated by kinship, rather than or in addition to social affiliation (e.g. Erhart and Overdorff, 1999). It also appears that the influence of the leaders was sufficiently strong to generate follower behaviour in the absence of 'herding' or any other forms of coercive behaviour, sometimes seen during conflicting interests within complex social systems (c.f. Henzi et al., 1998; Walther, 1991).

Whilst despotic decisions were the norm, group fissions and consensus non-visits were also seen to occur. In the first case, fission occurred in such a way that one small sub-group – comparable in size to the number of animals that could achieve consensus gains at the patch – would visit the patch, while the rest of the group would not. This would suggest that the fission event was driven by the consensus gains experienced by some individuals and the consensus costs experienced by others. Although the dominant male normally led this sub-group, his presence does not appear to have been sufficient to generate the usual pattern of follower behaviour across the rest of the group. Given the importance of social relationships in mediating follower behaviour, and the fact that fission events were only observed in the large group (Figure 7.8), I suspected that this might reflect variation between the two groups in the strength of social relationships connecting the leader and other group members. To test this prediction, I compared the daily time spent in social activity (grooming) in the two groups, together with the size of the leader's social networks i.e. grooming clique size (Kudo and Dunbar, 2001) (Chapter 2). I found that not only did individuals spend less time grooming in the larger group (Mann-Whitney tests: W=2226049, $n_{large}=1644$, $n_{small}=1096$, $P=0.05$) but also that a smaller proportion of individuals interacted socially with the leader (0.50 versus 0.33 of adult females in the small and large group, respectively). Both results support the interpretation that strong social relationships between leaders and followers are necessary for the emergence of despotic group decisions. My findings are also consistent with a wider pattern of time budget stress in large groups that links reduced social time with a higher probability of fission (see Dunbar, 1992).

Non-visits are likely to reflect a different process. Specifically, in light of the results already discussed, non-visits might be associated with a switch in leader incentives. Consistent with this expectation, I found that the dominant male was mate-guarding an oestrous female in the majority of non-visits by the small group, whereas he was never mate-guarding on those days the group visited the patch. Although only based on a comparison of small sample size, and more experiments over a number of female reproductive cycles are required to reach a clear conclusion, these results are consistent with a switch in leader incentives. During mate-guarding (consortship) in baboons, males follow females closely, and so it is the female who guides and constrains her male partner's behaviour (Alberts et al., 1996). Since the oestrous female who was being mate-guarded in this particular case was only mid-ranking in the dominance hierarchy (4/10 within females, and 8/14 overall), and experienced a net consensus cost from patch visits, there was no incentive for her to lead the dominant male to the patch.

In summary, these field experiments on wild baboons indicate that despotic group decisions can emerge when an individual has both a strong incentive to lead and sufficient social influence to elicit follower behaviour. Follower behaviour occurred despite consensus costs, but where social ties were weaker group fission was more likely. The influential role of the leader was further highlighted by the observation that groups failed to visit the food patch when the leader's priorities changed. My findings emphasise the importance of leader incentives and social relationships in group decision-making processes and the emergence of despotism.

Chapter 8 – Discussion

In this thesis I have focussed upon three unifying concepts upon which the benefits (and many of the costs) of grouping are reliant: information transfer, coordinated behaviour and leadership. A growing number of theoretical (e.g. Conradt and Roper, 2003; Couzin et al., 2005) and empirical (e.g. Fischhoff et al., 2007; Kerth et al., 2006; Ward et al., 2008) studies have been developed in recent years which have allowed us to build a more complete understanding of each of these concepts. However, there is still room for useful development, especially in more complex and stable social groups. I have attempted to plug some of the holes that exist in this knowledge during this thesis. I will briefly run through some of the main findings in this final chapter. My primary focus will be on those patterns that are consistent (or different) across chapters, and what these might mean for our wider understanding for the behavioural ecology of group living animals. I discuss these patterns under following sub-headings: (i) Social interactions; (ii) Reproductive patterns; (iii) From individual to group behaviour; (iv) Understanding leadership; (v) Developing and testing models presented. I will then end with some final concluding remarks.

Social interactions

The consequences of individual behavioural patterns interacting with one another were considered throughout this thesis. In Chapter 3 I investigated when individual baboons joined the food discoveries of their group-mates. I found (after controlling for ecological and spatial factors) that individuals were less likely to join the group-mates with whom they had weak social affiliations. I also found an independent effect of dominance rank: individuals joined dominants infrequently and subordinates more frequently. Both of these patterns were mirrored in Chapter 7, where dominant 'leader' animals monopolised experimentally provided food patches, and those with strong social affiliation to indentified leaders exhibited closest follower behaviour. The finding that social affiliation and dominance were crucial in both natural and experimental conditions suggests that such social interactions (and constraints) play a critical role in both individual and group decision-making for complex vertebrate groups (Beauchamp, 2006; Sueur and Petit, 2008 respectively).

Understanding how dominance and affiliation mediate collective decision-making (Chapters 3 and 7) is therefore vital for advancing our knowledge of the costs and benefits of group living (Krause and Ruxton, 2002). I have already described that the primary benefit of grouping is that it provides safety from predators (see Chapter 1; Cowlishaw 1994). But through quantifying social relationships within the framework of group decisions, I can speculate about how these relationships alter the relative balance of other costs and benefits of grouping. For instance, social relationships can mediate access to food (Chapter 3) or coalitionary support during aggressive interactions (Noe, 1984; Silk et al., 2004) and ultimately increase offspring survival (Silk, 2007a; Silk et al., 2003). In Chapter 7, where opportunity for maintaining social relationships with key individuals are limited (i.e. in the larger group), and where individuals experienced high competition for resources (see Figure 7.9), groups were seen to fission, albeit infrequently. Although further study is required to support the interpretation that this pattern was the result of reduced expression of social relationships, and therefore decreased individual grouping benefits (see discussion of Chapter 7), this is a starting point which can now be developed further. One potential avenue would be to explore the role of social relationships, and specific key individuals, upon group stability through removal experiments. Research in this area looks promising and has been developed in captivity (Flack et al., 2003), and experiments are ongoing in wild populations (Clutton-Brock, personal communication). If key individuals provide fitness benefits via the social relationships they hold with group-mates, then through their removal, you would predict lower levels of group cohesion, and ultimately group fission.

A key social factor that was explored in this study, but which was found not to contribute significantly to any of the results (see Chapters 3 and 7) was kinship. This is surprising. However, this does not mean that kinship is not relevant. On the contrary, kinship may well be important to the social lives of baboons (see Silk, 2002 for a discussion), but just not under the conditions considered here (cf. Langergraber et al., 2007). The primary reason for this may be that all of my analyses focus on adult individuals, yet half of each group under consideration comprised sub-adults and juveniles. From my own observations of the baboons whilst foraging, although youngsters are difficult to identify, they do associate closely with kin – their mothers and siblings. Between these closely related dyads then, the role of kinship in patterns of producer-scrounger dynamics or leader-follower behaviour may be large. Indeed, early interactions with adults mediate the development of a variety of behavioural strategies in group-living vertebrates (e.g. see Chapman et al., 2008 for a recent example). In future, expanding my analyses to include non-adults in Chapter 3 (which would require more data collection) and Chapter 7 (for which data are available) would allow me to test the prediction that kinship is important, but only at higher levels of relatedness – i.e. parent-offspring dyads. It is also worthy to note that although full-sibling pairs share the same degree of kinship as parent-offspring pairs, I do anticipate these being so important, as these are relatively rare in baboon societies, due to slow rates of reproduction and relatively high turnover in the alpha male position. As a result, the parent-offspring pattern is the only type of relationship with higher-level (50%) relatedness.

Reproductive patterns

Female reproductive state has been the focus of much research in baboons, and primates in general (e.g. Bielert and Anderson, 1985; Huchard et al., 2008; Semple, 2001). But the role of reproductive state in wider group-level patterns of behaviour is poorly understood. I hope that I have gone some way to addressing this paucity of knowledge in this thesis. I have shown that female reproductive state can impact on social foraging tactics (Chapter 3), and contribute to overall levels of behavioural synchrony within groups (Chapter 5). The findings presented in both chapters were interpreted as a consequence of (i) energetic requirements of females and (ii) the influence of female state on male behaviour. I would suggest that these patterns of social foraging behaviour and behavioural synchrony are explicitly linked. On the one hand, more scrounging should lead to higher behavioural synchrony since more animals are feeding in patches concurrently (and are also more likely to be leaving patches at similar times when food is depleted). On the other hand, more producing leads to asynchrony since individuals will be finding, feeding within, and exiting multiple food patches at different times from one another.

Individual reproductive state therefore has the potential to play a surprisingly influential role in shaping the behaviour at the group level. Indeed, in Chapter 7, I provided anecdotal evidence that the change of reproductive state in one female baboon can change the daily course of action for more than 60 individuals by virtue of her influence upon other group members (particularly the dominant male's) behaviour. These findings suggest that more detailed investigation of the role of individual reproductive state upon group-level patterns of behaviour between species and between contexts will be an important avenue for future research. One way to investigate the role of female reproductive state on conspecific relations and grouping patterns would be to experimentally manipulate reproductive cycles. This may seem totally unfeasible, but in fact is a part of management regimes in many zoos in which populations are growing too rapidly and cannot be supported by zoo resources. Thus, in captive UK primate populations, females are often provided with implants to reduce birth rates (e.g. Hamadryas baboons, *Papio hamadryas*: Plowman et al., 2004). This acts to increase the number of sexually swollen females, and decrease numbers of pregnant females. Such regimes, which are present and integrated parts of captive management schedules, lend themselves well to answering questions concerning the influence of female state on group behaviour.

From individual to group behaviour

The synchronisation of group members' behaviour allows coordination of different individuals' actions, thereby permitting group cohesion and maximising many of the benefits of group-living (Conradt and Roper, 2005; Pitcher and Parrish, 1993). The synchronisation of individual behaviours can result via a variety of processes. The simplest route to synchrony can be where group members respond simultaneously to a common stimulus, independently of conspecific behaviour. This might be stimuli as simple as the sun rising in the morning; the example of a starter's gun to begin a race is another commonly cited example (Krause and Ruxton, 2002; Meunier et al., 2008). Thus, the fact that individuals perform the same activity at the same time does not imply that such a phenomenon is coordinated by inter-individual attractions/interactions. In

Chapter 5, I was able to show that baboon groups altered their degree of behavioural synchrony (i.e. concurrence of broad state behaviour) in accordance with a number of behavioural and ecological conditions. The fact that these levels of synchrony varied significantly more than would be expected by a simple simulation model in which all baboons behave independently, suggests that baboons were actively coordinating their behaviours and not simply responding to the same external stimuli. The results of Chapter 7 support this interpretation: high-status individuals induced synchronous group travel to a particular location, even where the majority of the group did not benefit from travelling to this destination. Together, these findings clearly indicate that behavioural synchronisation is not coincidental but the result of active individual coordination. Future work might aim to uncover the underlying mechanisms through which such synchronisation and coordination is achieved.

At this point, it is also worthy to note that the individual and collective behaviour in one group can also impact upon the behaviour of an entirely different species. In Chapter 6 I investigated such an interspecies interaction. In some circumstances, one species may derive foraging benefits from associating with another, through one species 'flushing' prey items for the other. This need not necessarily involve a cost to the species that flushes the prey, since flushed individuals are effectively lost to them, or are of no interest. Chapter 6, to my knowledge, is the first time that the behavioural synchrony of the flushing species has been investigated. I found that when a majority of baboons were travel foraging, the association of kestrels was significantly higher than when few individuals were performing this behaviour, or engaged in other activities. I would not however, argue that travel foraging synchrony *per se* increased kestrel associations. Instead, it is likely that since there were more individuals travel foraging, more prey items were being flushed. This interpretation is consistent with the group size effect that was also detected. For a wide range of taxa, we have evidence of individuals preferentially choosing one group over another (Couzin, 2006; Croft et al., 2005b), and that this non-random assortment can provide fitness benefits (e.g. Croft et al., 2005a). The findings of chapter 6 suggest that interspecies interactions can also vary according to the properties of the groups involved. Kestrels appeared to preferentially associate with larger groups, and with groups in which the majority of individuals were performing behaviours that increase flushing of prey.

Understanding leadership

I will now return to the problems associated with maintaining coordination in groups has been emphasised throughout this thesis. I have discussed the variety of mechanisms that animals can use to solve these problems (Chapters 1, 5, 7), which are now relatively well understood (Conradt and Roper, 2003; Couzin et al., 2005). Until recently, however, the challenge remained to ascertain how, and why, certain individuals might dictate the actions of other group members. Coercion by a dominant individual is one potential mechanism. However, this may be difficult to achieve either because it is physically unable to coerce a sufficiently number of individuals (particularly in large groups), or because the leader would not gain sufficiently to outweigh the costs of coercion (see Conradt and Roper, 2005 for a discussion). Thus, consensus decisions involving conflicts of interest are perhaps more likely to be made through voluntary compliance, as presented in Chapter 7.

The findings of Chapter 7 and a number of recent studies (e.g. Fischhoff et al., 2007; Sueur and Petit, 2008) suggest social constraints can play critical roles with regard to follower behaviour and 'voluntary compliance' for animals that live in stable and complex social systems (see discussion of 'Individual behaviour' above). However, whilst it is now clear that social factors can induce follower behaviour, whether these leader-follower interactions are based on simple rules of thumb (e.g. move when animal A moves), or are the result of a more complicated negotiation between animals (e.g. move when animal A moves, but only where this has been supported by animals B, C, and D), is unclear. Investigation into the proximate mechanisms that are the pre-cursors to leadership and 'followership' will therefore be useful. In baboons and other social primates, the proximate mechanisms through which the preference of a single individual is communicated to other group members appears to be specialised vocalisations or movements (see also Leca et al., 2003; Stueckle and Zinner, 2008; Trillmich et al., 2004). When accepted, this preference may be adopted by the rest of the group, allowing this individual to direct group movements. I have collected a dataset that examines the use of such explicit signals in this study system, as well as associated behaviours that may provide incidental information on the motivations of individual group members. These data relate to how groups coordinate their morning departure from their sleeping sites. I have not been able to analyse this dataset for inclusion here, but further analyses are planned that will aim to elucidate the proximate behavioural mechanisms necessary for leader-follower behaviour to occur in baboons.

Developing and testing of models presented

In chapter 4, I developed a model to consider when individual animals should use social information according to the quality of information individuals possess, and the number of individuals sharing this information. The expansion and testing of this model might provide new insights into these processes. One clear extension would be to incorporate differential costs to the use of personal and social information. Such analyses may not only provide a more realistic model, but be useful in explaining the evolution of the diversity of signals used to transmit information by social animals (Endler, 1992; Schwartz and Freeberg, 2008) – especially when there are conflicts of interest between signallers and receivers (Greenfield, 1994; Johnstone, 1999; Lachmann et al., 2001). For instance, there are no food calls associated with scrounging in baboons (Chapter 3), despite their presence in a number of foraging systems (Brown et al., 1991; Hauser and Marler, 1993; Wilkinson and Boughman, 1998). So under what conditions are such signals expected to evolve (see Hauser and Nelson, 1991)? Through incorporating differential costs of information use, and perhaps through modelling the evolution of perception using artificial neural networks and genetic algorithms (e.g. Ioannou et al., 2008; Tosh and Ruxton, 2007), we might be able to answer such questions. At the same time, it would be important to compliment such an approach with investigations in the field, considering how other factors, like social structure, kinship, food patch sizes and habitat visibility, can each drive the evolution of food-calls.

The model presented in Chapter 4 could also be tested empirically. Baboons would perhaps be too complicated a starting point, but gregarious fish species might be suitable (e.g. see Ward et al., 2008). Individual fish could be taught to expect a reward at one of two locations via a visual cue. Some fish would always be rewarded at location one, 100% of the time, others would be rewarded 80% of the time at this location, and 20% of the time at location two, and so on. Thus, individual fish would receive information that was correct only a proportion of the time. By putting fish together in their respective 'level of information' categories, the responses of fish alone, and in a group could be compared to their performance in a group, and the model predictions tested.

Final conclusions

The complexity of interactions in groups like primates makes it incredibly difficult to study the connections between individual- and group-level patterns of behaviour. Indeed, the entire philosophy of data collection on which the primate literature (and most literature about animal groups in general) is based stems from individual focal animal sampling. It is this philosophy that has allowed individual behaviours to be compared and contrasted, and for massive advances in our understanding of subjects like kin selection, reciprocal altruism, communication and cognition. But all of these processes occur in the context of a group. A group which is required to stick together, remain coordinated, and make joint decisions about what they, as a whole, are going to 'do'. This is where there remains a lack of understanding.

Recent research on the processes that govern the evolution and maintenance of grouping behaviour in eusocial insects, fish, and birds has generated a great deal of interest (see Chapter 1). These studies also provide a valuable platform for understanding group-level phenomena in more socially complex systems. Researchers can now draw upon this growing understanding of both (1) the functional aspects, i.e. leadership, and (2) the mechanistic aspects, i.e. interactions of social forces, of collective decision-making. It is possible that the same group-level phenomena found in 'simpler' systems may operate in more 'complex' social systems, and future research may reveal similar basic processes of information transfer, coordination, and leadership that occur in each. However, at the same time we know that many of these approaches are deliberately missing what we know to be true about complex groups. Individuals often differ with respect to dominance, kin and grooming relationships (Chapter

2), which can vastly alter the manner in which individuals interact (Chapters 3, 5). Individuals can also differ according to their reproductive or energetic state (Chapters 2, 3, 5), and level of information (Chapter 4). Each of these factors may have important consequences for how collections of animals make group-level decisions (Chapter 7). Indeed they are also likely to impact upon heterospecifics with which they share their environment (Chapter 6). Therefore, I believe that we must complement and build upon the existing frameworks with empirical and theoretical investigations that consider dominance relationships, social and kin networks, as well as variations in individual state, in more complex systems. I hope that the findings of this thesis have begun to do that.

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Appendix

1. **King, A. J.** & Cowlishaw, G. (2007) When to use social information: the advantage of large group size in individual decision-making. *Biology Letters* 3, 137–139.

2. **King, A. J.** & Cowlishaw (2009) Foraging opportunities drive interspecific associations between rock kestrels and desert baboons. *Journal of Zoology.*

3. **King, A. J.** (2008) Dictators of the Desert. *BBC Wildlife.* 26, 50-55.

4. **King, A. J.**, Douglas, C. M. S., Huchard, E., Isaac, N. J. B. & Cowlishaw, G. (2008) Dominance and affiliation mediate despotism in a social primate. *Current Biology* 18, 1833-1838.

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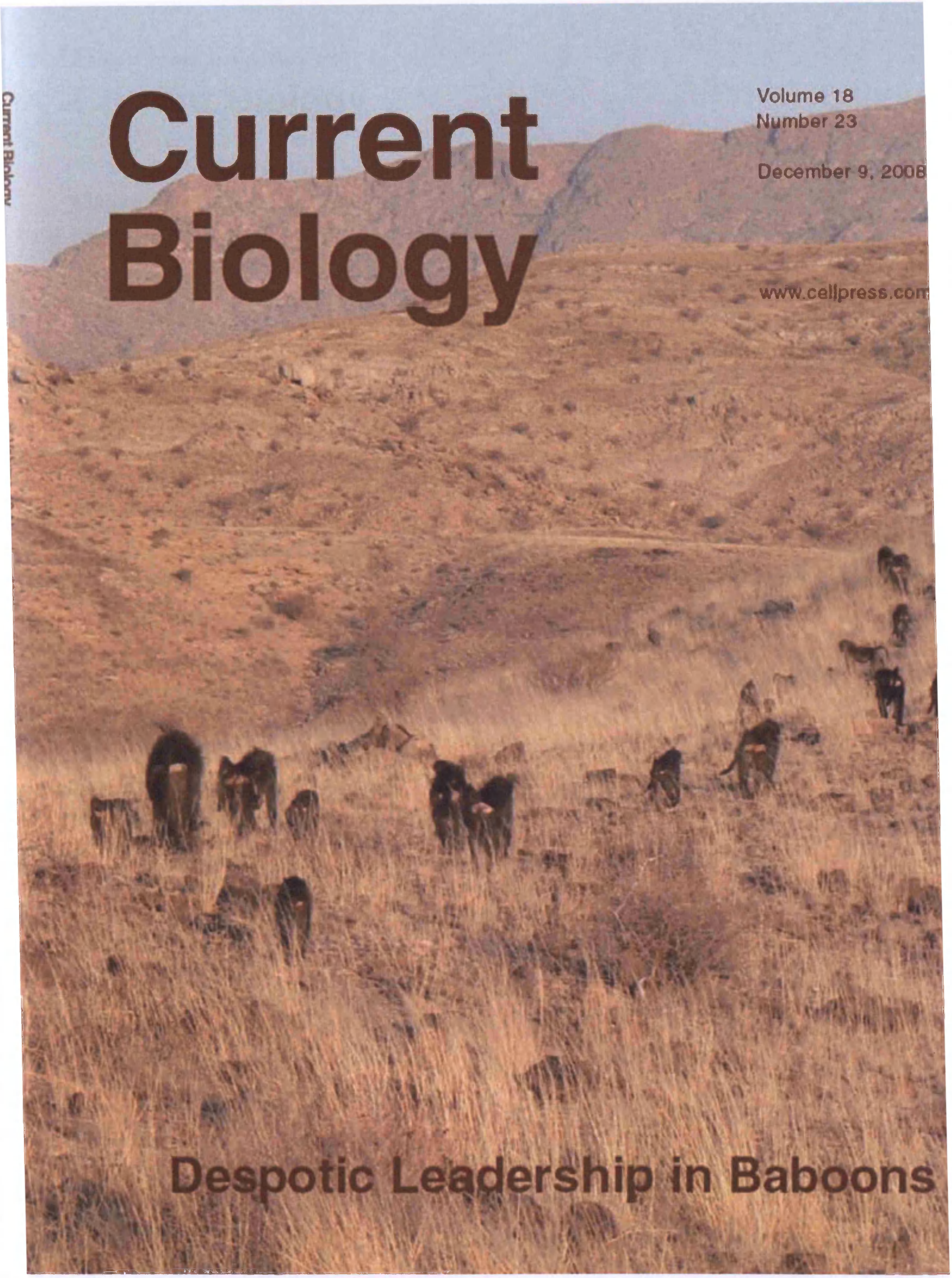

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On the cover: In this issue, King et al. (pages 1833–1838) conducted a foraging experiment with groups of chacma baboons (*Papio ursinus*), found at the edge of the Namib Desert in Namibia, to gain new insights into group decision making. They found that "despotic" group decisions were the norm. Groups were led by the individual who acquired the greatest benefits from those decisions, namely the dominant male. Recent theoretical models predict the opposite — that "democratic" decisions would be widespread — because they result in lower costs for the group as a whole. However, the researchers found that subordinate group members followed the leader despite considerable costs (in terms of foraging benefit). King et al. suggest that follower behavior was mediated by social ties to the leader, and they found that where these ties were weaker, group fission was more likely to occur. These findings highlight the importance of leader incentives and social relationships in group decision-making processes and the emergence of despotism. Image courtesy of Hannah Peck/ZSL Tsaobis Baboon Project.

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Report

Dominance and Affiliation Mediate Despotism in a Social Primate

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Summary

Group-living animals routinely have to reach a consensus decision and choose between mutually exclusive actions in order to coordinate their activities and benefit from sociality [1, 2]. Theoretical models predict "democratic" rather than "despotic" decisions to be widespread in social vertebrates, because they result in lower "consensus costs"—the costs of an individual foregoing its optimal action to comply with the decision—for the group as a whole [1, 3]. Yet, quantification of consensus costs is entirely lacking, and empirical observations provide strong support for the occurrence of both democratic and despotic decisions in nature [1, 4, 5]. We conducted a foraging experiment on a wild social primate (chacma baboons, *Papio ursinus*) in order to gain new insights into despotic group decision making. The results show that group foraging decisions were consistently led by the individual who acquired the greatest benefits from those decisions, namely the dominant male. Subordinate group members followed the leader despite considerable consensus costs. Follower behavior was mediated by social ties to the leader, and where these ties were weaker, group fission was more likely to occur. Our findings highlight the importance of leader incentives and social relationships in group decision-making processes and the emergence of despotism.

Results and Discussion

The way in which group-living animals coordinate their actions is fundamental to our understanding of the evolutionary and ecological basis of sociality. The benefits of group living are largely reliant on animals remaining cohesive, which often requires consensus choices from mutually exclusive actions [3]. Thus far, empirical work on consensus decision making has primarily concentrated on the eusocial insects [6], large insect swarms [7], fish schools [8], and bird flocks [9], in which collective behavior can emerge from simple rules of self-organization [10, 11]. Much less is known about the mechanisms underlying decision making in socially complex and heterogeneous groups, in which individuals are often related and have long-term social relationships with one another [2] (e.g., social birds, carnivores, and primates). In these groups, individual group members often differ with respect to optimal activity budgets [12], levels of information [13], and ability to monopolize resources [14]. Such differences lead to conflicts of interest that can impede the achievement of consensus decision making [15]. In the face of such conflict, two different modes of decision making might be adopted. First, consensus decisions can be reached democratically, whereby all group members contribute to the decision, independent of their individual identities or social status. At the other extreme, a decision can be despotic, taken by a single animal ("leader") with other members ("followers") abiding by this decision [2]. Theoretical models predict the former to be most common in nature [1, 3], and this is supported by a number of empirical examples [2]. However, despotic decisions are also widespread among group-living vertebrates [4], including humans [16]. The profusion of despotic decision making in nature therefore presents a significant challenge to our understanding of sociality.

There are conceivably several different types of animals that might emerge as a leader. In group movements, for instance, the individuals with the greatest incentives [17] or the most pertinent information [18] often lead groups, and are normally—but not always [19]—at the front of group progressions. Yet, the incentives or information required to create leaders does not necessarily generate following, and both processes are necessary for a despotic decision. New insights into group decision making may therefore be acquired by an understanding of not only what incentives may be necessary for leaders to emerge but also why followers accept a leader's decisions, especially when this compromises their own activity [2]. In the latter case, one possibility is that long-term benefits derived from social or genetic ties with the leader outweigh the short-term costs associated with accepting the leader's current decision. This explanation is supported by recent research indicating that follower roles may be primarily associated with stable vertebrate social systems [20, 21] in which kin support one another during conflicts [22] and the cultivation and exploitation of social relationships with those who are not kin can also enhance fitness [23]. In this study, we ask (1) whether the acquisition of foraging benefits by a minority of individuals creates incentives for them to lead; (2) whether group-mates are willing to follow leaders despite large consensus costs; and (3) whether such follower behavior is mediated by social and/or genetic ties to the leader.

We used an experimental approach in wild chacma baboons to estimate the benefits to leaders and costs to followers for democratic and despotic decisions. Baboon groups are an ideal model system in which to explore such questions. Previous observations of baboon movement patterns suggest that their group decisions may be largely democratic in nature but also have the potential for active leadership by both male and

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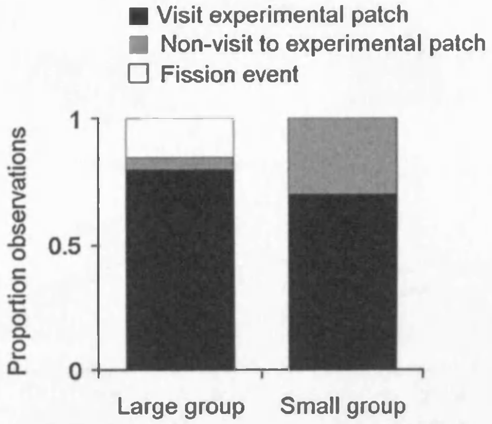

Figure 1. Group-Decision Outcomes

Two baboon groups (large, small) were presented with the opportunity to visit experimental food patches. These patches were designed to create benefits for a minority of individuals but costs for the majority. Group decisions that resulted in patch visits are shown in black, whereas nonvisits are shown in gray. Group fissions, in which groups did not reach a consensus but rather split, are shown in white.

female group members [19, 24–26]. Groups comprise a complex social system with a linear dominance hierarchy and are heterogeneous in composition. The dominance hierarchy also results in large asymmetries in resource-holding potential [14] and, thus, potentially high consensus costs from despotic foraging decisions in which dominant animals have incentives to lead. Furthermore, genetic and social ties among group members can influence individual behavior [22], providing fitness benefits [23].

Democratic or Despotic Group Decisions?

Two wild-baboon groups (one large, one small) were presented with an experimental food patch within their home range. This patch was of a size and shape predicted to create highly skewed foraging benefits among group members, relative to naturally occurring food resources. Thus, patches were expected to create consistent incentives for a minority of dominant individuals to lead and to result in consensus costs for the majority of followers. We therefore interpreted visits to experimental food patches as being the result of despotic decisions and visits to natural food patches as the result of democratic decisions.

We found that both baboon groups consistently visited the experimental food patch in preference to natural patches (Figure 1), indicating that despotic group decisions were the norm. The pattern of patch visits suggested that these decisions were made intentionally rather than opportunistically: at sunrise, the groups usually traveled directly from their sleeping sites to the patch (median travel time: 58 min). Groups then spent a large proportion of their normal foraging time at the patch location or, for those individuals who rarely entered the patch, at its periphery (mean ± SE: 83 ± 5 min). This is comparable to >30% of the baboons' normal daily foraging time. The groups normally visited the location just once on any given day during the experimental period (median visits/day = 1) and left the patch only after it was completely empty. Additionally, examination of group daily travel routes showed that the groups passed through the experimental food patch locations significantly more often when food was present ($\chi^2_1 = 6.13$, $p = 0.01$; **Figure S1**, available online).

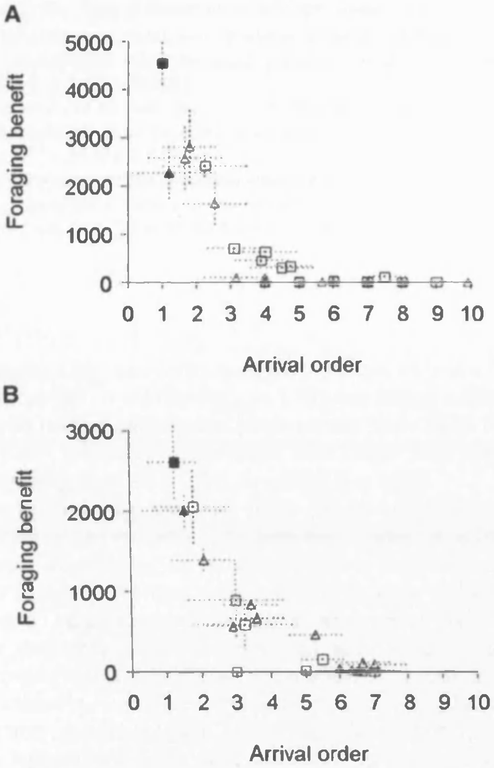

Figure 2. Leader Incentives and Identity

The mean ± SE foraging benefit attained in experimental patches, as a function of mean ± SE arrival order, for the large group (A) and the small group (B). Data for high-contest- and low-contest-competition treatments are shown in squares and triangles, respectively, and standard errors are depicted by dotted lines. The dominant male (filled symbols) usually arrived first and gained the highest foraging benefits, except in the large group during low-contest conditions, when his attempts to monopolize a larger area and chase off competitors resulted in a reduced intake rate. Indeed, the dominant male tended to acquire the highest foraging benefits in the high-contest-competition treatment, when food was more easily monopolized (t tests between treatments: $T_{large} = -2.25$, df = 30, $p = 0.04$; $T_{small} = -1.91$, df = 25, $p = 0.098$).

Leader Incentives and Follower Costs

During our experiments, we also varied the degree to which the experimental food patches could be monopolized. Patches were provided in two treatments: "low"- and "high"-contest competition. The low-contest treatment presented the same amount of food as the high-contest treatment but over twice the area. This design allowed us to investigate patterns of despotism in relation to different configurations of benefits to leaders and consensus costs to followers. The leader was defined as the animal that arrived first at the patch [21, 27], with others defined as followers.

In both treatment types, the dominant male was usually the first to arrive at the food patch (**Figure 2**). Dominant males, therefore, acted as leaders more frequently than expected by chance (Binomial tests: $p < 0.001$ for each group). Dominant males also tended to obtain more food in the high-contest patches than in the low-contest patches (**Figure 2**). Nevertheless, the incentives for leaders in the low-contest treatment were still sufficiently high to result in despotic decisions. Later arrivals at the patch acquired progressively less food in both treatments (**Figure 2**). We also found that the influence of social rank on arrival extended beyond the leader, producing a linear

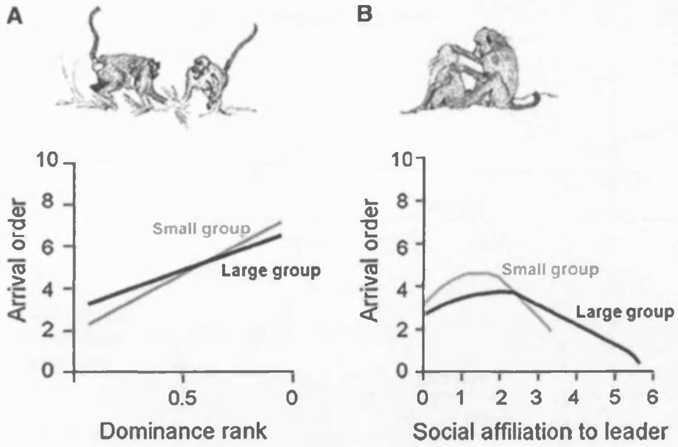

Figure 3. The Role of Dominance Rank and Social Affiliation

(A) High-ranked animals arrived earlier at experimental food patches than subordinates (GLMMs: small group, $\chi^2_1 = 32.9$, $p < 0.001$; large group, $\chi^2_1 = 2.9$, $p < 0.001$).

(B) The effect of an individual's social affiliation to the leader on that individual's arrival order (GLMMs: small group, $\chi^2_1 = 37.4$, $p < 0.001$; large group, $\chi^2_1 = 33.8$, $p < 0.001$).

The lines shown are the predicted effects from GLMMs controlling for all other significant effects and for repeated observations of individuals across days. See Table S1 for the full model results.

increase in arrival order with rank (Figure 3A). Previous research has indicated that under natural foraging conditions, leadership may be more evenly distributed across the group [28], a pattern also observed in this population (Figure S2), suggesting that the active leadership by the dominant male reported here was linked to his foraging benefits.

We then estimated the individual costs and gains of despotic decisions as the difference in consumption between natural and experimental conditions. Our analyses revealed that a minority of group members visiting the experimental patch obtained consensus gains, but the majority experienced substantial consensus costs (Figure 4). Moreover, these costs were more strongly skewed under conditions of high-contest competition than low-contest competition: the binomial skew index *B* [28] increased by 27%–76% between treatments in the large and small groups, respectively (Figure 4).

These findings indicate that a majority of subordinate individuals will accept despotic decisions, even where this compromises their own activity. This result is consistent for decision outcomes that differ in costs and for groups of different size and is coherent with high-ranking individuals having a particularly strong influence on the behavior of other group members [29, 30]. This influence was sufficiently strong to generate follower behavior in the absence of "herding" or any other forms of coercive behavior [31, 32].

Why Accept Despotism?

This leaves an important outstanding question: given that many followers experienced high consensus costs of following dominant-led group decisions, why follow? To answer this, we explored whether despotic group behavior could be explained by genetic and/or social ties to leaders (dominant males). We found that individuals with stronger social affiliation to the leader followed more closely. However, this was not a linear effect, since some individuals were close followers despite low affiliation (Figure 3B). These individuals were adult males who arrived closely behind the leader by virtue of their dominance rank rather than their social relationship. We found no effect of an individual's genetic relationship to the leader on follower behavior (Table S1). We also tested for a more complex "chain" effect, in which an individual's follower behavior is determined by the social or genetic relationship to the animal directly ahead of it rather than to the leader. Thus, we compared the strength of social affiliation and genetic relatedness between sequential pairs (dyads) in the arrival order with that of an average pair in the group. We found no differences for social affiliation (Wilcoxon tests across all trials: $W_{large} = 2967$, $n = 527$, $p = 0.68$; $W_{small} = 1721$, $n = 226$, $p = 0.99$) or for genetic relatedness in the large group ($W = 3860$, $n = 527$, $p = 0.10$), whereas relatedness was lower than average in the small group ($W = 1381$, $n = 226$, $p = 0.04$).

These findings suggest that close-follower behavior is more likely when social relationships between leaders and followers are strong. Therefore, we suggest that the long-term benefits derived from social ties with the leader may outweigh the short-term costs associated with accepting the leader's current decision. Close association with these individuals may provide females and their dependent offspring with direct fitness benefits, such as increased infant survival [33] and protection from predators [34]. Taken together with the preceding results, follower behavior appears to emerge as a combination of social rank and affiliation to the leader. In the first case, high-ranking animals most likely follow out of an interest in acquiring a share of the food in the patch (Figure 2), whereas in the second case, lower-ranked animals appear to follow primarily as a consequence of social affiliation (Figure 3B). The absence of a kinship effect on follower behavior might appear puzzling. However, in this case, the leader was most often the dominant male, who is an immigrant into the group and thus unrelated to other group members.

Group Fissions and Consensus Nonvisits

Occasionally, the groups did not collectively visit the experimental patch. Rather, the groups either fissioned into two subgroups of which only one visited the patch (n = 6/80) or remained cohesive but failed to visit the patch entirely (n = 14/80) (Figure 1). In both cases, there was no clear temporal pattern to suggest that subordinates were learning to resist costly despotic decisions (Figure S3), nor was there any spatial pattern suggesting that group members were less inclined to visit on those days when travel costs were higher (t tests comparing distances between sleeping site and patch when $n \geq 6$ cases: fission, $t_{large} = 1.03$, $df = 5$, $p = 0.35$; nonvisits, $t_{small} = 0.73$, $df = 13$, $p = 0.48$). Therefore, we must seek alternative explanations for group fission and nonvisits.

Fission events occurred in accordance with the foraging benefits derived from the experimental patches, i.e., the minority subgroup was comparable in size to the number of animals acquiring a net consensus gain (Figure S4). Given the importance of social relationships in mediating follower behavior, we predicted that the distribution of fission events, which were only observed in the large group (Figure S3), reflected variation between the two groups in the strength of social relationships connecting the leader and other group members. To test this prediction, we compared the daily time spent in social activity (grooming) in the two groups, together with the size of the leader's social networks (i.e., grooming-clique size [35]). We

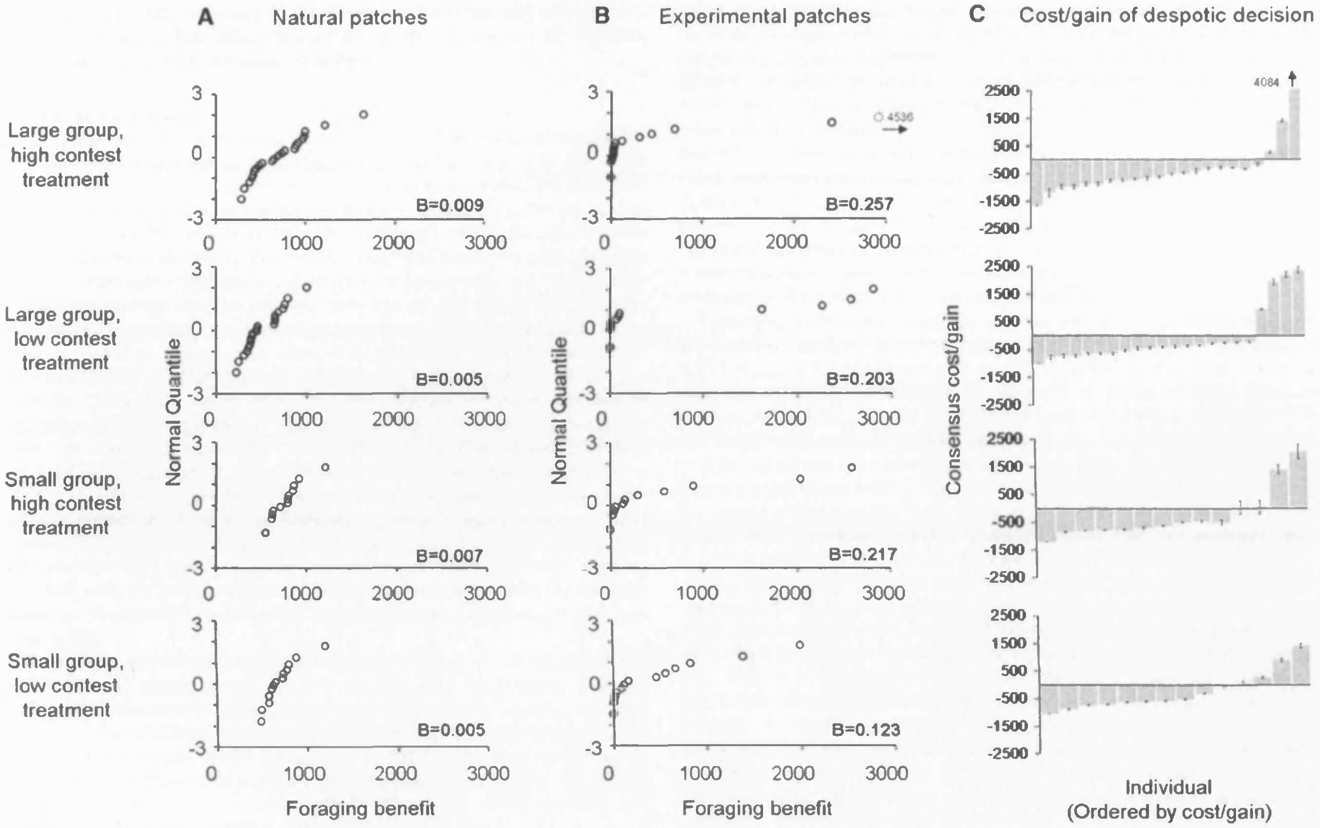

Figure 4. Foraging Benefits of Alternative Decisions and Consensus Costs of Despotism

Shown are normal quantile plots for the mean foraging benefits obtained by individual baboons belonging to the large and small group when at (A) natural and (B) experimental patches for comparable time periods, under two contest-competition treatments. Normal quantile plots are used to indicate skew from normality: where the distribution is normal, the points fall along a straight line. In addition, a binomial "*B*" skew index [28] is given, in which zero indicates a random distribution and higher values indicate increasing skew. The mean daily consensus cost or gain ± SE for decisions to visit experimental patches over natural patches (i.e., foraging benefits in experimental patch minus foraging benefits in natural patch) is also shown, in panel (C).

found that not only did individuals in the larger group spend less time grooming (Mann-Whitney tests: $W = 2226049$, $n_{large} = 1644$, $n_{small} = 1096$, $p = 0.05$), but a smaller proportion of individuals interacted socially with the leader (0.50 versus 0.33 of adult females in the small and large groups, respectively). Both results support the interpretation that strong social relationships between leaders and followers are necessary for the emergence of despotic group decisions. We also considered the possibility that fission was driven by higher consensus costs, but these results did not differ between groups (Mann-Whitney tests: "high" treatment, $n_{large} = 16$, $n_{small} = 11$, $W = 266$, $p = 0.83$; "low" treatment, $n_{large} = 16$, $n_{small} = 17$, $W = 248$, $p = 0.73$) **(Figure 4)**. Our findings are consistent with a wider pattern of time-budget stress in large groups that links reduced social time with a higher probability of fission [36].

Nonvisits are likely to reflect a different process. Specifically, in light of the preceding results, we anticipated that nonvisits might be associated with a switch in leader incentives. Consistent with our expectation, the dominant male was mate-guarding an oestrous female on the majority of nonvisiting days by the small group (9/12 cases; **Figure S3**), whereas he was never mate-guarding on the days that the group visited the patch (Fisher's exact test: $p < 0.001$). No mate-guarding was recorded in the large group, and non-visits were correspondingly rare (n = 2/40). During mate-guarding (consortship) in baboons, males follow females closely, so it is the female who guides and constrains her male partner's behavior [37]. Because this particular oestrous female was only midranking (4/10 within females, and 8/14 overall) and experienced a net consensus cost from patch visits, there was no incentive for her to lead the dominant male to the patch.

Conclusions

Our field experiments on wild baboons indicate that despotic group decisions can emerge when an individual has both a strong incentive to lead and sufficient social influence to elicit follower behavior. Follower behavior occurred despite consensus costs, but where social ties were weaker, group fission was more likely. The influential role of the leader was further highlighted by the observation that groups failed to visit the food patch when the leader's priorities changed. Our findings emphasize the importance of leader incentives and social relationships in group decision-making processes and the emergence of despotism.

Experimental Procedures

Study Site and Subjects

We conducted our study at Tsaobis Leopard Park, a wildlife reserve in the Karibib District of Namibia, Southern Africa (15° 45′E, 22° 23′S), with two groups of wild chacma baboons, *Papio ursinus* ($n_{large} = 60$; $n_{small} = 32$), that were habituated to direct observation at close range and were individually recognizable. Our study focuses on adults only (n_{large} = 22: 4 males, 18 females; n_{small} = 14: 4 males, 10 females).

Foraging Experiments

Each group was offered an experimental food patch placed at a single location within in its core home range (**Figure S5**). Patches were provided in two treatments: high-contest competition (20 days) and low-contest competition (20 days), both of which were of a size and shape that allowed access by only a minority (<50%) of baboons (although the high-contest patch excluded more individuals). The patch design was based on prior observation of the baboons' abilities to monopolize naturally occurring high-quality food patches. High-contest patches were 315 m^2 and 160 m^2 for large and small groups, respectively, equivalent to an available area of approximately 12.5 m^2 per adult baboon. Low-contest patches were increased by a factor of two, to 630 m^2 and 320 m^2, equivalent to approximately 25 m^2 per baboon. For each patch condition, the amount of food—dry maize kernels—presented remained constant per individual within groups, so that the large group received more than the small group, at approximately 80 g of maize per adult baboon in each case (each kernel was 0.39 ± 0.01 g). Low-contest patches followed high-contest patches, with an intervening period of at least 10 days during which no experiments were conducted. Consecutive experimental days started once the group had encountered the patch by chance. One experiment was run for each group, the first with the large group (6/15/06 to 8/5/06) and the second with the small group (8/24/06 to 10/15/06), during the same dry season [38] (see **Figure S3**).

Two observers followed the baboon groups on foot for full days throughout the study period, recording the group's daily route taken and any approach to the experimental food patches (taking group coordinates using handheld Garmin Etrex GPS units at 30 min intervals). Upon approach and entry into the patch, these observers recorded individual arrival order, bite rates, and time spent in patch for all baboons (see below). To identify any fission events and to corroborate arrival orders, a third observer was positioned at the food patches before sunrise each day.

Measuring Foraging Benefits

Foraging benefits for individuals during group visits to experimental food patches, defined as the number of kernels ingested per visit, were calculated from the time an individual spent in the experimental patch (rather than outside the patch) and his or her mean bite rate during this time (one kernel is consumed per bite). These data were obtained from patch scans and bite-rate observations, respectively. The patch scans recorded the number and identity of all individuals on the experimental patch at 5 min intervals. The bite-rate observations were 1 min focal watches, in which all hand-to-mouth consumptions of corn kernels were recorded, collected sequentially for all individuals in the patch. In total, 957 scans were completed: n_{large} = 553 (272, 281: scans for high-contest and low-contest patches, respectively) and n_{small} = 404 (138, 267). Similarly, n_{large} = 1036 bite-rate observations (601, 435 for high-contest and low-contest patches, respectively) and n_{small} = 331 (128, 203) were collected. Individually, each baboon appeared in 64 ± 1 scans and was sampled for 34 ± 1 bite-rate observations.

To measure the corresponding foraging benefits in natural food patches, one-hour focal watches on foraging adults were conducted during full-day follows. To control for any variation in foraging due to time of day, all individuals were sampled equally across both morning and afternoon observation periods. Focals were only begun once groups had been foraging for more than 20 min, to exclude periods of inactivity when resting, at waterholes, or at sleeping sites. During focals, all time spent feeding in patches (rather than traveling between patches) was recorded by continuous monitoring. Bite-rate observations were also made on individuals opportunistically during focal watches when visibility permitted. This allowed us to calculate the average food bites consumed per unit of time spent feeding in natural patches for each individual. This, in turn, allowed us to compare the number of bites obtained during feeding in the experimental patch versus the number of bites obtained over a comparable time period during feeding in natural patches: the consensus cost or gain. The natural foraging benefits corresponding to the high- and low-contest experimental patches were derived from a 20 day period preceding or following these patches, respectively (**Figure S3**). A mean ± SE of 15 ± 2 hr was recorded per individual, during which 25.5 ± 1.5 bite-rate observations were recorded. During these observations of natural foraging, the groups were never observed to fission.

Measures of Dominance, Social Affiliation, and Genetic Relationships

Dominance relationships were established on the basis of approach-avoid interactions (active supplants and displacements) between individuals. Dominance ranks were stable, so data were drawn from across the entire field season (May–December 2006) to provide a larger sample. These data were collected ad libitum (n_{large} = 1485, n_{small} = 1698 interactions), and their frequencies were recorded in actor-recipient matrices. Dominance hierarchies were then determined with Landau's linearity index (h) implemented in Matman [39], and linear hierarchies were found in both groups (h_{large} = 0.65, $p < 0.001$; h_{small} = 0.93, $p < 0.001$). All males outranked all females. Individual dominance ranks were then scaled by group size and assigned a value between 0 and 1, with 1 indicating the highest rank (i.e., dominant male) and 0 the lowest (i.e., most subordinate female).

Grooming is a standard measure of social affiliation in primates e.g., [40]. We used a matrix of grooming interactions collected ad libitum (n_{large} = 2,535, n_{small} = 1,727 interactions) over the course of the field season to calculate an index representing the strength of social affiliation between pairs of individuals (dyads). Because we were concerned with how evenly social contacts were distributed across dyads, our actor-recipient matrix was folded across the main diagonal and corresponding cells were summed to yield a triangular matrix. We then calculated the frequency of grooming for dyad *ij* divided by the mean frequency of grooming for all dyads in the group. High values of the index represent dyads that had stronger bonds than expected, and low values represent those with weaker bonds.

Variation in grooming time was calculated from scan data at 30 min intervals over the entire field season, excluding experimental periods (n_{large} = 1645 scans over 78 days, n_{small} = 1097 over 54 days). Scans began 30 min after the baboons left the sleeping site and ended at dusk at the sleeping site. Data on the proportion of baboons that were in view and engaged in five broad categories of activity were recorded: (1) traveling, (2) resting, (3) feeding, (4) grooming, and (5) drinking. Traveling was defined as brisk locomotion; feeding was defined as travel foraging (slow locomotion while searching for, manipulating, and ingesting food) and stationary foraging (searching for, manipulating, and ingesting food while remaining in one location); resting described the baboons' sedentary state in which they were not traveling or foraging and included sleeping; grooming involved affiliative allogrooming; and drinking referred to drinking from a waterhole.

Genetic relatedness between group members was derived from DNA analysis. We obtained DNA for adults in both groups from tissue (n = 35) and fecal (n = 1) samples as part of a wider investigation into relatedness in the Tsaobis baboon population (Cowlishaw et al., unpublished data). Individuals were genotyped at 17 microsatellite loci. See **Table S1** for more details on the analysis of these data.

Statistical Analysis

Simple bivariate relationships were tested with standard two-tailed parametric tests (or nonparametric tests when the data could not be normalized). Arrival orders were analyzed with generalized linear mixed models (GLMMs). We conducted one model for each group and explored the effects of individual dominance rank, as well as social affiliation and genetic relatedness to the individual who arrived first. We also tested for the overall effects of treatment (high-contest patch, low-contest patch) and sex (male, female) on arrival order. All two-way interactions were tested, but none were found to be significant. We incorporated "day" and "individual ID" as random effects in our models, in order to control for nonindependence of repeated observations of individuals over experimental days. Backward elimination was used in selecting the minimal adequate model and included only those factors that contributed significantly ($p < 0.05$) to the explanatory power. The significance of fixed terms is presented as Wald statistics evaluated against the Chi-square distribution. Full model results are presented in **Table S1**.

Supplemental Data

Supplemental Data include five figures and one table and can be found with this paper online at **http://www.current-biology.com/supplemental/S0960-9822(08)01417-6**.

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Supplemental Data

Dominance and Affiliation Mediate Despotism in a Social Primate

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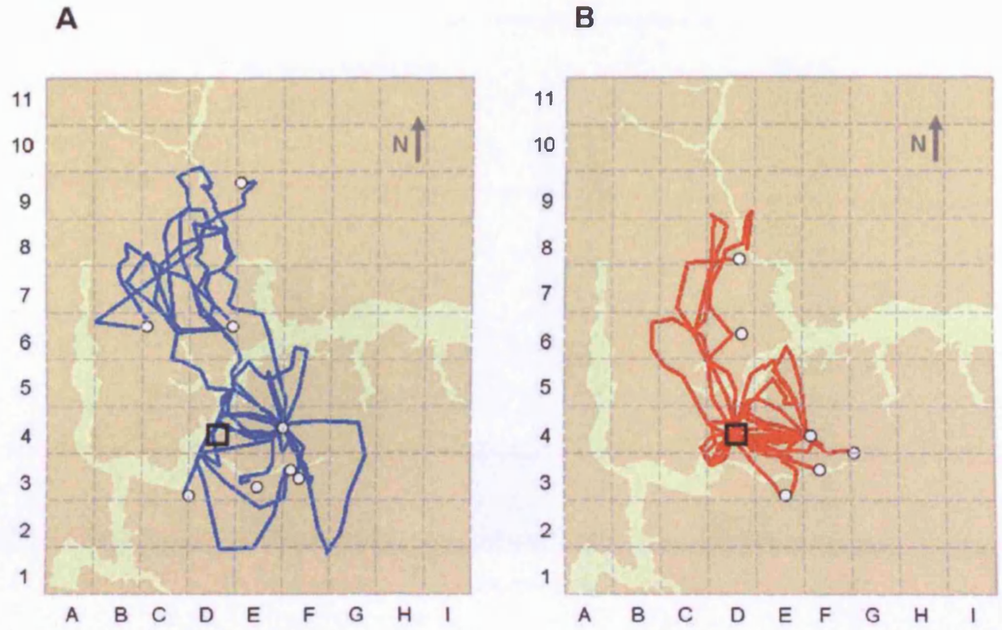

Figure S1. Baboon Group Travel Routes. An example of the daily travel routes for the large group when no food was presented, n=13 days (A), versus when food was presented experimentally as a 'high contest competition patch', n=16 days (B) at grid location D4 marked with a black square. (A) represents the time period shown in row 1 of Figure S3 and (B) represents row 2 of Figure S3. Days when the group fissioned (n=3), or did not visit the experimental patch (n=1) in (B) have been excluded. For an example of a travel route during group fission, see Figure S4. Sleeping site locations, where the group started and ended each day are shown by white-filled circles. Light shaded areas represent the (dry) Swakop River and its tributaries. Grid cells represent 1km by 1km.

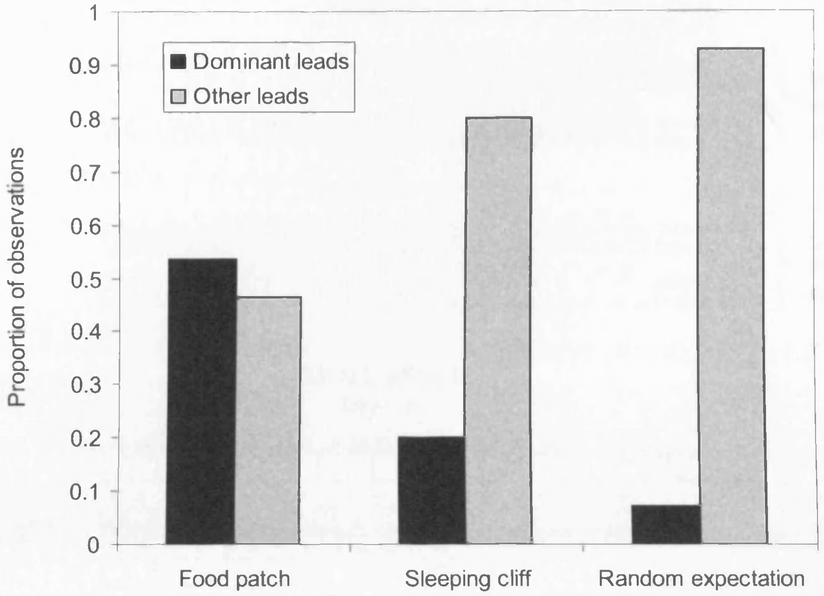

Figure S2. Patterns of Leadership. Proportion of cases where the dominant male or another individual leads the small group, under three conditions. In the first case, food patch data describe patterns of leadership during the experimental trials (n=28 patch visits). In the second case, sleeping cliff data describe patterns of leadership away from the sleeping cliff under natural foraging conditions (n=40 days: 27/06 – 26/11/2005). In this case, leaders were defined as those individuals who moved a distance of at least 20m beyond the periphery of the group, after/during which all adult group members departed from the sleeping site in the same direction [see also 1, 2, 3]. In the third case, the pattern of leadership is shown according to random expectation, i.e. given the number of adults in the group (n=14 adults). These patterns indicate that the frequency of leadership by the dominant male was higher during the experimental trials than under natural foraging conditions. Although the two may not be directly comparable, since different definitions of leadership are used in each case, a statistical comparison indicates a significant difference (X^2=8.29, df=1, P=0.004). The plot also shows that the dominant male was more likely to lead the group under both conditions than would be expected by chance (binomial tests: P<0.001). The finding that the dominant male also actively leads the group under natural foraging conditions (a pattern also recently reported in [3]) is consistent with the fact that he can monopolise natural food patches as well as experimental ones.

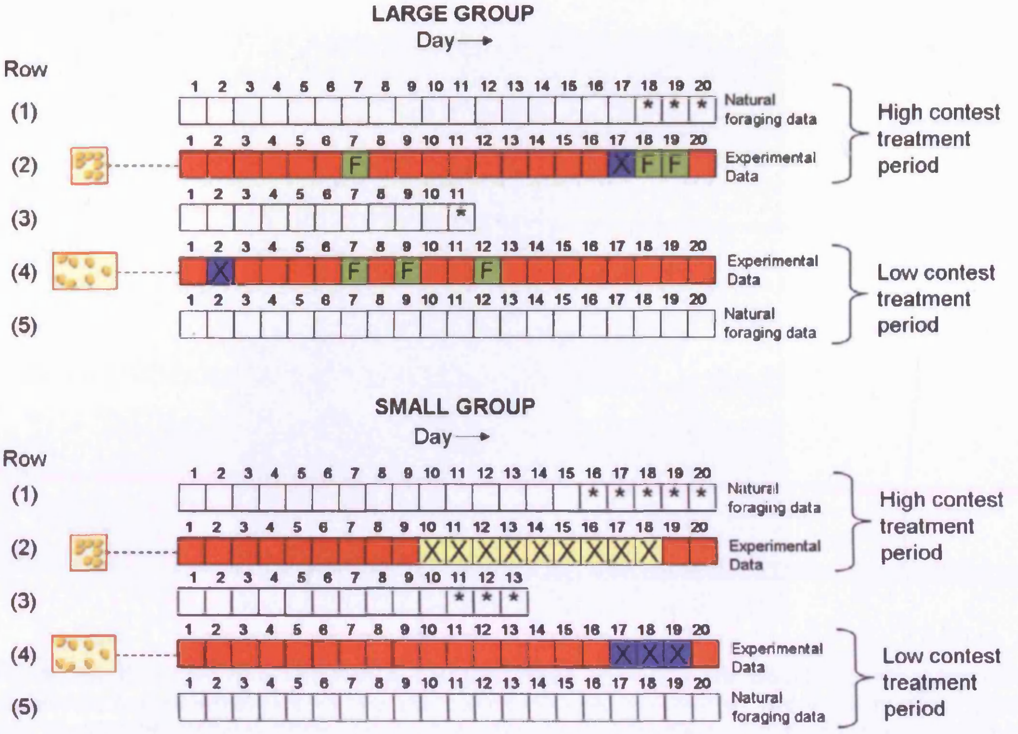

Figure S3. Summary of Decision Outcomes by Trial Number. Rows 1-5 show up to 20 consecutive days over five consecutive periods for the small and large study groups. Boxes in rows (1), (3) and (5) are natural foraging days. Data on natural foraging were collected during rows (1) and (5). The '*' boxes in rows (1) and (3) represent days on which the experimental food patch was introduced to the baboon groups but it was not found. Rows (2) and (4) show days during which the baboon groups had the opportunity to visit the high-contest patch and low-contest patch, respectively, once it had been located on day 1. The colours and contents of boxes indicate decision outcomes on that day. Red boxes are group visits to the patch; blue 'X' boxes are days on which groups did not visit but naturally foraged; yellow 'X' boxes are days during which groups did not visit when the dominant male was in a consortship; and green 'F' boxes are days during which the groups did not reach a consensus and fissioned.

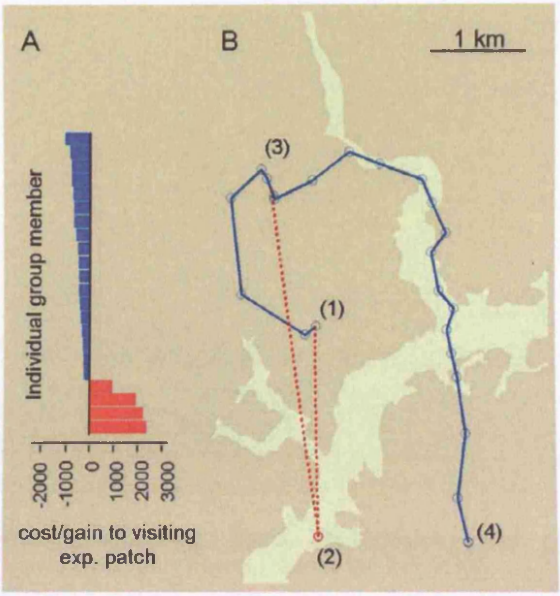

Figure S4. Example of a Temporary Fission Event. During group fission, a small subgroup visited the experimental patch while the majority foraged elsewhere. The minority group size was comparable to the number of animals acquiring a net consensus gain: mean ± SE = 3.8 ± 1.3. (A) shows the average consensus cost/gain of the decision to visit the experimental food patch for all group members during the treatment period (from Figure 4C in the main paper). (B) shows the group's travel route for a fission event observed on 21/06/06 (row 2, day 7 in Figure S3). At point (1) all group members are at their sleeping site (06:00). A minority of four group members (red line and corresponding red coloured bars) fission from the main group and travel directly to the experimental food patch (2), arriving at 06:21 and departing at 07:31. The remainder of the group (blue line) leave the sleeping site in a different direction, and are rejoined by the red subgroup at 08:15. The full group remain cohesive for the remainder of the day arriving at a different sleeping site at 16:30 (4). Light shaded areas represent the (dry) Swakop River and its tributaries. The blue travel route is based on GPS locations taken every 30 minutes (open circles). The red travel route shows the straight line travel distance between observations of the sub-group, i.e. observed at the sleeping site (observer 1), experimental patch (observer 2), and when rejoining the main group (observer 1).

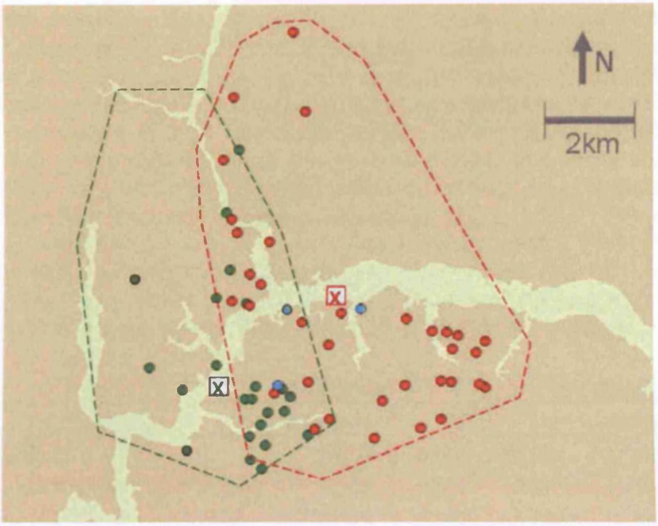

Figure S5. Home Range, Sleeping Sites, Waterholes, and Experimental Patch Locations. Minimum convex polygon home ranges for the 2006 study field season for the large (green) and small (red) study group are shown by dashed lines. Each group's sleeping sites are indicated by filled circles of the same colour. Waterholes are shown by blue filled circles. The small group used all three waterholes; the large group was seen to only use the most southerly waterhole. Experimental food patches are indicated by locations marked with an 'X'. Sites were chosen on the basis of comparable visibility, surrounding foraging opportunities, and proximity to key sleeping sites and water sources. Site locations also had to be outside the ranging area of the neighbouring group. Light shaded areas represent the (dry) Swakop River and its tributaries.

Table S1. Factors Affecting the Arrival Order of Baboons to the Experimental Food Patches. GLMM analysis with a normal error structure, controlling for repeated observations on individual focal animals across days (each entered as random effects) were conducted in MLwiN [4]. Table shows parameter estimates (Estimate), standard errors (SE) and associated *P* values, evaluated against a chi-squared distribution. Values for non-significant terms were obtained from fitting terms individually to the minimal model, and there were no significant two-way interactions. Genetic affiliation was measured using four common estimators of pairwise relatedness [5]: Wang [6], Queller & Goodnight [7], Lynch & Ritland [8], and Triadic identical by decent IBD [9]. All four were calculated in Coancestry v1.0. [10], and all were strongly correlated with one another (Spearman's r_s >0.70; n=36, *P*<0.001 in all cases). Each estimator was entered individually into the model, but all were found to have similar (non-significant) effects. The results for the Triadic IBD [9] estimator are presented here.

	Large group			*Small group*		
Effects	Estimate	SE	*P*	Estimate	SE	*P*
Dominance rank (scaled)	2.858	0.579	<0.001	3.488	0.608	<0.001
Social affiliation to leader (grooming index)	1.503	0.502	0.002	2.129	0.497	<0.001
Social affiliation to leader^2 (grooming index)	-0.319	0.088	<0.001	-0.753	0.153	<0.001
Genetic affiliation to leader (relatedness)	0.993	1.108	0.370	2.147	2.303	0.351
Treatment						
Low contest competition	0.000	0.000	-	0.000	0.000	-
High contest competition	-0.239	0.283	0.398	-0.342	0.241	0.157
Sex						
Male	0.000	0.000	-	0.000	0.000	-
Female	0.190	0.447	0.670	-0.825	0.503	0.101
Constant	3.553	0.236	-	2.844	0.370	-
Individual identity (random effect)	0.000	0.000	-	0.272	0.155	-
Day of experiment (random effect)	2.077	0.273	-	1.359	0.300	-

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