

**Social foraging behaviour in a varying  
environment**

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Cover photo: 'Ebola' – the best baboon, and therefore the best primate, and therefore the best animal in the world. (paraphrasing Andrew Cockburn; Photo credit: Hannah Peck)

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## **Declaration of Originality**

This thesis is result of my own work. Any contribution to this work by others is appropriately acknowledged.

Harry Marshall, September 2012.

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## Abstract

Social foraging behaviour has an important influence on individuals' survival and reproduction through its role in the acquisition of food resources. It also determines the amount of foraging time required in differing environments, and so the amount of time available for other activities, such as socialising and resting, which have been implicated in an individual's fitness, as well as the stability of the wider social group. In this thesis I explore the links between these two processes by investigating the drivers of social foraging behaviour, and how the foraging time budgets that this behaviour produces vary between environments. I do this using data collected from a wild population of chacma baboons (*Papio ursinus*) in Namibia, under both natural and field-experimental conditions, and through the development of an individual-based model (IBM). I show that baboon foraging decisions are influenced by social and non-social factors, but that the relative influence of these factors is dependent on the characteristics of the forager and the habitat it is in. These differences in decision-making appear to allow all individuals in a group to experience similar foraging success under natural conditions, but this pattern breaks down in extreme conditions. Using these findings to build an IBM of social foraging, I show that the time individuals need to spend foraging can increase rapidly in a deteriorating environment to the point where they are no longer able to gather enough resources. Overall, the findings of this thesis contribute to the growing appreciation that social foragers can exhibit a high degree of behavioural flexibility. These findings also emphasise the long-standing recognition that individual-level behaviours have an important influence on higher-level ecological patterns and processes and that an appreciation of this is important, not only for our understanding of these patterns and processes, but also for informing conservation and management.

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# Chapter 1

## Introduction

Behavioural ecology is a well-established field of research that investigates the ecological and evolutionary drivers of animal behaviour (Krebs & Davies 1997; Davies et al. 2012). As this field has progressed it has become increasingly apparent that these individual-level behaviours can have important influences on higher-level patterns, with implications for conservation (Sutherland 1996; Gosling & Sutherland 2000). This is particularly the case in social species where individual survival and reproduction are often highly dependent on the behaviour of other group members (Courchamp et al. 1999a,b; Krause & Ruxton 2002). For example, earlier work on shorebirds has shown how individual foraging behaviour and success could be used to predict variation in population densities (Goss-Custard et al. 1995a,b; Stillman et al. 2000; Pettifor et al. 2000). This work has subsequently been used to predict how populations will be affected by anthropogenic effects such as habitat loss or changes in its usage (Goss-Custard et al. 1995c,d; Stillman et al. 2003; Durell et al. 2005, 2006). Other studies have also shown how social animals' grouping patterns, and the behavioural synchrony and network of affiliations within these groups, can be predicted by individual behaviours (Conradt & Roper 2000; Ruckstuhl & Kokko 2002; Rands et al. 2003; Ramos-Fernández et al. 2006; Sueur et al. 2010b). However, despite these studies, the understanding of how individual-level behaviours scale up to higher-level patterns and processes still remains relatively limited (Stillman & Goss-Custard 2010; Evans 2012).

Many studies of how individual-level behaviour influences higher-level patterns have focussed on individuals' foraging behaviour as it is intrinsically linked to their survival and reproduction. Foraging behaviour is strongly influenced by individual decisions about where to feed

and what to feed on (Stephens & Krebs 1986; Stephens et al. 2007). An understanding of the how these decisions are made is, therefore, an important step in the appreciation of how foraging behaviour influences higher-level ecological patterns. This is particularly the case in social species where individuals' foraging decisions will not only be influenced by the characteristics of the surrounding habitat and forager's own traits (as in solitary species), but also by the traits and behaviour of other group members (Giraldeau & Caraco 2000; Waite & Field 2007). Consequently, there has been a considerable amount of theoretical work exploring how foragers (social and solitary) should make these decisions (reviewed in Giraldeau & Caraco 2000; Stephens et al. 2007; Giraldeau & Dubois 2008; Hamilton 2010). These theoretical studies have been complemented by empirical work testing their predictions (see reviews in Chapter 2 and Nonacs 2001; Valone 2006; Stephens et al. 2007; Giraldeau & Dubois 2008). However, in comparison to the wealth of theoretical work, empirical tests remain relatively limited, meaning there is still considerable debate about how individuals make foraging decisions.

These foraging decisions will determine the amount of time an animal needs to devote to foraging to gather enough resources, and so the time remaining for other activities. In social species this remaining time is particularly important as these other activities include socialising (Dunbar 1992; Pollard & Blumstein 2008; Dunbar et al. 2009). Limitations to this social time can restrict the strength and quality of the social bonds that an individual can maintain with other group members (Lehmann et al. 2007), and so have negative effects on that individual's fitness (Silk et al. 2003; Silk 2007a; Cameron et al. 2009; Barocas et al. 2011). If social time is limited not just for particular individuals but across groups, it can also have a significant impact on group size (Dunbar 1992; Pollard & Blumstein 2008; Dunbar et al. 2009) and habitat use (Korstjens et al. 2010), with further implications for how local populations are affected by climate change (Lehmann et al. 2010). Understanding the mechanics of how these time budget patterns emerge from individuals' decisions

is, important, therefore, not only in our understanding of how social species interact with their environment, but also in our ability to predict how they are likely to be affected by future environmental change.

## **Thesis Aims and Structure**

In this thesis I aim to address these gaps in our knowledge by addressing two overarching research questions:

- What are the drivers of social foraging decisions and success, and how do these drivers vary between individual foragers and habitats?
- How do these social foraging behaviours influence the amount of time an individual needs to spend foraging in different habitats?

I do this using a wild chacma baboon (*Papio ursinus*) population as a model system. Throughout, however, I endeavour to focus on the general implications of each chapter's findings for our wider understanding of social foraging behaviour across species and systems, especially keeping in mind the implications for social species' conservation and management. These chapters are written as separate review or research papers (except for Chapters 3 and 8) and are structured as follows.

*Chapter 2* provides a more comprehensive review of the literature concerning the issues touched on in this brief introductory chapter. It explores the current understanding of the drivers of social foraging behaviour, and individual- and group-level time budgets. It highlights the limited understanding of the mechanistic links between these two areas, reviewing the previous studies that



have attempted to explore these links. It then argues that individual-based modelling may provide a powerful approach to tackling this problem (as used in Chapter 7).

*Chapter 3* introduces the study system in more detail, including background information about the study species and a description of the study site (The Tsaobis Baboon Project, Namibia). It then provides an overview of the general data collection methods used in the next four data chapters.

*Chapter 4* explores the determinants of foragers' decisions about which food patch to feed in. It employs discrete choice analysis, a relatively novel technique to behavioural ecology, and shows how this technique can be used to explore the effects of multiple social and non-social factors on foraging decisions. It then investigates how the relative importance of these different factors varies depending on both the habitat the decision is made in and the characteristics of the individual making the decision.

*Chapter 5* tests theoretical predictions about how foragers decide when to leave a food patch. In particular it tests hypotheses that foragers use fixed rules against hypotheses that they use more flexible rules informed by their recent foraging experiences. The support for these hypotheses is compared in data collected under natural conditions and during a field experiment.

*Chapter 6* investigates the drivers of foraging aggression and foraging success. In particular it investigates suggestions that the effects of individual social traits, such as rank, social bonds and kinship, on foraging behaviour may be dependent on local environmental conditions. It does this by comparing the effect of these social traits on the rates of aggression and foraging success an individual experiences in natural and field-experimental conditions.

*Chapter 7* uses the findings from Chapters 4, 5 and 6 to build an individual-based model of social foraging behaviour, predicting the proportion of time an individual must spend foraging in a given environment. This model is validated by comparing its predictions against observed variation in foraging time budgets under known environmental conditions. Following model validation, the model predictions are then explored over a wider range of environmental conditions.

*Chapter 8* highlights common themes in the previous chapters' findings and discusses their overarching implications for improving our understanding of social foraging systems. It also considers how this improved understanding might have implications for social species' conservation and management.

## Chapter 2

# Linking social foraging behaviour with individual time budgets and emergent group-level phenomena

A version of this chapter has been published as:

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### Abstract

A social group's time budget is an emergent property of individual-level decisions about how to allocate time. One fundamental determinant of these time allocation decisions is foraging success. Yet while there is a growing appreciation of how social animals optimise their foraging behaviour, our understanding of the mechanisms that link this behaviour with individual time use, and thus group-level time budgets, is relatively poor. In this review chapter, I explore the current understanding of social foraging behaviour and time budgets at the individual level and emergent group-level time budgets. I highlight how research into individual-level differences in time budgets is comparably limited. I then explore how individual-based mechanistic modelling may provide a useful tool for elucidating how social foraging behaviour drives individual time budget patterns, and how these patterns in turn give rise to group-level time budgets. An improved understanding of the links between these three phenomena will not only allow us to address more challenging

evolutionary questions, but also enable us to better predict and manage the impacts of a changing environment on social animals in the future.

## **Introduction**

How individuals allocate time to different activities can provide valuable insights into how animals trade-off different fitness-enhancing behaviours. In social groups, individuals not only need to allocate enough time to successfully gather resources and reproduce, but also to successfully manage their relationships with other group members (Dunbar et al. 2009). Our understanding of how they do this comes from three related areas of behavioural research: social foraging behaviour and time budgets at the individual-level, and emergent patterns in group-level time budgets. Social foraging behaviour, where individuals' foraging decisions and payoffs can influence and be influenced by the foraging behaviour of others, can vary considerably as a consequence of individual traits, the social environment and the underlying physical environment (Giraldeau & Caraco 2000; Krause & Ruxton 2002; Waite & Field 2007; Giraldeau & Dubois 2008). Time budgets describe the amount of time devoted to feeding, travelling, resting and socialising, with other activities considered negligible (Pollard & Blumstein 2008; Dunbar et al. 2009). Research into individual-level time budgets has tended to focus on how the time each individual allocates to these different activities varies with traits such as sex or social rank (Ruckstuhl 2007; Hamel & Cote 2008; Main 2008). In contrast, research into group-level time budgets has tended to focus on how the amount of time a group allocates to these activities (i.e. the emergent property of individual time budgets) varies with physical and social factors such as food availability and group size (Dunbar et al. 2009; Grove 2012). However, despite substantial recent advances in these fields – especially in

individual-level foraging behaviour and group-level time budgets – there is surprisingly little understanding of the mechanisms that link them together.

In this review chapter, I argue that the elucidation of these mechanisms is a priority, in particular the mechanisms by which variation in social foraging behaviour drives individual-level time budget differences. There is a growing appreciation that to study group-level patterns of behaviour it is necessary to understand how these emerge from individual-level behaviours (Conradt & Roper 2000; King et al. 2008; Lihoreau et al. 2010; Petit & Bon 2010). A classic example of this is in social insects where colony- (or group-) level phenomena such as social networks (Fewell 2003; Naug 2009) and collective foraging (Sumpter & Pratt 2003; Lihoreau et al. 2010) and decision-making (Passino et al. 2007; Marshall & Franks 2009) are the product of the behaviours of each individual colony member. It follows, therefore, that to study group-level time budgets it is necessary to understand how each group member decides how to allocate their time. These individual-level decisions will be strongly influenced by social foraging success, and so individual-level time budgets clearly play a critical mediating role between social foraging behaviour and group-level time budgets. To date, the determinants and consequences of individual time budgets have received relatively little attention, although individual-level differences in time budgets have been implicated in group-level cohesion and behavioural synchrony, which play an important role in the functioning of social groups and so the performance of the individuals within it (Conradt & Roper 2000; Ruckstuhl 2007; Main 2008; Sueur et al. 2011a). Furthermore, a greater understanding of individual-level time budgets will provide insight into group-level time budgets, which have themselves been implicated in constraining the group's size (Dunbar 1992; Korstjens et al. 2006; Pollard & Blumstein 2008) and, through the requirements of minimum group size for population viability, species' geographic ranges (Dunbar 1998b; Lehmann et al. 2006, 2010; Korstjens et al. 2010).

Here, I synthesise the current understanding each of these three research areas and explore the relevant work in each which has started to investigate the mechanistic links between them. Finally, I discuss how future research might work towards a better understanding of these links, in particular by making better use of individual-based mechanistic modelling techniques.

## **Individual-Level Social Foraging Behaviour**

The amount of time an individual needs to forage to meet its daily nutritional requirements is a key component of its time budget, as it will determine the amount of time it has left to devote to other activities such as resting and socialising (Dunbar et al. 2009). An understanding of an individual's social foraging behaviour, therefore, plays an important role in the understanding of its time allocation decisions. In the last two decades research into social foraging behaviour has been particularly active (Giraldeau & Caraco 2000; Waite & Field 2007; Giraldeau & Dubois 2008) and has revealed how this behaviour is influenced by a broad range of factors. In this section I review these factors, grouped under three broad headings: the ecological environment, e.g. food distribution and quality; the individual characteristics of the forager, e.g. age and sex; and the social environment, e.g. the number and relatedness of co-foragers in the group.

### Ecological Environment

A habitat's food distribution plays a key role in determining decisions made by foragers, such as which patch to exploit and when they leave a patch in search of another (Giraldeau & Caraco 2000; Nonacs 2001; Waite & Field 2007; Giraldeau & Dubois 2008; Hamilton 2010). Recent empirical studies of the influence of food distribution on social foraging have tended to be

confined to group-foraging birds. They do, however, broadly support theoretical predictions that foragers should (1) consider the underlying patch qualities and co-forager characteristics and distribute themselves across patches to maximise individual benefits (e.g. shorebirds, Folmer et al. 2010; the ideal-free distribution, Fretwell & Lucas 1969, reviewed in Waite & Field 2007; Hamilton 2010) and (2) leave patches earlier in higher quality habitats (e.g. common cranes, *Grus grus*, Alonso et al. 1995; red knots, *Calidris canutus*, van Gils et al. 2003; the marginal value theorem, Charnov 1976, reviewed in Nonacs 2001). A habitat's food distribution can also influence the type of feeding competition experienced within social groups. Increased levels of feeding aggression, that is contest (or interference) competition rather than scramble (or depletion) competition, have been shown in habitats with increased patch quality (Wrangham 1980; Hamilton 2002; Stillman et al. 2002), defensibility (Van Schaik 1989; Isbell 1991; Sterck et al. 1997) and clumping (i.e. resources concentrated in fewer patches) (Vahl et al. 2005; Tanner et al. 2011; Tanner & Jackson 2012).

It has also become increasingly apparent that the information a forager possesses about its environment, and whether it collects this by directly searching the environment or by monitoring the behaviour of others, plays an important role in social foraging behaviour (Valone & Templeton 2002; Danchin et al. 2004; Dall et al. 2005). The availability of these two sources of information, and a forager's ability to monitor them both simultaneously, can be determined by a habitat's physical structure (Templeton & Giraldeau 1995; Coolen et al. 2001). For example, where habitat characteristics restrict visibility, and so the distance over which individuals can search for their own foraging opportunities, they may more readily exploit the food discoveries of others (capuchin monkeys, *Cebus apella*, Di Bitetti & Janson 2001; Ruxton et al. 2005; bison, *Bison bison*, Fortin & Fortin 2009). The importance of these two sources of information and whether they can be collected simultaneously is recognised by producer-scrounger (P-S) and information sharing (I-S) models of

social foraging behaviour (Giraldeau & Beauchamp 1999; Giraldeau & Caraco 2000; Ruxton et al. 2005; Beauchamp 2008b). Both describe how, in a group of foragers, an individual can either search for food themselves or monitor others and exploit their discoveries. They are differentiated by whether or not they treat these behaviours as compatible, as in I-S models, or incompatible (i.e. an individual must do one or the other, produce or scrounge, at any one time) as in P-S models. Empirically, P-S models appear to have received more direct support (spice finches, *Lonchura punctulata*, Mottley & Giraldeau 2000; zebra finches, *Taeniopygia guttata*, Mathot & Giraldeau 2010a), although searching and monitoring can be compatible under some circumstances (violating P-S assumptions). For instance, the ability of starlings (*Sturnis vulgaris*) to assess patch quality was enhanced when the environment allowed them to concurrently feed and monitor others more easily (Templeton & Giraldeau 1995). Similarly, food type can also affect foragers' abilities to collect information by determining whether they can handle a food item and simultaneously scan for other foraging opportunities (samango monkeys, *Cercopithecus mitis erythrarchus*, Cowlshaw et al. 2004), as well as directly influencing foraging success by determining the handling time required per food item (European blackbirds, *Turdus merula*, Cresswell et al. 2001; roe deer, *Capreolus capreolus*, Illius et al. 2002; grass-cutting ants, *Acromyrmex heyeri*, Bollazzi & Roces 2011) and its nutritional benefit (baboons, *Papio* spp., Whiten et al. 1991; spider monkeys, *Ateles chamek*, Felton et al. 2009).

Social foraging behaviour can also be influenced by a habitat's predation risk, with increased risk leading to greater individual vigilance requirements (Brown 1999) and foraging group sizes, resulting in increased feeding competition (Barton et al. 1996; Barton 2000). Furthermore, high predation risk can inhibit or reduce foragers' use of a habitat altogether. Studies on chacma baboons (*Papio ursinus*), bison (*Bison bison*) and vervet monkeys (*Cercopithecus aethiops*) have shown that groups will trade-off habitat quality with predation risk, often resulting in



them using habitats which are not the most resource rich (Cowlshaw 1997; Fortin & Fortin 2009; Willems & Hill 2009).

### Individual Traits

The importance of individual characteristics such as age, sex and morphology is widely recognised by ecologists (Bolnick et al. 2003) and can have important implications for foraging behaviour where these differences result in variation in individual energy requirements, e.g. sexual dimorphism (Key & Ross 1999; Isaac 2005). Larger individuals, e.g. males, may have greater energy requirements but also slower metabolisms (Key & Ross 1999; Ruckstuhl & Neuhaus 2002; Bowyer 2004) and so may forage on lower-quality but more plentiful food types (reviewed in Ruckstuhl & Neuhaus 2002; Ruckstuhl 2007; Main 2008) and/or have lower intake rates (Ruckstuhl et al. 2003). Similarly, female bighorn sheep (*Ovis canadensis*) may compensate for the greater energy requirements of lactation with higher intake rates (Ruckstuhl & Festa-Bianchet 1998; Ruckstuhl et al. 2003). Body size differences can also simply restrict the habitats accessible to individuals. For example, larger male green woodhoopoes (*Phoeniculus purpureus*) forage more on thicker branches than the smaller females (Radford & Du Plessis 2003). In the case of individual age differences, older animals may forage more successfully due to experience. This can also benefit other group members, such as in the case of African elephant (*Loxodonta africanus*) groups led by older matriarchs who have more accurate knowledge of their environment (McComb et al. 2001).

Individual characteristics can also influence a forager's spatial position within a group, and so its foraging behaviour. In general, as an individual moves towards the centre and away from the leading edge of a foraging group they experience greater feeding competition but also reduced

predation risk (Hirsch 2007; Morrell & Romey 2008). An individual's position on this competition-predation gradient tends to be determined by their competitive ability. In species such as ring-tailed coatis (*Nasua nasua*) and forest buffalo (*Syncerus caffer nanus*) adult males tend to occupy central positions whilst juveniles tend to be on the periphery (Melletti et al. 2010; Hirsch 2011). However, in species with more complex intra-group social structures, competitive ability, and so spatial position, tends to be determined by factors such as rank (chacma baboons, *Papio ursinus*, Cowlshaw 1999; capuchin monkeys, Di Bitetti & Janson 2001; see "Social Environment" below).

Our understanding of the influence of individual characteristics on social foraging is still incomplete. In many cases individual variation in foraging behaviour has been identified but without a particular cause or correlate (e.g. European blackbirds, Cresswell et al. 2001; capuchin monkeys, Di Bitetti & Janson 2001). It is likely that further research into the influence of individual characteristics such as age, sex and morphology, and especially into more recently identified sources of individual variation such as information use (Galef & Giraldeau 2001; Danchin et al. 2004; Dall et al. 2005) and personality (Dall et al. 2004; Réale et al. 2007), will prove fruitful. Empirical studies of these latter sources of variation are relatively recent but growing rapidly in number. For instance, personality has been shown to effect foraging behaviour in fallow deer (*Dama dama*, Bergvall et al. 2010) and both foraging behaviour and social information use in barnacle geese (*Branta leucopsis*, Kurvers et al. 2010a,b, 2011).

Individual variation in social foraging behaviour, particularly when linked to differences in individual energy requirements, are likely to result in differences in energy reserves, which in turn are predicted to feedback on social foraging tactics (Barta & Giraldeau 2000; Rands et al. 2003; Morrell & Romey 2008; Mayack & Naug 2011). Barta & Giraldeau's (2000) risk-sensitive producer-scrounger model predicts that individuals should scrounge (exploit others' food

discoveries) more when they have lower energy reserves. This prediction has been empirically validated (house sparrows, *Passer domesticus*, Lendvai et al. 2004; zebra finches, Mathot & Giraldeau 2010b) but validation of other energetic models has proven more difficult due to the technical challenges associated with directly and non-invasively measuring energy reserves. New techniques, such as urinary C-peptide analysis (Higham et al. 2011), may allow empirical tests of such models in the future.

### Social Environment

A social forager's behaviour is strongly affected by the number of other individuals in the foraging group, especially as individual foraging reward is classically seen as having a humped relationship with group size (Krause & Ruxton 2002; Waite & Field 2007; Earley & Dugatkin 2010). In this relationship the benefits of grouping initially increase faster than the costs. These benefits include the dilution of predation risk, reduced individual vigilance and/or an increased ability to detect predators (Lima 1995; Roberts 1996; Beauchamp & Livoreil 1997; Quinn & Cresswell 2004; Beauchamp 2008a; Ward et al. 2011; Finkbeiner et al. 2012), as well as increased information about the location and quality of food resources (Valone & Templeton 2002; King & Cowlshaw 2007; Rieucou & Giraldeau 2011) and a greater ability to defend these resources (Rasmussen et al. 2008). However, past a threshold group size the benefits of grouping are exceeded by the costs – mainly feeding competition (Moody & Houston 1995; Stillman et al. 1996; Folmer et al. 2010; Rutten et al. 2010) – and the overall benefits of grouping, such as foraging reward, declines.

An individual's social position and relationship with other group members are also influential determinants of social foraging behaviour. Social groups commonly contain dominance

hierarchies, the presence and strength of which are thought to indicate the balance of scramble and contest competition both within and between groups, particularly in primates (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997). Where contest competition is high, dominance ranks are likely to be strongly linear, with higher ranked individuals experiencing greater foraging success (Milinski & Parker 1991; Barrett et al. 2002). Dominant individuals often have a greater ability to monopolise better feeding sites (red-spotted masu salmon, *Oncorhynchus masou ishikawai*, Nakano 1995; Hamilton 2002), steal food from (kleptoparasitise) subordinates (capuchin monkeys, Di Bitetti & Janson 2001; pigs, *Sus scrofa*, Held et al. 2010) and occupy more central spatial positions in the group where, although foraging competition is more intense, the opportunities to exploit others' food discoveries are greatest (Di Bitetti & Janson 2001; ring-tailed coatis, Hirsch 2011).

Many social groups are also characterised by high levels of relatedness. Consistent with kin selection, aggression levels between closely related foragers tend to be lower (Siberian jays, *Perisoreus infaustus*, Sklepkovych 1997; Northwestern crows, *Corvus caurinus*, Ha et al. 2003). However, while kinship may result in reduced aggression, its effect on the exploitation of co-foragers' discoveries are less clear. For example, social foragers may exploit the foraging discoveries of close kin more often (Ha et al. 2003; Mathot & Giraldeau 2010a), in apparent contradiction to kin selection theory. In a recent modelling study, Mathot & Giraldeau (2010a) found that this behaviour could arise in a producer-scrounger system through the inclusive fitness benefits of being scrounged from by kin rather than non-kin. However, while this effect was supported in groups of zebra finches (*Taeniopygia guttata*) that were either related or unrelated, other studies have failed to find this pattern (Mexican jays, *Aphelocoma ultramarina*, McCormack et al. 2007; chacma baboons, King et al. 2009, 2011) or found the opposite (house sparrows, Tóth et al. 2009). Natural foraging groups usually include individuals with varying levels of relatedness, rather than being all kin or non-kin as in Mathot and Giraldeau's (2010a) study. The effect of

kinship on the exploitation of co-foragers' food discoveries may, therefore, be dependent on the level of intragroup relatedness.

Individuals in groups can also form affiliative, or social, bonds with other group members (reviewed by Silk 2007a,b). The function of these bonds is still debated, but there is growing evidence that, in the short-term, they can be used to negotiate tolerance from co-foragers (Barrett et al. 1999; King et al. 2009, 2011; Fruteau et al. 2009; Tiddi et al. 2011). One suggested mechanism for this is through a biological market (Noë & Hammerstein 1995), with several recent studies showing that foragers can trade their contribution to social bonds for tolerance at feeding sites (chacma baboons, Barrett et al. 1999; vervet monkeys, Fruteau et al. 2009; capuchin monkeys, Tiddi et al. 2011). There is, however, alternative evidence from studies on baboons that the primary proximate function of social bonds is not the short-term negotiation of services or resources, but rather longer-term benefits they provide through social support (Cheney et al. 2010) and stress relief (Crockford et al. 2008). Since most group members form social bonds with multiple social partners, this gives rise to social networks (reviewed in Fewell 2003; Croft et al. 2008). Social networks are often characterised as containing clusters of long-term and strongly bonded individuals, often kin (guppies, *Poecilia reticulata*, Croft et al. 2004; social wasps, *Ropalidia marginata*, Naug 2009; spider monkeys, *Ateles geoffroyi*, Ramos-Fernández et al. 2009; chacma baboons, Silk et al. 2010b), with bonds between individuals from different clusters being ephemeral and dependent on ecological conditions (African elephants, Wittemyer et al. 2007; chacma baboons, Henzi et al. 2009). This seems to suggest that the longer-term function of social bonds, such as stress-relief, could be fulfilled by these strongly-bonded clusters, whilst the ephemeral bonds could fulfil shorter-term functions, such as the negotiation of foraging tolerance. Studies of the influence of social bonds on foraging behaviour have, however, mainly focussed on primate systems (but see Beauchamp 2000b; Carter et al. 2009 for examples in zebra finches and eastern grey kangaroos,

*Macropus giganteus*). Future work might explore whether these effects are also found in non-primate systems.

## **Time Budgets**

The underlying environment clearly has a strong influence on social foraging behaviour and success (see ‘Individual-Level Social Foraging Behaviour’ above). A poor environment can require animals to devote more time to foraging to meet their daily requirements, in response to both reduced food availability and quality (Isbell & Young 1993; Doran 1997; Hill & Dunbar 2002; Alberts et al. 2005; Hamel & Côté 2008; Dunbar et al. 2009), and to the thermoregulatory demands of harsher climates (Dunbar 1992; Bronikowski & Altmann 1996; Hill & Dunbar 2002; Dunbar et al. 2009). Variation in these foraging demands, and decisions about how to reallocate time to meet these demands, act at the level of the individual forager. Despite this, studies investigating variation in time budgets at the individual level are relatively few compared to those that have investigated such changes at the group level. This seems an oversight, since it is clear that individual-level time budgets play a key mediating role in translating variation in foraging success into changes in group-level time budgets. A better understanding, therefore, of the drivers of individual time budgets appears to be needed, especially since individual and group-level time budgets have been implicated not only in the cohesion and function of social groups (Dunbar 1992; Conradt & Roper 2000; Pollard & Blumstein 2008; Asensio et al. 2009; Lehmann & Dunbar 2009; Sueur et al. 2011b), but also in the emergence of broader macroecological patterns such as species geographic ranges (Korstjens et al. 2010; Lehmann et al. 2010).

### Individual-Level Time Budgets

Sexual dimorphism in ungulates is one of the few instances where individual differences in time budgets have been comprehensively investigated. Males' larger body size means they have a slower metabolism and larger rumen and so have lower nutritional requirements per unit body mass and longer, more efficient rumination bouts (Ruckstuhl 1998; Ruckstuhl & Neuhaus 2002; Bowyer 2004). These physical differences have been cited, in numerous cases, as the reason why females spend more time feeding and less time resting (and ruminating) than males (Ruckstuhl 1998; Neuhaus & Ruckstuhl 2002; Ruckstuhl & Neuhaus 2002; Pelletier & Festa-Bianchet 2004). Other studies, however, have failed to find this effect (Shi et al. 2003; Hamel & Côté 2008; Shannon et al. 2008) or found the opposite (du Toit & Yetman 2005; reviewed in Ruckstuhl 2007). Similarly, relatively higher energy requirements may also explain the increased travel times or distances recorded in female ungulates (Neuhaus & Ruckstuhl 2002) or smaller-bodied ungulate species (Du Toit & Yetman 2005). Again, though, other studies have failed to find this pattern (Pelletier & Festa-Bianchet 2004; Shannon et al. 2008). It now appears that the differences between ungulate sexes' activity budgets can be due to differences not only in energy requirements, but also in predation risk (Ruckstuhl 1998; Pépin et al. 2009) and reproductive strategies (see Bowyer 2004, Ruckstuhl 2007 and Main 2008 for reviews of these hypotheses). Furthermore, these patterns may be climate dependent since, in tropical ungulates, larger individuals/species have been found to spend more time feeding (rather than less, as above). This may be due to daily fluctuations in temperature having less of an influence on these individuals/species, allowing them to be more active during the hotter part of the day, when most observations are made, rather than during the cooler night (Mysterud 1998; du Toit & Yetman 2005).

The influence of sexual dimorphism on individual energy requirements has also been recognised in other species (Key & Ross 1999; Isaac 2005; Scantlebury et al. 2006), although its influence on individual time budgets is less clear. For example, in some primate species, similar to the ungulate pattern above, males have been shown to spend less time feeding and/or more time resting (Prates & Bicca-Marques 2008; Masi et al. 2009; Shanee & Shanee 2011) but in others no difference was found (Isbell & Young 1993). Similarly, whilst there is evidence that males travel for less time or over shorter distances in some species (Eurasian badgers, *Meles meles*, Revilla & Palomares 2002; Western lowland gorillas, *Gorilla gorilla gorilla*, Masi et al. 2009) the opposite is true in others (Alberts et al. 1996; Ramos-Fernández et al. 2004; Sueur et al. 2011a). Further differences in individual energy requirements can also lead to individual differences in time budgets. Older individuals, whose energy needs for growth are lower, tend to spend less time feeding and/or more time resting (Neuhaus & Ruckstuhl 2002; Shi et al. 2003; Pelletier & Festa-Bianchet 2004; Prates & Bicca-Marques 2008; Sueur et al. 2011b; but see Hamel & Côté 2008). However, in apparent contradiction to this, there is also some evidence that older or larger individuals have greater travel distances (Aivaz & Ruckstuhl 2011; Sueur et al. 2011b, but see Prates & Bicca-Marques 2008; Shanee & Shanee 2011). Finally, in mammals, lactating females spend more time feeding than non-lactating females (Neuhaus & Ruckstuhl 2002; Ruckstuhl & Neuhaus 2002; Hamel & Côté 2008) especially as their infant grows and its energy needs increase (Lycett et al. 1998; Dunbar et al. 2002; Barrett et al. 2006). Females also tend to devote less time to feeding and travelling when sexually receptive (Rasmussen 1985) and males show a similar change whilst mate-guarding (Rasmussen 1985; Alberts et al. 1996; Willis & Dill 2007).

There is clearly a lack of consensus as to how time budgets vary with classic individual traits such as age, sex and body size in social species. This may be partly due to individual energy requirements, reproductive strategies and predation risk varying differently with these attributes



both within and between species (Ruckstuhl 1998, 2007; Ramos-Fernández et al. 2004; Main 2008; Sueur et al. 2011b). However, this may also be because, in many social species, age and sex are confounded by social characteristics such as individual rank, social bonds and kinship. These social characteristics can influence an individual's foraging behaviour (see 'Individual-Level Social Foraging Behaviour') and so it is reasonable to expect them to likewise influence an individual's time budgets. Indeed, the few studies that have investigated rank-effects on individual time budgets have consistently found that dominant individuals spend less time feeding than subordinates (yellow baboons, *Papio cynocephalus*, Altmann & Muruthi 1988; bighorn sheep, Pelletier & Festa-Bianchet 2004; mountain goats, *Oreamnos americanus*, Hamel & Cote 2008). In contrast, the evidence for the effect of rank on travel time is limited and mixed (vervet monkeys, Isbell & Young 1993; Rands et al. 2006). If other studies had been able to disentangle rank effects from those of age and sex, they might have found an effect of rank on individual time budgets, and after controlling for this found more consistent effects of age and sex.

To my knowledge no study has yet investigated how time budgets vary between individuals with differing social networks and kinship bonds with other group members. Additionally, despite some indirect evidence (e.g. vervet monkeys, Isbell & Young 1993; chacma baboons, Barrett et al. 2006), I know of no study that has directly investigated how the re-allocation of resting and/or social time to incorporate extra feeding requirements in poorer environments varies between individuals, and how this may lead to some individuals being time-budget stressed with consequences for their health, condition and, ultimately, fitness. Furthermore, most studies of individual time budgets tend to consider how time is allocated to activities over fairly long periods, e.g. months. However, individuals can also alter when during the day they allocate time to different activities in response to changes in food availability and climate (McNamara et al. 1987; Bednekoff & Houston 1994; Owen-Smith 1998; du Toit & Yetman 2005; Brodin 2007; Shannon et al. 2008),

and this may vary between individuals of differing rank (Ekman & Lilliendahl 1993; Brodin 2007). Therefore, the effects of age, sex and rank on time allocation decisions may potentially be manifested through differences in the timing of activities across the day rather than differences in the absolute time allocated to activities, e.g. subordinate individuals allocating more time to feeding later in the day (King & Cowlshaw 2009).

### Group-Level Time Budgets

Group-level changes in time budgets, in contrast to individual-level differences, have been relatively well explored. Research has generally focussed on two related areas: how the physical and social environment affects groups' foraging-related travel costs (Chapman et al. 1995), and the knock-on consequences of this on the time available for activities such as resting and socialising (Dunbar 1992; Dunbar et al. 2009). These two areas have largely been treated separately in the literature, and so I review them separately here. Recently, however, Grove (2012) unified these two themes showing, theoretically and empirically, how a social group's size could be limited by one or both of these mechanisms through restricting its ability to efficiently acquire enough resources to fulfil its energy needs.

### *Foraging-Related Travel Requirements*

At the group level, a great deal of research has focussed on the causes and consequences of daily ranging distances, with obvious implications for how individuals allocate time to travel. One particular focus has been on how group size relates to travel distance. The ecological-constraints hypothesis proposes how social groups' travel requirements vary with group size and with the environment (Milton 1984; Janson 1988; Isbell 1991; Wrangham et al. 1993; Chapman et al. 1995;

Chapman & Chapman 2000; Gillespie & Chapman 2001; Chapman & Pavelka 2005). It describes how either a reduction in habitat quality (Gillespie & Chapman 2001) or increase in group size (Chapman et al. 1995; Chapman & Chapman 2000; Chapman & Pavelka 2005) leads to increased intragroup scramble competition. This leads to a reduction in per capita resource availability such that groups have to cover a greater area each day to meet their energy requirements, ultimately constraining any further increases in group size (Chapman et al. 1995; Gillespie & Chapman 2001). Correspondingly, reductions in food availability have been associated with increased day ranges in primates (Gillespie & Chapman 2001; Asensio et al. 2009; Mbora et al. 2009; Harris et al. 2009), carnivores (Wrangham et al. 1993) and elephants (Wittemyer et al. 2007). Where these increased ranging costs are sustained over longer time scales (e.g. months rather than days) this can lead to groups fissioning to offset these costs (Asensio et al. 2009). An alternative, and not mutually exclusive, response to increased intragroup scramble competition is for groups to spread out more, such that each individual has a larger search area (Altmann 1974a; Janson 1988; Isbell 1991; Chapman & Chapman 2000). This second scenario has received much less attention, perhaps because the constraints on group spacing imposed by habitat visibility and predation risk make it a less common response than changing day range. Nevertheless, it has been demonstrated in primates (Henzi et al. 1997; Isbell et al. 1998; Cowlshaw 1999; Gillespie & Chapman 2001) and implicated in other species of mammals (Thouless 1990; Hirsch 2011) and birds (Moody et al. 1997).

It is not the case, however, that a group's travel costs always co-vary with resource availability. In some situations, group sizes and travel costs are constrained by other costs and benefits of grouping besides scramble competition. For instance, in their meta-analysis of primate and carnivore grouping patterns, Wrangham et al. (1993) suggested that those populations and species which have greater-than-expected group sizes were subject to higher predation risk. In this situation, predation risk keeps group sizes at the maximum allowable given local foraging

conditions meaning the per capita food share, and so travel costs, remains constant across group sizes (Chapman & Chapman 2000). Social costs, such as aggression and infanticide, may also constrain group sizes in some situations, leading to smaller group sizes and lower travel costs (Treves & Chapman 1996; Steenbeek & van Schaik 2001; Chapman & Pavelka 2005; Snaith & Chapman 2007, 2008).

### *Reallocation of Resting and Social Time*

The amount of time which an animal has to allocate to activities is finite. Where more time needs to be devoted to foraging – feeding and moving – there will necessarily be less time for other activities. These are primarily resting and, in group-living animals, socialising (Dunbar 1992; Pollard & Blumstein 2008; Dunbar et al. 2009). How this reallocation of time happens has been the subject of recent research as it has become increasingly recognised that sacrificing resting and social time can have fitness consequences (Lehmann et al. 2007; Pollard & Blumstein 2008; Dunbar et al. 2009; Korstjens et al. 2010).

Time spent resting was often assumed to be ‘free’ and available for use in other activities if required (e.g. Altmann & Muruthi 1988; Dunbar 1992) despite the suggestion that it may be important in physiological processes such as digestion and thermoregulation (Herbers 1981). More recent studies have supported this suggestion, showing that groups spend more time resting when under greater heat stress (Stelzner 1988; Dunbar 1992; Di Fiore & Rodman 2001; Hill et al. 2004; Hill 2006; Korstjens et al. 2010) or when their diet contains less easily digestible food (Doran 1997; Korstjens & Dunbar 2007; Masi et al. 2009; Korstjens et al. 2010). Consequently, time allocated to resting is increasingly understood to include an ‘enforced’ component determined by the environment either directly through thermoregulation requirements or indirectly through digestion

requirements (Dunbar et al. 2009). The importance of this component has been highlighted by recent evidence in primates showing that enforced resting time predicts both biogeography (Korstjens et al. 2010) and group size (Pollard & Blumstein 2008).

Social bonds have been linked to indirect and direct fitness effects (Silk 2007b; Crockford et al. 2008; Fruteau et al. 2009) and are, in part, constrained by the amount of socialising time available (Lehmann et al. 2007). Social time is, therefore, expected to be conserved over 'free' resting time (Dunbar et al. 2009). This expectation is supported by previous studies in baboons showing that in environments requiring greater foraging times there was a corresponding decrease in group-level resting time but no change in social time (Dunbar & Dunbar 1988; Bronikowski & Altmann 1996). There is, however, some evidence that social time might contain a similar internal division to resting. As described in 'Individual-Level Social Foraging Behaviour', the structure of many social networks at the group level has been characterised as containing numerous closely bonded sub-groups (Connor et al. 1999; Croft et al. 2004; Wittemyer et al. 2005; Silk et al. 2006a,b; Hill et al. 2008) often containing close kin (Wittemyer et al. 2005; Silk et al. 2006a,b) or individuals of similar age (Lusseau & Newman 2004; Wey & Blumstein 2010). The bonds within these sub-groups are strong and relatively stable through time (Wittemyer et al. 2005; Silk et al. 2010a) whilst the bonds between these groups are weaker and vary with environmental conditions (Wittemyer et al. 2007; Henzi et al. 2009; Silk et al. 2010a). The social time necessary to maintain these weaker bonds may, therefore, be analogous to the 'free' component of the resting time budget and be more easily sacrificed, at relatively little cost. However, far greater costs are likely to be incurred when sacrificing the social time associated with stronger core bonds, analogous to 'enforced' resting time. Studies on baboons support this theory, showing that they will sacrifice resting time to cope with seasonal changes in the environment, and then social time in the face of longer-term changes

(Alberts et al. 2005), and, further, that this sacrificed social time tends to be associated with weaker short-term bonds (Dunbar & Dunbar 1988).

## **Linking Social Foraging Behaviour to Time Budgets: Individual-Based Modelling Approaches**

It is becoming increasingly apparent that to fully understand higher-level ecological patterns, and make accurate predictions about how environmental change might influence these patterns, an understanding of the individual-level mechanisms that drive them is key (Evans 2012). As I have described, individual-level time budgets play an important mediating role in determining how variation in individual-level social foraging behaviour drives changes in group-level time budgets. Despite this, our understanding of the mechanisms linking these phenomena is limited. In this final section, I review the work that has explored the group-level consequences of differences in individual-level time budgets. I then explore how individual-based modelling might provide a useful tool for building a greater understanding of the mechanisms linking individual-level foraging behaviour with individual- and group-level time budgets. Developing a greater and more integrated appreciation of these mechanisms is likely to be important in understanding how social individuals interact with their environment and so how they are likely to be influenced by changes in the environment in the future.

Despite the limited research into differences in individual-level time budgets, such variation has been implicated in emergent patterns of behaviour at the group level, which in turn can feedback to produce individual-level consequences. Greater differences within groups in individuals' time budget requirements is expected to lead to increasing conflicts of interests in the

timing and location of activities (Conradt & Roper 2000, 2005; Sueur et al. 2011a). Initially these increased conflicts are expected to lead to reductions in the group's behavioural synchrony (Rands et al. 2008; Sueur et al. 2011a), with individuals incurring costs such as reduced foraging success and predator detection as a result (Valone 2007; Ruckstuhl 2007; Sirot & Touzalin 2009; Aivaz & Ruckstuhl 2011). However, past a certain threshold this reduced synchrony may lead to a breakdown in group cohesion (Dunbar 1992; Henzi et al. 1997; Conradt & Roper 2000; Ruckstuhl 2007; Main 2008; Sueur et al. 2011a). Where a group is forced to split (fission), individuals in the smaller subgroups may benefit from reduced competition, but will also suffer from increased vulnerability to predators (Roberts 1996; Beauchamp & Livoreil 1997; Ward et al. 2011) and fewer other group members to provide information about the location of food (Danchin et al. 2004; Dall et al. 2005; Valone 2007). If group-level time budgets are stressed, individuals may also struggle to allocate sufficient social time to maintain their social networks (Lehmann et al. 2007; Lehmann & Dunbar 2009). It is becoming increasingly apparent that social bonds play an important role in a social group's functioning (Fewell 2003; Silk 2007b) and group decision-making (King et al. 2008; Sueur et al. 2010b, 2011a). Social bonds can also have an impact on the ability of individuals to negotiate tolerance from others at feeding sites (e.g. Fruteau et al. 2009) and to maintain their health (e.g. Crockford et al. 2008, see 'Individual-Level Social Foraging Behaviour').

These consequences of variation in individual and group-level time budgets highlight the need to better understand the mechanisms that drive this variation. Individual-based mechanistic modelling (or agent-based modelling) is likely to prove useful in building this understanding as it is specifically designed to examine how higher-level phenomena emerge from individual-level processes (Grimm & Railsback 2005). A similar approach is advocated by Sueur et al. (2011a) for the study of group cohesion and decision-making, and has been used to demonstrate how individual differences within groups influence collective decision-making (Couzin et al. 2005, 2011; Conradt

et al. 2009; Sueur et al. 2009, 2010a; Lihoreau et al. 2010) and patterns of group cohesion or fission (Conradt & Roper 2000; Ruckstuhl & Kokko 2002; Yearsley & Pérez-Barbería 2005; Sueur et al. 2010b). However, as this chapter has argued, gaining a greater understanding of how social individuals interact with their environment to produce emergent group-level phenomena requires explicit consideration of their foraging behaviour. Studies by Rands and colleagues provide a good example of how individual-based models can be used in this approach. They modelled social individuals using state-dependent foraging rules and demonstrated that varying food availability and distribution could lead to differences in individual energy reserves, movement patterns and group sizes (Rands et al. 2004). Furthermore, they highlighted the importance of considering individual differences (in dominance), since incorporating them in the model led to greater differences in individual energy reserves and movement (Rands et al. 2006). In a separate dynamic game model of a foraging pair, they also showed that, where a cost to solitary foraging existed, synchronised foraging spontaneously emerged with one individual consistently leading the other (Rands et al. 2003). Again they highlighted the importance of individual differences, showing that when these differences were incorporated in the model the patterns of leader and follower emergence became more complex and harder to predict (Rands et al. 2008). Recently, Rands (2011) further extended this model, showing that although the subordinate member of the pair experienced a foraging cost, this also had implications for the dominant animal since the subordinate was likely to become the leader, deciding when the pair foraged.

Unfortunately, many of these individual-based modelling studies did not compare their model outputs to empirical data, and none of the exceptions among the aforementioned studies explicitly considered foraging behaviour (red deer, Conradt & Roper 2000; tonkean macaques, *Macaca tonkeana*, Sueur et al. 2009, 2010b; golden shiners, *Notemigonus crysoleucas*, Couzin et al. 2011). The value of doing so is demonstrated by numerous studies of shorebirds in which analyses



of individual foraging behaviour have been used to build individual-based models simulating this behaviour. These models have then accurately described the observed variation in individual foraging success, the interference competition they experience and their distribution across resources (Goss-Custard et al. 1995a,b; Stillman et al. 1997, 2000, 2002; Amano et al. 2006). The foraging successes these models predict have then been extended to accurately predict observed population sizes and levels of mortality (Stillman et al. 2000, 2003; Pettifor et al. 2000), and have been applied to predict the effect of anthropogenic environmental change in shorebird populations (Durell et al. 2005, 2006). However, despite these models sometimes predicting the time that individuals spend feeding (Stillman et al. 2000; Stillman 2008), they have not linked their individual-level predictions of foraging behaviour to time budgets (instead making assumptions about individual energy requirements to predict population parameters from individual foraging success, e.g. Goss-Custard et al. 1995b).

To my knowledge, Ramos-Fernández et al. (2006) is the only study that has developed an individual-based model of social foragers to explore emergent individual and group-level phenomena. They found that, despite the use of simple foraging rules, complex sub-grouping patterns and social networks could emerge. When the model had intermediate food distribution values and foragers only had partial knowledge of their environment, these emergent patterns matched those observed in spider monkeys (*Ateles* spp.). However, this model did not incorporate individual differences in the foragers, which may well explain why some of the model outputs were a poor quantitative fit to the observed values. In fact, the authors deliberately kept the model simple, as a “null” model. This model, and the models of shorebird foraging behaviour may, therefore, provide a useful starting point for future research investigating the mechanisms linking individual-level social foraging behaviour with time budgets at the individual and group level. In this endeavour, the inclusion of individual differences, such as differences in energy requirements or

rank-related competitiveness, would seem an obvious first step. Furthermore, there is growing evidence that social foragers can alter their decision-making to suit the habitat they are in or social position they occupy (Devenport & Devenport 1994; Sargeant et al. 2006; Biernaskie et al. 2009; Marshall et al. 2012a/Chapter 4). Future modelling work might, therefore, also seek to include this flexibility in decision-making and explore how such flexibility influences individuals' and groups' abilities to maintain sustainable time budgets across differing environments.

In general, individual-based modelling is likely to provide a powerful tool for studying how social foraging behaviour drives time budgets at the individual-level, and how these in turn lead to emergent patterns in group-level time budgets. As this chapter has shown, these individual- and group-level time budget patterns can have implications for the fitness of individuals and the functioning of the social groups in which they live. However, as yet there is only a limited understanding of the individual-level mechanisms linking social foraging behaviour and time budgets. These mechanisms also play an important role determining how social individuals interact with their environment and so how social animals are likely to be influenced by changes in the environment. Gaining a greater appreciation of these mechanisms should, therefore, be a research priority for behavioural ecology, population ecology and conservation science.

## Chapter 3

### Study System and General Methods

This thesis's study system was a population of chacma baboons (*Papio ursinus*) at Tsaobis Leopard Park, Namibia, that are part of the Zoological Society of London's long-term Tsaobis Baboon Project (see Figures 3.1 and 3.2). Fieldwork was carried out over two field seasons, from May to November 2009 and May to September 2010. In this section I provide a brief background to baboons, with particular reference to their suitability as a study system for this thesis. I then provide a brief description of the Tsaobis environment and baboon population during the study period. Finally, I give a general overview of the data collection methods used.

#### Study System

##### Chacma Baboons

Baboons are large, omnivorous primates that are the most widely distributed primate in sub-Saharan Africa (Estes 1991). They are particularly suited as a study species for research on social foraging behaviour as they live in large and discrete social groups numbering from as few as ten to over one hundred individuals (Estes 1991; Alberts et al. 2005; Cheney & Seyfarth 2008) which contain complex social structures based on dominance rank, kinship and affiliative social bonds (Silk et al. 2006a,b; Cheney & Seyfarth 2008; Henzi et al. 2009; Silk et al. 2010b). Individual baboons negotiate this complex and dynamic social landscape on a day-to-day basis, recognising

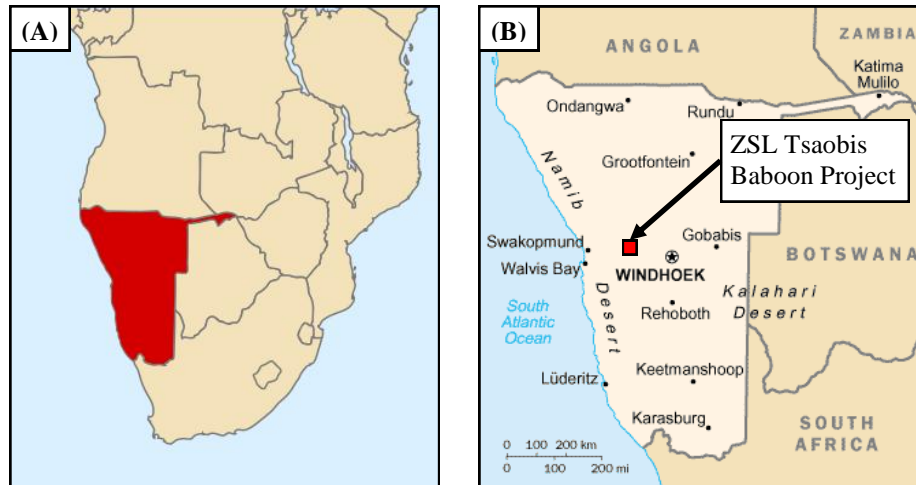


Figure 3.1. The (A) location of Namibia in Southern Africa and (B) approximate location of the study site, ZSL's Tsaobis Baboon Project, in Namibia. The GPS coordinates for the study site are 22°23'S, 15°45'E.

other group members and their social relationships with them. Furthermore, unlike many other primates, they are predominantly terrestrial and live in open, savannah habitats, making conditions for behavioural observations particularly favourable. Consequently, over the last 40 years, baboon behaviour and ecology has been particularly well studied (reviewed in Alberts et al. 2005; Cheney & Seyfarth 2008) providing an excellent platform for this thesis to ask challenging questions about social foraging behaviour.

### The Tsaobis Environment

The environment at Tsaobis Leopard Park predominantly consists of two habitats: open desert and riparian woodland (Figure 3.3). The open desert, hereafter 'desert', is characterised by alluvial plains and steep-sided hills. Desert vegetation mainly consists of small herbs and dwarf shrubs and trees such as *Monechma cleomoides*, *Sesamum capense* and *Commiphora virgata* (see Table 3.1 for full list of plant species recorded at Tsaobis during the study period). The riparian woodland, hereafter 'woodland', is associated with the ephemeral Swakop River that bisects the site

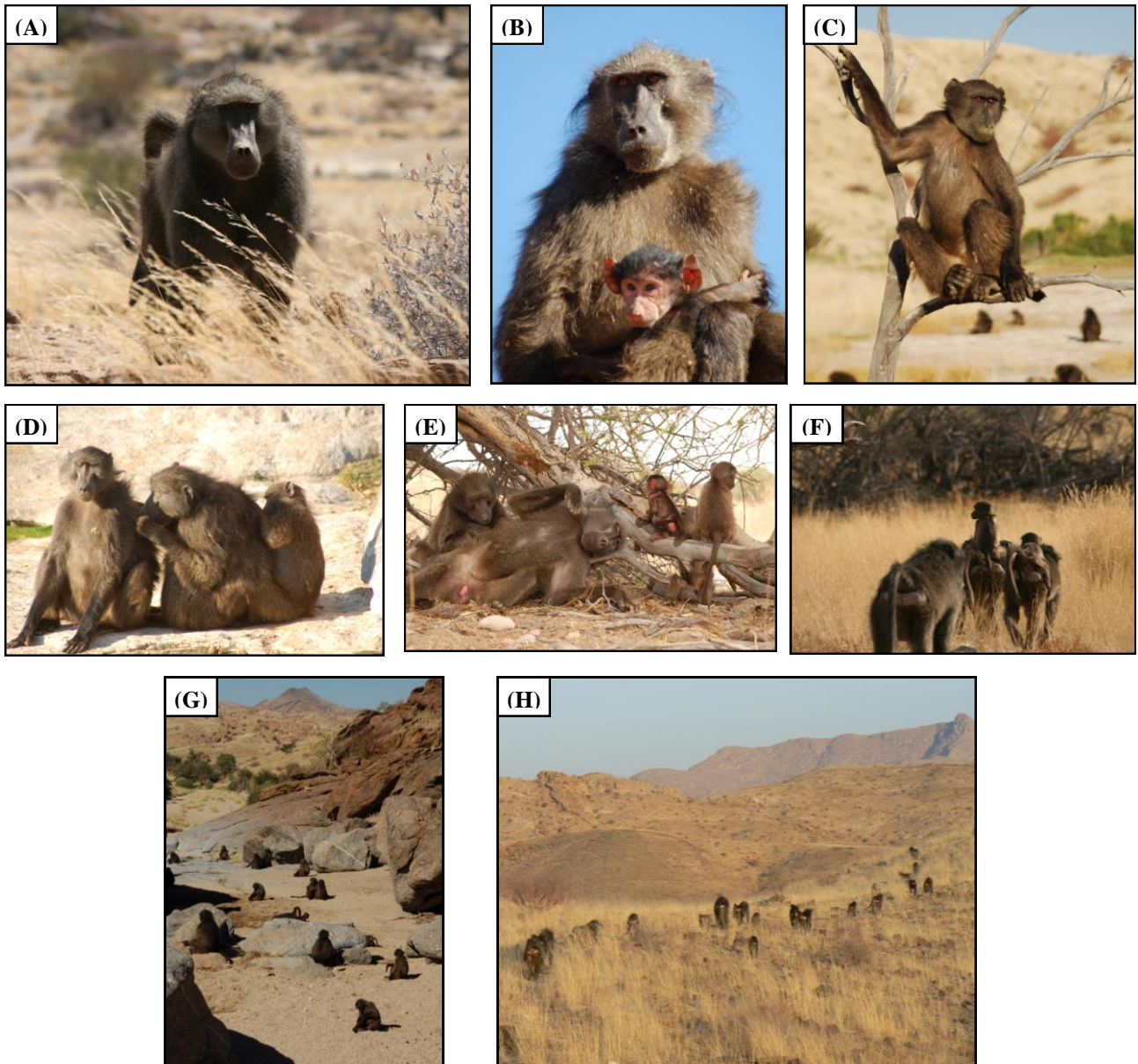


Figure 3.2. Chacma baboons (*Papio ursinus*) at ZSL's Tsaobis Baboons Project. Troops contain adult (A) males and (B) females and (B and C) juveniles. They function as discrete and stable units in which individual baboons socialise with one another (D and E) and travel between food patches (F), drinking points (G) and sleeping cliffs (H). Photo credits: (A,F) Tim Davies, (H) Hannah Peck, (all others) H.M.

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and covers a relatively small area of the field site (see Figure 3.3). The river channel's subsurface water means the woodland vegetation is dominated by large trees and bushes such as *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica* (see Table 3.1, Cowlshaw & Davies 1997 for more ecological detail of the site and Jacobsen et al. 1995 for a detailed review on Namibian river system ecology). The local Tsaobis climate is also highly seasonal. Local annual rainfall is low (median = 156 mm, range = 34 – 633 mm, n = 22 years) with most falling between December and April (149 mm, 32 – 599 mm), and little falling between May and November (10 mm, 0 – 97 mm; C. Douglas, unpublished data). Temperature is also highly variable with the maximum daily temperature across the study period ranging from 23 to 42 degrees Celsius (median = 35, n = 277 days), and the minimum daily temperature ranging from 3 to 24 degrees Celsius (median = 14, n = 272).

The baboons at Tsaobis forage almost exclusively on the discrete herbs, shrubs and trees of the desert and woodland (the remainder of their diet typically consists of insects). In the desert these discrete food patches are small, and so can usually only accommodate two to three foraging baboons at most (Figure 3.5). In contrast, woodland patches are large and can often potentially accommodate a whole troop (30-40 baboons, see Figure 3.5). Furthermore, as well as this spatial variation between habitats in food patch configuration (the number of patches containing food and the amount of food in each), the seasonal climate means that these configurations also vary temporally across the study period (see Table 7.2 in Chapter 7), making Tsaobis an ideal site to study the effects of environmental change on social foraging behaviour.

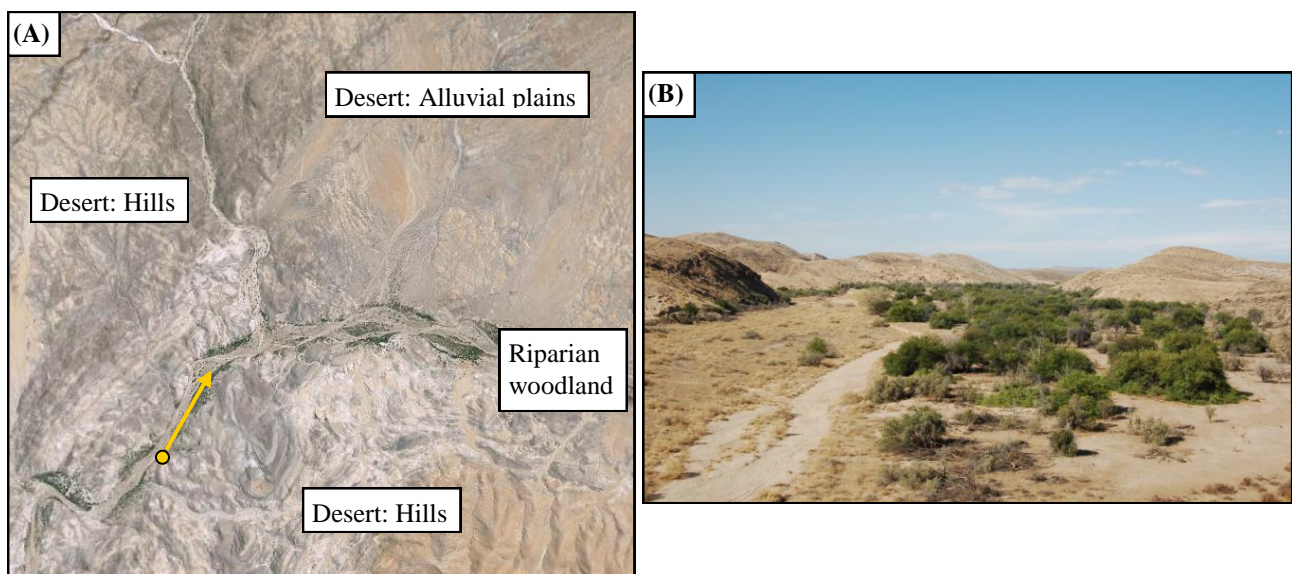


Figure 3.3. The Tsaobis environment. (A) A Google Earth image of the study site with the desert and riparian woodland habitats marked. The yellow dot and arrow mark the approximate location of the photo in (B) showing the riparian woodland of the Swakop River with the desert hills on either side.



Table 3.1. The plant species recorded at the field site during the study period and the parts of each plant that the baboons were observed eating. Species were identified using Burke (2003) and Mannheimer & Curtis (2009).

Species name	Parts baboons observed eating	Species name	Parts baboons observed eating
<u>Large trees and bushes</u>		<u>Small herbs and dwarf shrubs (contd.)</u>	
<i>Acacia erioloba</i>	flowers, immature pods, seeds	<i>Datura stramonium</i>	-
<i>Acacia tortilis</i>	flowers, seeds	<i>Euphorbia glanduligera</i>	roots
<i>Faidherbia albida</i>	flowers, immature pods, seeds	<i>Euphorbia virosa</i>	plant flesh
<i>Prosopis glandulosa</i>	bark, flowers, new leaves, seeds	<i>Foveolina dichotoma</i>	flowers
<i>Salvadora persica</i>	berries	<i>Gisekia sp.</i>	flowers
<i>Tapinanthus oleifolius*</i>	flowers, new leaves, seeds	<i>Gossypium anomalum</i>	seeds
<u>Small herbs and dwarf shrubs</u>		<i>Mesembryanthemum guerichianum</i>	roots
<i>Adenolobus garipensis</i>	seeds	<i>Monechma cleomoides</i>	flowers
<i>Aloe sp.</i>	-	<i>Petalidium variabile</i>	seeds
<i>Boscia foetida</i>	-	<i>Ruella diversifolium</i>	-
<i>Calicorema capitata</i>	-	<i>Senecio inaequidens</i>	flowers
<i>Catophractes alexandrii</i>	flowers, seeds	<i>Sesamum capense</i>	flowers, roots, seeds
<i>Citrillus ecirrhosus</i>	-	<i>Tribulus zeyheri</i>	flowers, roots, seeds
<i>Cleome augustifolia</i>	-	<i>Trichodesma africanum</i>	
<i>Commiphora spp.</i>	bark, new leaves, roots	<i>Tripteris microcarpa</i>	flowers
<i>Curroria decidua</i>	seeds	<i>Zygothymum simplex</i>	seeds
<i>Cyperus difformis</i> or <i>Limeum aethiopicum</i>	-		

\* epiphyte of trees and shrubs



### Tsaobis Baboons

The baboon population at Tsaobis has been studied continuously since 2000 as part of the Zoological Society of London's Tsaobis Baboon Project (e.g. Cowlishaw 1997; King et al. 2008; Huchard et al. 2009). During this thesis's study period there were two troops under study: J and L Troop (see Table 3.2 for troop demography). All individuals were habituated to the presence of human observers at close proximity and all those over the age of two years were individually recognisable using ear notches and other distinguishing features (Figure 3.4). Ear notches were made by a veterinarian during whole-troop capture events prior to the study period. These tissue samples were also previously analysed to provide data on the baboons' dyadic relatedness (details in Huchard et al. 2010). In this thesis, J and L Troop are usually referred to as the 'large' and 'small' troop, respectively.

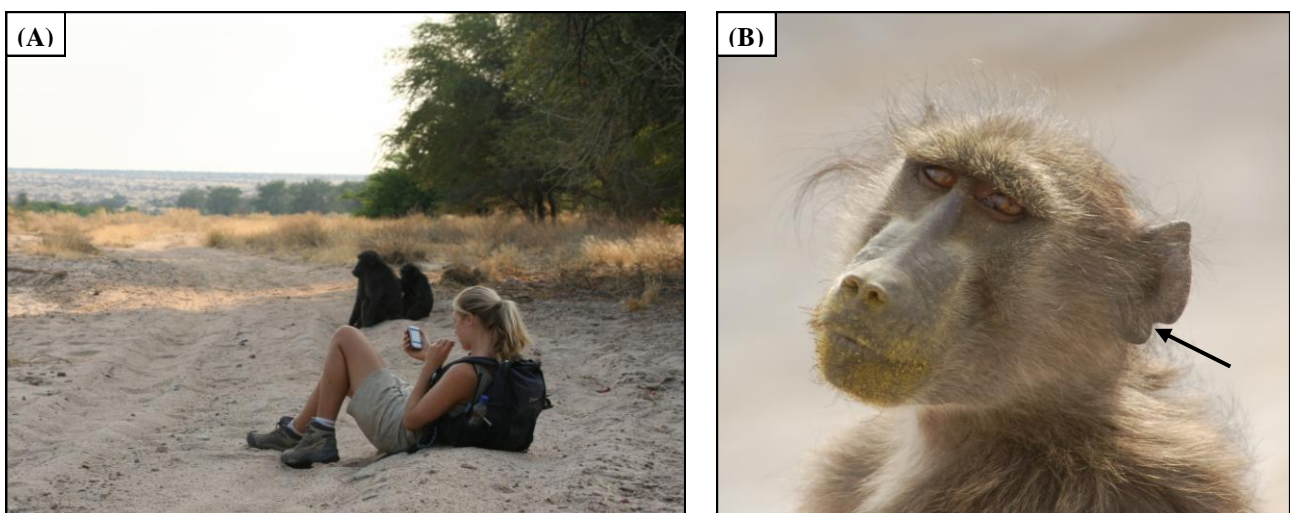


Figure 3.4. Baboon observation at Tsaobis. The baboons are (A) habituated to the presence of observers in close proximity and (B) individually identifiable using ear notches (black arrow) and other naturally occurring features (e.g. scars). Photo credits: (A) Tim Davies, (B) H.M.

Table 3.2. Demographic composition of each study troop at the start of each field season. Age-sex classes follow Altmann et al. (1977).

Start of field season	Troop	Adult males	Adult females	Sub-adults	Juveniles	Infants	Total
2009	J	3	14	8	11	8	44
	L	1	10	4	8	8	31
2010	J	2	15	7	16	3	43
	L	1	13	3	14	3	34

## General Data Collection Methods

Data were collected at Tsaobis during two field seasons running from May to November 2009 and May to September 2010, in collaboration with another PhD student, Alecia Carter, who was studying the evolution of personality in social species (Carter et al. 2011; Carter et al. 2012). During these field seasons we were assisted by six to eight volunteers who were given training to individually recognise each baboon and implement the data collection protocols. Data collection had two components: phenological surveys of baboon food availability; and the recording of individual baboon behaviour, both under natural conditions (2009 and 2010) and during a large-scale field experiment (2010 only). The phenological surveys and recording of natural baboon behaviour required a consistent definition of a baboon ‘food patch’ to ensure comparability between the measures of food availability and foraging behaviour that each provided. Therefore, in this section I first describe the definition of a food patch, and the rationale behind it, used in this thesis. I then provide an overview of each of the data collection methods used in the thesis. Specific details of each of these data collection methods are given within the relevant data chapters.

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### Definition of a Food Patch

The aim of this thesis was to explore how social foraging behaviour decisions and success are influenced by (1) individual patch characteristics, such as patch food availability and type, individual forager traits, such as social rank, and social influences, such as the forager's social bonds with other foragers in the patch, and (2) a habitat's patch configuration, such density and overall food availability (see Chapter 1). The 'food patch' is central to these aims and so it was important to identify a definition of a food patch to be used throughout the thesis.

The thesis aimed to investigate explanatory factors, such as food type and co-forager identity, and processes, such as foraging decisions, which primarily operate and vary at a local-level: i.e. between individuals and over a matter of metres rather than between social groups or populations and across habitats. The baboons at Tsaobis forage almost exclusively on discrete herbs, shrubs and trees which can accommodate varying numbers of individuals (see Figure 3.5 and Table 3.1). This suggested that the appropriate definition of a patch for this thesis would be based around an individual herb, shrub or tree. This was supported by the observation that when they were foraging on these 'patches' baboons spent the majority of their time foraging (searching for or processing food such as flowers or pods), but moving away from these 'patches' required baboons to stop foraging until they reached another 'patch'. There were, however some cases where parts of two of more conspecific herb, shrubs or trees overlapped (e.g. the canopies of two *Faidherbia albida* met) and so baboons were able to move between them without stopping foraging. Different species rarely produced food (e.g. flowers) at the same time and so this was not an issue where two different species overlapped. It was necessary, therefore, to include a provision for this, resulting in this thesis using the following definition of a food-patch: An individual herb, shrub or tree with no conspecific within one metre (see Figure 3.5).

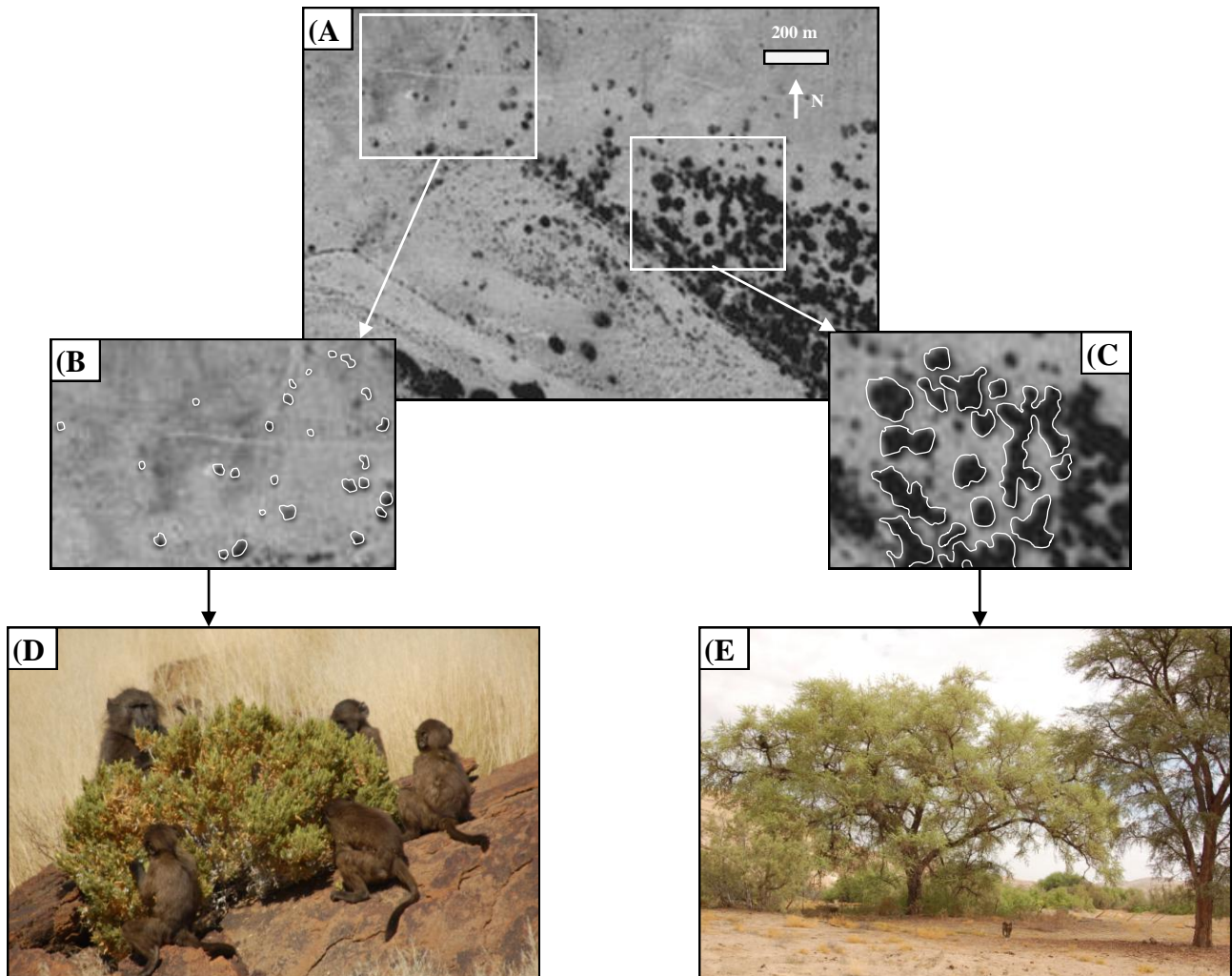


Figure 3.5. Food patches in the desert and woodland habitats. (A) An aerial photo of the Tsaobis study site showing the desert habitat to the north and woodland habitat, and associated Swakop riverbed to the south. Enlarged photos of the desert (B) and woodland (C) show the baboon food patches defined by this study in white. (D) and (E) show typical photos of the contrasting vegetation in each habitat. The desert contains small herbs and dwarf shrubs such as the *Monechma cleomoides* bush in (D). The woodland is characterised by large trees and bushes such as the *Acacia erioloba* tree in (E). To compare the difference in scale, note the baboons pictured in (D) and (E).

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### Phenological Surveys

Phenological surveys were conducted over three days spanning the 1<sup>st</sup> of each month during the study period, yielding nine monthly surveys. Each of these survey periods was split between the woodland (two survey days) and the desert (one day) habitats.

The woodland surveys were a continuation of on-going monitoring of the woodland habitat at the Tsaobis Baboon Project. During each survey, we visited a representative sample of 110 patches (trees and large bushes, see Figure 3.6) and estimated the abundance of each food type in each patch (see Table 3.1 for food types). These patches were selected in a stratified manner from an earlier survey of all 5,693 woodland patches carried out by the Project in 2001, ensuring a representative sample of patch species, locations and sizes. During this earlier survey the height and area covered by each patch was measured by observer assessments and differential-GPS perimeter analysis, respectively.

I developed the desert surveys in 2009 to complement the woodland surveys and provide a more complete picture of the monthly variation in food patch configuration at Tsaobis. The desert surveys consisted of eight 50m x 1m transects placed at random points around the troops' core sleeping cliffs (four of the top five most frequently used cliffs in 2008, see Figure 3.6). Each month, the number of food items in each patch falling within these transects was estimated (mainly small herbs and shrubs, see Table 3.1). The height, width and depth of each patch was also recorded in the first survey of each field season (desert patches only produce new growth during the wetter periods between field seasons).



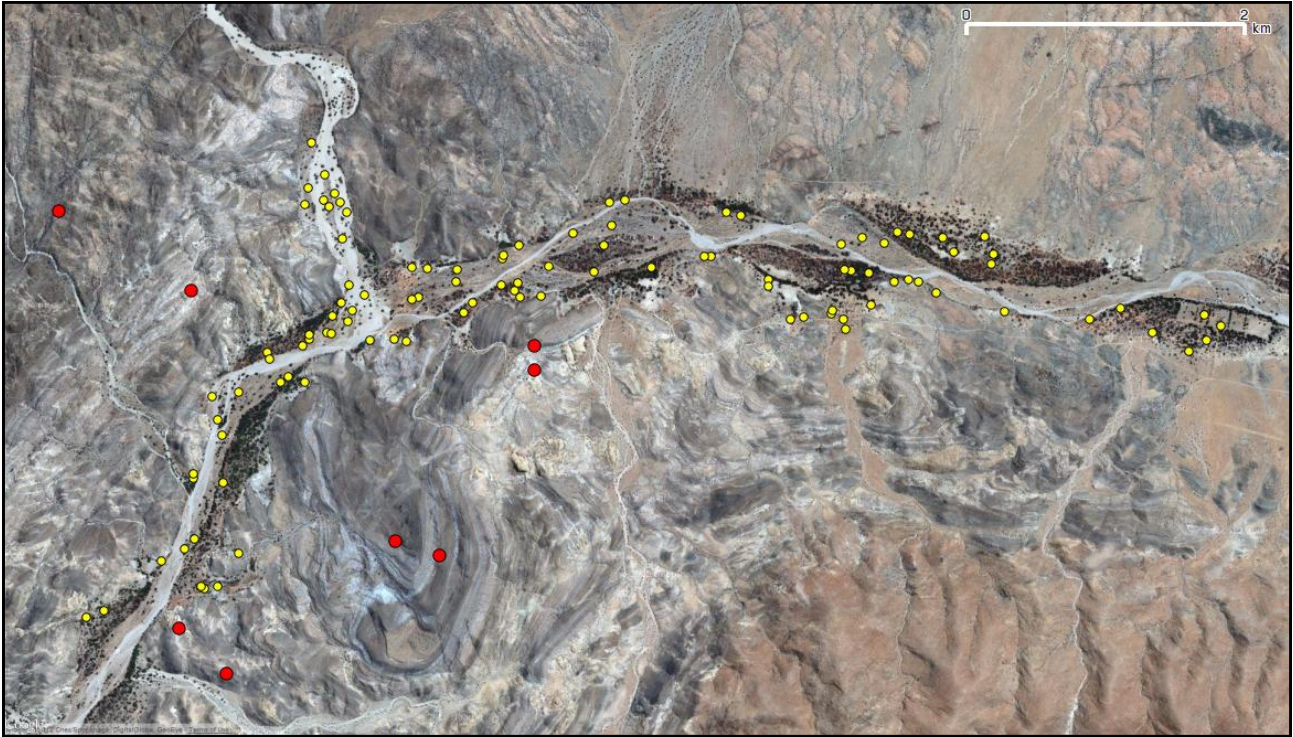


Figure 3.6. The location of the 110 woodland patches (yellow dots) and eight desert transects (red dots) visited in the monthly phenology surveys. Satellite image from Google Earth.

### Behavioural Data Collection: Natural Conditions

During the field seasons, each study troop was followed on a daily basis (Figure 3.4). Observers met each troop at their overnight sleeping cliff at dawn, and followed them on foot throughout the day until they reached their next sleeping cliff at dusk ( $n_{\text{large}} = 269$  days,  $n_{\text{small}} = 257$  days). During these troop follows, data on individual behaviour were collected using focal follows (Altmann 1974b) under two independent protocols: ‘general’ and ‘patch use’ (see details of each below). Data were recorded on handheld Motorola MC35 and Hewlett-Packard iPAQ Personal Digital Assistants using a customised spreadsheet in SpreadCE version 2.03 (Bye Design Ltd 1999) and Cybertracker v3.237 (<http://cybertracker.org>), respectively. Focal animals were selected in a stratified manner to ensure even sampling from four three-hour time blocks (6 – 9am, 9am – 12pm,

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12 – 3pm and 3 – 6pm) across the field season, and no animal was sampled more than once per day under each protocol.

‘General’ focal follows were designed to provide an overview of the baboons’ time use, social behaviour (affiliative and agonistic) and, in 2010, foraging behaviour (see patch use focals below for foraging behaviour recorded in 2009). Observers followed individual focal animals for up to one hour (any focals in which the focal animal was lost before twenty minutes of data were recorded were discarded). They recorded (1) the focal baboon’s activity, as feeding, travelling, resting, grooming or drinking; (2) the occurrence of any agonistic interactions with other troop members, including supplants, displacements, attacks, chases and threats; and (3) the partner identity and direction of both agonistic and grooming interactions. In 2010 they also recorded when the focal entered and exited a food patch. Patch entry was defined as the focal moving into and eating an item from the patch (to rule out the possibility that they were simply passing by or through the patch), and exit defined as the focal subsequently moving out of the patch. Patches were defined as herbs, shrubs or trees (see Table 3.1) with no other conspecific plant within one metre (closer conspecifics, which could potentially be reached by the forager without moving, were treated as part of the same patch). At each patch entry, observers scored the patch’s size (see Tables 3.3 and 3.4) and recorded its type (species and food part eaten, Table 3.1), the number and identity of other baboons in it and, where possible, the number of bites the animal took in the first ten seconds. Under this protocol, focal animals were selected from all individually recognisable baboons, i.e. those over two years old. This yielded a total of 3,356 hours of general focal follows with a mean  $\pm$  s.d. of  $56 \pm 25$  hours per individual ( $n = 60$ ).

Table 3.3. The criteria used to score the size of large bushes and trees in the woodland habitat. All areas are in metres<sup>2</sup> and heights are in metres.

Size scoring			<i>Acacia erioloba</i>	<i>Acacia tortilis</i>	<i>Faidherbia albida</i>	<i>Prosopis glandulosa</i>	<i>Salvadora persica</i>					
Overall	Area	Height	Area	Height	Area	Height	Area	Height				
1		1	<6	<8	<9	<6	<2.5					
2	1	2	<60	>6-8	<60	>8-10	<90	>9-12	<100	>6-8	<160	>2.5-3.5
3		3	>8	>10	>12	>8	>3.5					
4		1	<6	<8	<9	<6	<2.5					
5	2	2	>60	>6-8	>60	>8-10	>90	>9-12	>100	>6-8	>160	>2.5-3.5
6		3	>8	>10	>12	>8	>3.5					

Table 3.4. The criteria used for scoring the size of herbs and shrubs (including *Tapinanthus oleifolius*) in the woodland and desert habitats.

Size Score	Patch can accommodate, at the same time:
1	only one adult feeding on it
2	two adults feeding on it
3	three or more adults feeding on it
4	one or more adults feeding on it more than 10 meters away from each other



'Patch use' focal follows were designed to record more detailed information about the baboons' foraging decisions and patch-use patterns. Observers followed focal baboons whilst they were foraging over two patch visits. At the first patch, they recorded the time the focal entered and exited, the patch's food-density (see below), size (Tables 3.3 and 3.4), type (species and food part eaten, Table 3.1), the number and identity of other baboons in the patch and, where possible, the number of bites the animal took in the first ten seconds. Patch food-density was scored using a ten-point scale for large bushes and trees in the woodland habitat, and a four-point scale for all herbs and dwarf shrubs in the desert habitat. On both scales a score of one indicated the patch was empty and an increasing score indicated progressively higher food-item densities for that patch-species/food-item combination (observers were trained to recognise the range of food densities available prior to data collection). At the second patch visit, the observers recorded the same information (except for bite rate) from the patch the focal fed from, and from all other patches within 5 metres (desert) or 20 metres (woodland), i.e. data collection switched from a focus on the individual baboon to the wider foraging environment. (The different distances used in each habitat reflects the differences in patch spacing in each).

The rationale behind these wider patch scans was that the characteristics of all available patches will be important in a forager's decision about which one to feed from. Once a baboon had selected a patch to feed from it was not possible to record the characteristics of the other available patches and continue to follow the baboon at the same time. Therefore, it was not possible to include these wider patch scans in the general focal follows and so this separate 'patch use' protocol was developed. This protocol thus permitted the collection of information on forager patch choice in relation to the available patches (at the second patch) and on the baboons' foraging rewards (at the first patch visit). Under this protocol only adult baboons were selected as focal animal, yielding a total of 703 patch use focals with a mean  $\pm$  s.d. of  $24 \pm 5$  per individual ( $n = 29$ ) at the end of the

2009 field season. This provided an adequate sample size for the analysis of baboon foraging decisions (Chapter 4), and so the collection of data on baboons' foraging reward from a patch was included in the general focal follows in 2010.

### Behavioural Data Collection: Field Experiments

In the 2010 season we conducted a large-scale field experiment on the baboons' foraging behaviour. The purpose of this experiment was to complement the natural behavioural data (above) by (1) providing more detailed data on baboon social foraging dynamics through video-recording foraging behaviour on a known configuration of artificial food patches, and (2) broadening the range of environmental conditions for which data on foraging behaviour was available by providing higher quality food patches than usually found naturally.

Here, I provide a brief overview of the experimental setup and procedure, with greater detail given in Chapter 5. Experiments were conducted at an open, flat and sandy area in each troop's home range (one site per troop, see Figure 3.7), and involved three large and two small artificial food patches of loose maize kernels. Because troop J was approximately 25% larger than troop L the area of their experimental patches was increased by the same factor to keep the per-animal feeding area constant. The experiment for each troop was run over two 14-day periods. Logistical constraints meant experiments could not be run simultaneously on both troops, so each 14-day period was run on each troop alternately (Table 3.5). The patches' food content was varied between each period, and inter-patch distance was varied within each period (Table 3.5). Experimental food patches were marked out with large stones, painted white, and maize kernels were evenly scattered over the patch area before dawn each morning. Panasonic SDR-15 video cameras (one per patch, started simultaneously when the first baboon was sighted) were used to record the baboon activity

on each patch, with trained observers narrating the identity of all individuals. Video camera error on day 11 of J troop's experiment meant that data from this day were unreliable and so were excluded from all analyses. This left 320 hours of video with a mean  $\pm$  s.d. of  $5.8 \pm 1.7$  hours per day ( $n = 55$  days). Data on the individual's entering and exiting each patch, their foraging success (bites per 10 seconds) and any agonistic interactions they had with others were later transcribed from these videos.

Table 3.5. Patch configurations used during the field experiment and the dates (all 2010) they were run on each study troop. Further details about the experimental setup are given in Chapter 5.

14-day period	Patch food content	Inter-patch distance	J troop dates	L troop dates
1 <sup>st</sup>	low	low	30/06- 06/07	06/06- 12/06
	low	high	07/07 - 13/07	13/06 - 19/06
2 <sup>nd</sup>	high	high	31/08 - 06/09	07/09 - 13/09
	high	low	12/08 - 18/08	19/08 - 25/08

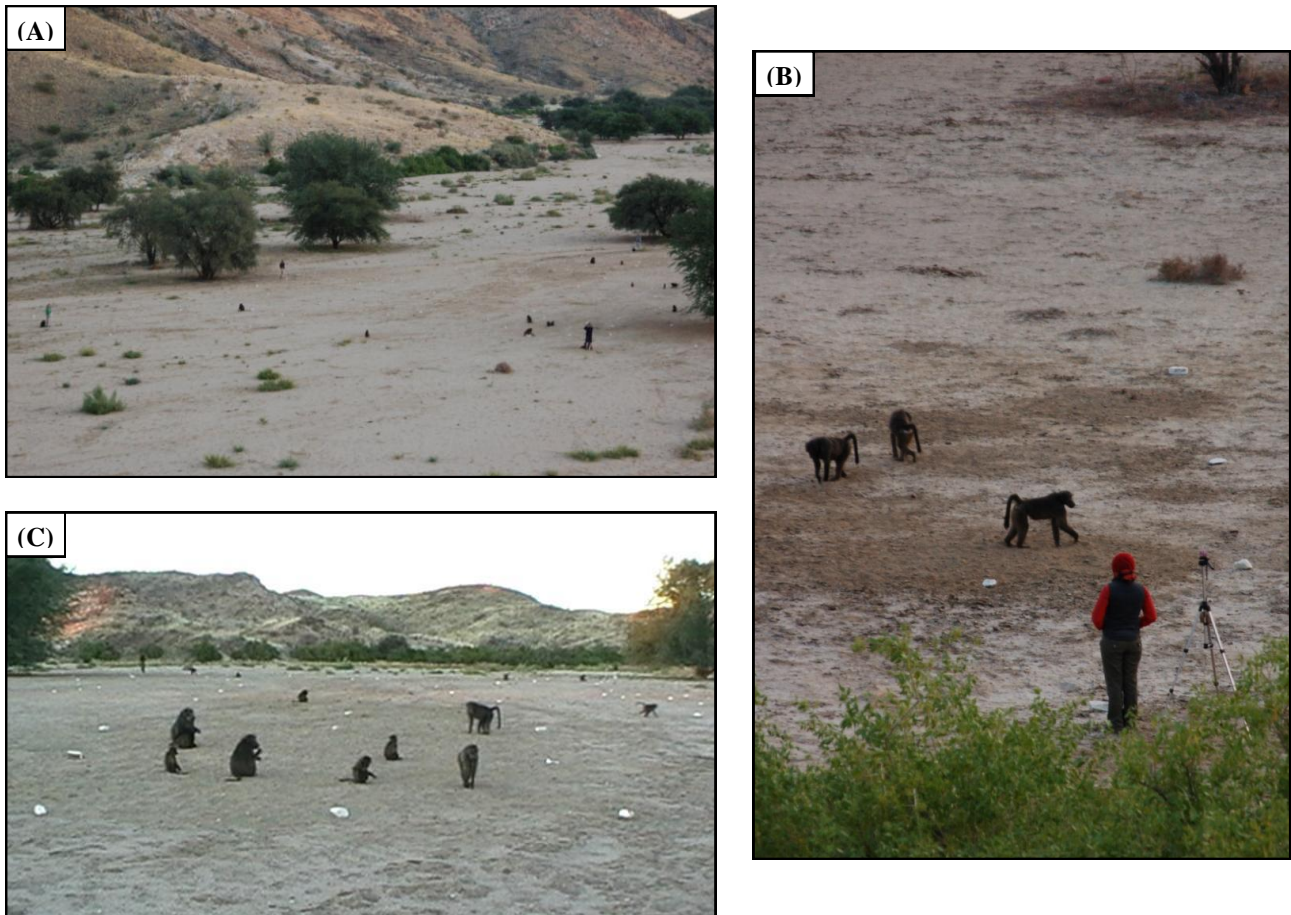


Figure 3.7. The 2010 large-scale field experiment. (A) The large, open area in which L troop's experiments were conducted. (B) A trained observer, with a video camera to her right, recording the activity on an artificial food patch. (C) A still taken from a video recording of the experiments showing an artificial food patch (marked by the white stones) containing seven foraging baboons.

## Chapter 4

# Exploring foraging decisions in a social primate using discrete choice models

A version of this chapter is published as:

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### Abstract

There is a growing appreciation of the multiple social and non-social factors influencing the foraging behaviour of social animals, but little understanding of how these factors depend on habitat characteristics or individual traits. This partly reflects the difficulties inherent in using conventional statistical techniques to analyse multi-factor, multi-context foraging decisions. Discrete choice models provide a way to do so, and I demonstrate this by using them to investigate patch preference in a wild population of social foragers (chacma baboons, *Papio ursinus*). Data were collected from 29 adults across two social groups encompassing 683 foraging decisions over a six-month period, and the results interpreted using an information theoretic approach. Baboon foraging decisions were influenced by multiple non-social and social factors, and were often contingent on the characteristics of the habitat or individual. Differences in decision-making between habitats were consistent with changes in interference competition costs but not changes in social foraging

benefits. Individual differences in decision-making were suggestive of a trade-off between dominance rank and social capital. My findings emphasise that taking a multi-factor, multi-context approach is important to fully understand animal decision-making. I also demonstrate how discrete choice models can be used to achieve this.

## **Introduction**

How social foragers decide which patch to use is an important component of their foraging behaviour. At any given decision point, an individual's patch preference may be influenced by many non-social and social factors, such as patch food content or the number of resident conspecifics, whose relative importance can vary depending on the wider characteristics of the habitat and the forager itself (Giraldeau & Caraco 2000; Waite & Field 2007). However, the differential influence of multiple factors depending on the habitat and forager's characteristics are yet to be fully explored. Most previous studies have either investigated the effects of a relatively wide range of factors but not how their influence varies with habitat or individual characteristics (Smith et al. 2001; Di Bitetti & Janson 2001; Ha et al. 2003; Kazahari & Agetsuma 2008; King et al. 2011), or have explored the influence of habitat and individual characteristics but only on a narrow range of factors (Lendvai et al. 2004; Johnson et al. 2006; Sargeant et al. 2006; Kurvers et al. 2010b; Metz et al. 2011).

Only two studies have attempted to consider the relative importance of a wide range of factors across different contexts (habitats or individuals) by adopting a multi-factor, multi-context approach, and both these studies have suffered limitations. In the first case, Fortin & Fortin (2009) investigated how bison (*Bison bison*) resource selection tactics varied with seasonal habitat

changes. However, they were unable to identify individuals and so examine either how foraging tactics varied between individuals with differing traits, or how co-forager traits influenced these tactics. In the second case, King et al.'s (2009) study of chacma baboon (*Papio ursinus*) foraging tactics was able to individually identify focal foragers and co-foragers. However, this study only considered the effects of the nearest co-forager on patch preference rather than the effects of all individuals in either the chosen patch or nearby alternative patches, and did not investigate the effects of the patches' non-social characteristics.

The need to consider the many characteristics of multiple alternative patches, whose identity is likely to change between each decision, may have prohibited previous studies of foraging decisions from taking a multi-factor, multi-context approach. Conventional statistical techniques used in ecology either do not allow the set of alternatives to change between decisions (e.g. Resource Selection Functions: Manly et al. 2002) or do not allow the consideration of more than two alternative patches (binomial models). Both, however, are allowed by discrete choice analysis: a technique developed in the study of human consumer choice (Ben-Akiva & Lerman 1985; Train 2003). Within ecology, discrete choice analysis has been used in studies of broad-scale habitat use (reviewed in Cooper & Millspaugh 1999; Manly et al. 2002), but it has only been used twice in behavioural ecology, to consider cheetah (*Acinonyx jubatus*) hunting decisions (Cooper et al. 2007) and to investigate female greater prairie-chicken (*Tympanuchus cupido*) mate choice (Noor & Sandercock 2008).

Discrete choice analysis is designed to explore the factors influencing individual decision-making, a topic that many studies in behavioural ecology aim to explore. An increased appreciation and application of this analytical tool may, therefore, lead to greater insight into animal decision-making. In this chapter I aim to demonstrate this potential by using it to explore the factors

influencing foraging decisions in a wild population of social foragers: chacma baboons (*Papio ursinus*). I start by using it to identify the non-social and social influences on ‘baseline’ patch preference, and then show how it can be used to explore how the factors influencing patch preference differ between two habitats and between individuals with differing social traits.

## Methods

### The Discrete Choice Model

The discrete choice model assumes that, faced with a set of resources (the ‘choice set’), individuals seek to choose the resource that will give them the maximum utility (Cooper & Millspaugh 1999), where utility represents some measure of ‘satisfaction’. Behavioural ecologists might think of utility as measuring the cost-benefit ratio of the different available resources, for example in foraging decisions as the foraging reward of different food patches. In the model, the utility of the  $i$ th resource in the  $j$ th choice is defined as (Cooper & Millspaugh 1999):

$$U_{ij} = \beta_1 x_{ij1} + \dots + \beta_n x_{ijn} + \varepsilon_{ij} \quad (4.1)$$

Here,  $x_{ij}$  describe  $n$  attributes of the resources and surrounding environment,  $\beta$  represents the model parameters to be estimated for each of the  $n$  attributes and  $\varepsilon_{ij}$  is an error term. Knowing the utility of a single resource is, however, uninformative, since the probability of it being chosen will depend on the utility of all other resources in the choice set. This probability is described by the multinomial logit model, where  $k$  is the number of alternatives in the choice set (McCracken et al. 1998; Cooper & Millspaugh 1999):



$$P_j(i|k) = \frac{\exp(\beta_1 x_{ij1} + \dots + \beta_n x_{ijn})}{\sum_1^k \exp(\beta_1 x_{kj1} + \dots + \beta_n x_{kjn})} \quad (4.2)$$

This assumes that the error terms from equation 4.1 follow a type I extreme value, or Gumbel, distribution (McCracken et al. 1998; Cooper & Millsaugh 1999).

Here I demonstrate how the discrete choice model can be used in the study of animal decision-making by using it to analyse the foraging decisions made by wild baboons. In this context the values of  $i$ ,  $k$  and  $j$  in equations 4.1 and 4.2 represent a particular food-patch ( $i$ ) within a selection of patches (the choice set containing a total of  $k$  patches) at a particular decision point ( $j$ ). Equation 4.1 then represents the utility value of the particular patch to the baboon making this foraging decision and equation 4.2 describes the baboon's preference for the patch given the characteristics of it and the surrounding patches.

### Study System

Fieldwork was carried out at Tsaobis Leopard Park, Namibia (22°23'S, 15°45'E), from June to November 2009. Data were collected from all adults in two troops of chacma baboons (number of adults = 19 and 12, total troop sizes = 44 and 32, respectively), hereafter the 'large' and 'small' troop, on handheld Motorola MC35 Personal Digital Assistants using a customised spreadsheet in SpreadCE version 2.03 (Bye Design Ltd 1999). Trained observers followed each study troop on foot from dawn to dusk. All baboons were habituated to the presence of human observers at close proximity and were individually recognisable using unique ear notch combinations, made during

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previous capture events, and other naturally-occurring distinguishing features (see Huchard et al. 2010 for further details). Observation conditions at Tsaobis are excellent, allowing detailed observations of individual- and group-level foraging behaviour.

Baboons at Tsaobis forage predominantly in two habitats – the woodland and desert. Both contain discrete food patches but differ markedly in their patch types and distribution. The woodland habitat's food patches are mainly large trees and bushes (patch surface area: median = 156m<sup>2</sup>, inter-quartile range = 28 – 237m<sup>2</sup>: see below for sample sizes and calculations) such as *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica*, containing large numbers of food items (median = 87 items, inter-quartile range = 24 – 390 items such as pods, berries, flowers, and leaves). The surrounding desert habitat's food patches are mainly herbs and dwarf shrubs (patch surface area: median = 0.4 m<sup>2</sup>, inter-quartile range = 0.4 – 3.5 m<sup>2</sup>) such as *Monechma cleomoides*, *Sesamum capense* and *Commiphora virgata*, and contain small numbers of food items (median = 9 items, inter-quartile range = 7 – 33 items) (see Chapter 3 and Cowlshaw & Davies 1997 for further details). Baboon troops move through their environment as a coherent and behaviourally synchronised group (King & Cowlshaw 2009), such that all individuals are typically foraging in the same habitat.

### Data Collection

Data were collected using focal follows (Altmann 1974b) and monthly phenological surveys. Individual baboon foraging decisions were recorded using 'patch-preference' focal follows. In addition, data on the size and food content of patches, and the social relationships between the focal forager and patch occupants, were collected separately using monthly phenological surveys and 'social-behaviour' focal follows, respectively. In both focal protocols,

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individuals were selected to ensure even sampling from all times of day, throughout the field season and across all individuals. No individual was sampled more than once a day under each protocol. Two adult males emigrated from the large troop during the study and so were excluded from the analysis, leaving data from 29 adults (17 and 12 per troop).

Each patch-preference focal follow comprised one foraging decision – defined as the focal individual eating an item from a patch – and recorded the discrete choice set at this decision point. The choice set consisted of the chosen patch and all other patches within 5m and 20m in the desert and woodland habitats (reflecting the differences in patch spacing between these habitats), respectively. Patches were defined as herbs, shrubs or trees with no other conspecific plant within one meter (closer conspecifics, which could potentially be reached by the forager without moving, were treated as part of the same patch). The patch species sampled represented the vast majority of the baboons' diet during the austral winter season. In each focal, the observer scanned the choice set as soon as the focal forager made a decision and recorded the characteristics of the patches within it. The non-social characteristics recorded were the food-item density, patch size and food-item type. Food-item density was scored on a four (desert) or ten (woodland) point scale. Patch size was scored on a four (desert) or six (woodland) point scale (see text and Tables 3.3 and 3.4 in Chapter 3 for more details on these scoring systems). Food-item type was classified as having a handling time that was either low (flowers, leaves and berries) or high (pods, bark and roots). The social characteristics recorded were the number of occupants in each patch and the identity of any adult occupants. Overall,  $24 \pm 5$  (mean  $\pm$  s.d.) choice sets were recorded for each focal individual (generating 703 choice sets in total), with a median of 7 patches (range = 1 – 21) per choice set.

Patch size and food-item density scores were converted to patch quality (food content) and size ( $m^2$ ) estimates using more detailed patch information taken from monthly phenological surveys

in the two habitats. In the desert, 132 food patches, that fell within eight randomly placed 50m x 1m transects within the study troops' home ranges, were surveyed. In the woodland, 59 food patches, representative of patch species, size and location, were selected from an earlier survey of 3,444 woodland patches (the Swakop River Survey: G. Cowlshaw, unpublished data). In each monthly survey, each patch's food item density was scored as in the patch-preference focals (see above and Chapter 3) and the actual number of food items it contained was estimated. Each patch's size was also scored as in the patch-preference focals (see above and Tables 3.3. and 3.4) and in the desert survey each patch's height, width and depth in centimetres was also measured. The area and height of the woodland patches was already known, through differential-GPS perimeter analysis and observer assessments, respectively, from the Swakop River Survey. The conversion of patch size and food-item density scores to patch quality and size estimates is detailed below.

Further behavioural data describing the social relationships between troop members were recorded using social-behaviour focal follows. These lasted from twenty minutes to an hour (any lasting less than twenty minutes were discarded) and recorded the focal individual's grooming and aggressive interactions with others. In all cases the direction of the interaction and the partner's identity was recorded, and for grooming, the interaction's duration was also recorded. Focal individuals were sampled in a stratified manner at all times of day throughout the field season to ensure representative social-behaviour from all habitats and activities. In total,  $47.6 \pm 5.5$  hours (mean  $\pm$  s.d.) of social-behaviour focal follows were conducted for each of the 29 study animals. Aggressive interactions were also recorded *ad libitum*.

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## Data Processing

The food content of patches recorded in the choice sets was predicted from the relationship between the food content (the response variable) and the ordinal patch size and food density scores (fixed effects) estimated from the monthly phenological survey data using linear mixed-effect models (Appendix S1). Where possible, specific models for each food type and species combination (e.g. *Faidherbia albida* flowers) were calculated. However, where samples were too small, the data were pooled to create general food item (e.g. all flowers) or species (e.g. all *F. albida* items) models. Patch ID was included as a random effect in all models, while food-item type was included in general patch-species models and species was included in general food-item models. In all models, empty patches were removed, and the response variable was log-transformed to normalise the residuals (see Table S1.1 in Appendix S1).

To explore the physical constraints on forager space, it was necessary to estimate the size of patches on a continuous scale that would be comparable across all patches and habitats (the ordinal scoring systems for patch size in the choice sets were both species- and habitat-specific). To do this, data from the Swakop River Survey (for the woodland patches) and monthly phenological surveys (for the desert patches) were used to describe the relationship between the actual surface area of a patch (the response variable) and its ordinal size score (the explanatory variable) using linear models (Appendix S1). Surface area was selected as a measure of patch size since the majority of food items were found on the outer branches of plants, and was calculated from patch measurements (height, diameter) assuming patches were cylindrical. Species-specific relationships were estimated for trees/bushes in the woodland, whereas the great diversity of desert herb/shrubs meant the number of each species in our survey was too small for species-specific models, so a

general ‘herbs and shrubs’ model was estimated (Appendix S1). Surface area was log-transformed to normalise the residuals in all models (see Table S1.2 in Appendix S1).

To explore the effects of a forager’s social relationships on their patch preferences I calculated their mean rank difference, social capital and relatedness to the adult occupants of each patch in the choice set. Each troop’s adult dominance hierarchy was calculated from all dominance interactions recorded both during social-behaviour focals and *ad libitum* (total number of interactions per troop:  $n_{\text{large}} = 1655$ ,  $n_{\text{small}} = 1316$ ) using Matman 1.1.4 (Noldus Information Technology 2003). In both troops the hierarchy was strongly linear (Landau’s corrected linearity index:  $h'_{\text{large}} = 0.84$ ,  $h'_{\text{small}} = 1$ ,  $p < 0.001$  in both). To control for troop size, each individual’s rank was standardised to between 0 (most subordinate) and 1 (most dominant) using,  $1 - [(1-r)/(1-n)]$ . Here,  $r$  is an individual’s rank and  $n$  is the number of individuals in the hierarchy.

Social animals maintain affiliative bonds with other group members through social interactions. In primates, these bonds are commonly measured by grooming interactions, and there is evidence that they may ‘trade’ these interactions for commodities such as tolerance during foraging (Barrett et al. 1999; Fruteau et al. 2009). Social capital between foragers was therefore calculated using a grooming symmetry score (on the basis that a grooming asymmetry might indicate the ‘purchase’ of tolerance during co-feeding):  $[g_{ij}/(g_{ij} + r_{ij})] - 0.5$ . Here,  $g_{ij}$  is the proportion of focal  $i$ ’s social-behaviour focal time that it was observed grooming individual  $j$ , and  $r_{ij}$  is the proportion of this time that individual  $j$  groomed focal  $i$ . A score of -0.5 indicates that focal  $i$  received all grooming interactions from  $j$  (i.e. low social capital), +0.5 indicates  $i$  contributed all grooming interactions (i.e. high social capital), and 0 indicates that both  $i$  and  $j$  contributed equally.

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Pairwise relatedness ( $r$ ) between individuals was estimated on the basis of 16 microsatellite loci using Wang's triadic estimator (Wang 2007): see Huchard et al. (2010) for further details.

### Analysis

I analysed baboon foraging decisions using the discrete choice model (see equations 4.1 and 4.2). As there were multiple non-social and social factors that might influence patch preference, I used an information-theoretic approach to select estimates of the patch preference model in equation 4.2 (Burnham & Anderson 2002; Garamszegi 2011). I generated a set of candidate models (Table 4.1) assuming that foraging baboons were unable to consider the number of occupants in a patch without also considering its non-social characteristics and, similarly, unable to consider their relationship with the patch occupants without also considering their number. The relationship between group size and foraging reward is often shown to be humped as, initially, the benefits of group foraging (such as the reduced need for anti-predator vigilance and increased availability of social information) rise faster than the intraspecific competition costs before, past a certain co-forager number, this relationship reverses (Giraldeau & Caraco 2000; Krause & Ruxton 2002; Beauchamp 2007). Furthermore, the overall intensity of intraspecific competition, and so the particular form of this humped relationship, can be dependent on forager density (Rutten et al. 2010) and food items' handling times (Cresswell et al. 2001; Folmer et al. 2010). Therefore I included, respectively, a quadratic term for the number of patch occupants, and interaction terms between the number of patch occupants and both the patch size and food-item handling time. Patch size was included as a controlling physical factor in all models including social predictors (models 3-66).

Table 4.1. Candidate models explaining patch preference in foraging baboons.

No.	Model	Notation
	Null	$\beta_0$
<i>Non-social (models 1-2)</i>		
1	Food content	$\beta_0 + \beta_1\text{food}$
2	Food + handling time	$\beta_0 + \beta_1\text{food} + \beta_2\text{handling}$
<i>Non-social plus occupant number (models 3-10)</i>		
		$\beta_0 + \beta_1\text{food} + \beta_2\text{handling} + \beta_3\text{size} +$ :
3	Linear occupant effect	$\beta_4\text{occ}$
4	Non-linear occupant effect	$\beta_4\text{occ} + \beta_5\text{occ}^2$
5	Moderated by patch size	$\beta_4\text{occ} + \beta_6(\text{occ} \times \text{size})$
6		$\beta_4\text{occ} + \beta_5\text{occ}^2 + \beta_6(\text{occ} \times \text{size}) + \beta_7(\text{occ}^2 \times \text{size})$
7	Moderated by handling time	$\beta_4\text{occ} + \beta_8(\text{occ} \times \text{handling})$
8		$\beta_4\text{occ} + \beta_5\text{occ}^2 + \beta_8(\text{occ} \times \text{handling}) + \beta_9(\text{occ}^2 \times \text{handling})$
9	Moderated by patch size and handling time	$\beta_4\text{occ} + \beta_6(\text{occ} \times \text{size}) + \beta_8(\text{occ} \times \text{handling})$
10		$\beta_4\text{occ} + \beta_5\text{occ}^2 + \beta_6(\text{occ} \times \text{size}) + \beta_7(\text{occ}^2 \times \text{size}) + \beta_8(\text{occ} \times \text{handling}) + \beta_9(\text{occ}^2 \times \text{handling})$
<i>Non-social plus occupant number plus relationship with occupants (models 11-66)</i>		
		<i>Models 3-10 plus:</i>
11-18	Rank	$\beta_{10}\text{rank}$
19-26	Grooming symmetry score	$\beta_{11}\text{symmetry}$
27-34	Kinship	$\beta_{12}\text{kinship}$
35-42	Rank + grooming symmetry	$\beta_{10}\text{rank} + \beta_{11}\text{symmetry}$
43-50	Rank + kinship	$\beta_{10}\text{rank} + \beta_{12}\text{kinship}$
51-58	Grooming symmetry + kinship	$\beta_{11}\text{symmetry} + \beta_{12}\text{kinship}$
59-66	Rank + Grooming symmetry + kinship	$\beta_{10}\text{rank} + \beta_{11}\text{symmetry} + \beta_{12}\text{kinship}$

Table Note: Definitions of notations. food = number of food items in a patch, handling = food patch classed as requiring high (1) or low (0) food-item handling time, size = patch surface area (m<sup>2</sup>), occ = number of individuals (occupants) in a food patch, rank = mean rank difference between the forager and all adult patch occupants, symmetry = mean grooming symmetry score between the forager and all adult patch occupants, kinship = mean relatedness coefficient between the forager and all adult patch occupants.



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I then estimated the  $\beta$  parameters in equation 4.2 in nine separate analyses. The first analysis explored baseline patterns of patch preference (across all habitats and individuals); the next two analyses explored differences in patch preference between two habitats (desert and woodland); and the final six analyses explored differences in patch preference between individuals with different social characteristics (involving three measures of social ‘advantage’ and three of social ‘disadvantage’). Forager ID and habitat intercepts were included in all models to allow for unequal numbers of foraging decisions from each individual and habitat in the datasets, except in the habitat-specific analyses where each model only included data from one habitat type and so only forager ID intercepts were included. The datasets used in each of these analyses were constructed as follows.

To produce a balanced dataset, each choice set was randomly sampled without replacement to leave the chosen patch and three alternative patches. This resulted in 20 choice sets being discarded, leaving 683 sets in the full dataset. Each row in this dataset represented one patch and contained information as to whether it had been chosen (0/1), the choice set it was from, and a range of explanatory variables describing its non-social and social characteristics (the  $x$ 's in equations 4.1 and 4.2). To make comparisons between parameter estimates easier, each explanatory variable was standardised to have a mean of zero and standard deviation of one, except for the categorical handling time variable, which was dummy coded (1 = high, 0 = low). No explanatory variables were highly correlated in any dataset (Pearson's correlation coefficient,  $r < |0.5|$  in all cases), except for the patch size and number-of-patch-occupants terms ( $r > 0.5$  in 5 out of 9 datasets) and the linear- and quadratic-occupants terms ( $r > 0.75$  in all datasets). Each row also contained further information about the habitat in which each foraging decision occurred and the characteristics of the focal baboon.

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For the analysis of the baseline patch preference the full dataset was used. For the analysis of habitat-specific patch preference the choice sets were filtered according to whether the focal forager had been in the desert (number of choice sets,  $n = 452$ ) or woodland ( $n = 231$ ). For the analysis of individual trait-specific patch preference, the choice sets were filtered according to whether the focal forager was classed as ‘socially-advantaged’ or ‘socially-disadvantaged’. Foragers were classed as advantaged or disadvantaged if they scored higher or lower than the troop median for relative dominance rank (number of choice sets,  $n_{\text{high}} = 335$  and  $n_{\text{low}} = 328$ ), social capital ( $n_{\text{high}} = 323$ ,  $n_{\text{low}} = 340$ ), and number of close kin (relatedness coefficient  $\geq 0.25$ ;  $n_{\text{high}} = 250$ ,  $n_{\text{low}} = 277$ ). Choice sets from individuals that were equal to the troop median were excluded from that analysis. Individuals’ classification on each social axis was independent of their classification on other axes, i.e. if an individual was high ranked it was not more or less likely have high social capital or high numbers of close kin (Cochran-Mantel-Haenszel 3-way Chi-Squared Test,  $\chi^2 = 0.057$ , d.f. = 1,  $p = 0.81$ ).

For each of the nine analyses I estimated the parameters in equation 4.2 for each candidate model using a generalised linear model with a multinomial error structure and logit link. Following Burnham & Anderson (2002), in the baseline analysis  $n/k > 40$  (where  $n$  is the number of choice sets and  $k$  is the number of parameters in the maximal model) so AIC values were calculated for each candidate model, whilst in all other analyses  $n/k < 40$  and so  $AIC_c$  values were used. In all analyses, the overdispersion coefficient  $\hat{c}$  was less than 1. To identify final parameter values for each of the nine analyses I used full model set averaging as the maximum Akaike’s model weight in each analysis was low (maximum of 0.30 in the baseline analysis). This procedure uses the estimates for all models in the model set to calculate global coefficient and standard error estimates for each predictor. Global coefficient estimates are calculated as the sum of a predictors’ coefficient estimate in each model weighted by each model’s Akaike’s weight. Thus, predictors which have

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stronger effects in better models (those with higher Akaike's weights) have a stronger effect in the final averaged model compared to those which only appear or only have a strong effect in poorer models (those with lower Akaike's weights) (Lukacs et al. 2010; Symonds & Moussalli 2011). Global standard error estimates were calculated using the unconditional estimator recommended by Lukacs et al. (2010).

I explored the predicted effects of specific patch characteristics ( $x$ 's) by calculating a patch's 'selection index', defined by the numerator of equation 4.2:  $\exp(\beta_1 x_{ij1} + \dots + \beta_n x_{ijn})$  (Manly et al. 2002), over the observed range of  $x$ , keeping all other characteristics constant and using the back-transformed parameter estimates in the final averaged models. In Figures 4.1 and 4.3 plots of these calculations are presented. However, in Figure 4.2 it was necessary to present plots of the beta coefficients and patch utility (the natural logarithm of the selection index, see equation 4.1) respectively, to make comparisons between the desert and woodlands models easier. All analyses were carried out in R, version 2.12.1, using the lme4 package for mixed model estimation and the mlogit package version 0.1-8 for multinomial logit model estimation (Croissant 2010; R Development Core Team 2010; Bates et al. 2011).

## Results

In the baseline analyses (Table 4.2; see Table S1.3 for the 95% confidence model set) the final averaged model showed that both non-social and social factors strongly affected the baseline patch preference (Fig. 4.1). The relative probability of a patch being chosen increased by 20% for every standard deviation (s.d.) increase in food content, but declined by 42% if a patch had high handling time requirements (Fig. 4.1A). Patch size also had a negative effect, reducing the probability of a patch being chosen by 30% for every 1 s.d. increase in size. The final baseline

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model also showed an important effect of some, but not all, candidate social factors. The number and rank of patch occupants had strong effects: patch preference peaked at intermediate numbers of occupants (5-6 individuals), but the peak height was moderated by the mean rank difference between the occupants and the forager (Fig. 4.1B). Thus, independent of occupant number, a mid-ranking forager was 4.1 times more likely to choose a patch containing the lowest ranking occupant over a patch containing the highest ranking occupant. In contrast, the effects of the mean social capital or mean relatedness between the forager and patch occupants were weak. Finally, the interactive effect of occupant number and food handling time was also important. Patches with food requiring low handling times were preferred when they contained high ( $>7$ ) or low ( $<2$ ) numbers of occupants. However, at intermediate numbers of occupants preference was stronger for foods with high handling times, such that when patches contained five occupants a high handling-time patch was 63% more likely to be chosen (Fig. 4.1C). The effect of the interaction between patch size and number of occupants was weak.

In the woodland and desert analyses (Table 4.2; see Tables S1.4 and S1.5 for the 95% confidence model sets) there were marked differences in the important factors influencing patch preference in each habitat's final-averaged model (Fig. 4.2). Non-social factors had a much stronger effect on patch preference in the desert habitat: an increase of 1 s.d. in food content (Fig. 4.2A), a high handling time or a 1 s.d. increase in patch size (Fig. 4.2B), made a patch 41.3 times more likely and 1.6 and 2.9 times less likely to be chosen in the desert (compared to the woodlands), respectively. The mean rank difference between foragers and patch occupants was also more influential in the desert (Fig. 4.2B). Here a mid-ranking individual was 349 times more likely to choose a patch containing the lowest ranking occupant over one containing the highest ranking, but only 1.3 times more likely given the same foraging decision in the woodlands. Finally, the interaction between patch size and number of occupants was highly important in the desert but negligible in the

Table 4.2. Final averaged model for baseline, habitat-specific and individual trait-specific patch preference.

Model		<u>Non-social patch characteristics</u>			<u>Social patch characteristics</u>			<u>Non-social x Social</u>						<u>Sample sizes</u>	
		food	handling	size	occ	occ <sup>2</sup>	rank	symmetry	kinship	size x occ	size x occ <sup>2</sup>	handling x occ	handling x occ <sup>2</sup>	<i>n</i>	<i>i</i>
Baseline	$\beta$	0.18	-0.54	-0.34	0.83	-0.08	-0.16	0.01	-0.03	-0.004	0.001	0.77	-0.09	683	29
	s.e.	0.06	0.15	0.10	0.15	0.02	0.05	0.03	0.04	0.04	0.01	0.26	0.05		
Desert	$\beta$	3.97	-0.81	-1.41	1.61	0.02	-0.64	-0.05	0.01	2.40	0.25	0.16	-0.06	452	29
	s.e.	1.96	0.26	0.71	0.61	0.32	0.17	0.07	0.06	1.32	1.10	0.62	0.61		
Woodland	$\beta$	0.24	-0.34	-0.33	1.15	-0.12	-0.03	0.01	-0.03	0.00	0.001	0.26	-0.03	231	29
	s.e.	0.08	0.27	0.11	0.21	0.03	0.05	0.04	0.05	0.04	0.01	0.33	0.05		
High Rank	$\beta$	0.19	-0.62	-0.28	0.96	-0.10	-0.07	-0.03	-0.02	-0.01	0.01	0.75	-0.10	335	14
	s.e.	0.10	0.22	0.14	0.24	0.04	0.07	0.05	0.04	0.06	0.01	0.38	0.06		
Low Rank	$\beta$	0.22	-0.71	-0.43	0.97	-0.09	-0.08	0.19	-0.01	0.01	-0.002	0.07	0.00	328	14
	s.e.	0.09	0.21	0.15	0.24	0.03	0.09	0.08	0.05	0.06	0.01	0.21	0.03		
High grooming symmetry	$\beta$	0.10	-0.52	-0.10	0.65	-0.04	-0.15	0.02	-0.01	0.00	0.00	0.62	-0.10	323	14
	s.e.	0.08	0.22	0.13	0.23	0.04	0.08	0.05	0.04	0.05	0.01	0.43	0.11		
Low grooming symmetry	$\beta$	0.28	-0.56	-0.56	1.09	-0.12	-0.18	0.01	-0.04	-0.03	0.01	0.67	-0.05	340	14
	s.e.	0.10	0.22	0.15	0.24	0.04	0.08	0.04	0.06	0.08	0.02	0.40	0.07		
High number of kin	$\beta$	0.87	-0.78	-0.35	1.30	-0.36	-0.15	0.001	0.02	0.11	-0.03	0.04	0.03	250	11
	s.e.	0.31	0.26	0.18	0.44	0.14	0.11	0.05	0.05	0.20	0.06	0.39	0.16		
Low number of kin	$\beta$	0.10	-0.26	-0.28	0.69	-0.04	-0.16	-0.05	-0.15	0.06	-0.01	0.23	-0.03	277	12
	s.e.	0.08	0.23	0.17	0.31	0.04	0.08	0.07	0.08	0.11	0.02	0.36	0.06		

Note: Coefficient estimates ( $\beta$ ) and unconditional standard errors of estimates (s.e.) are given for each explanatory variable – see table 1 for definitions of variables' notations. *n* foraging decisions from *i* individuals were used to estimate each model. All explanatory variables except for the categorical handling time variable were standardised to a mean of 0 and standard deviation of 1.

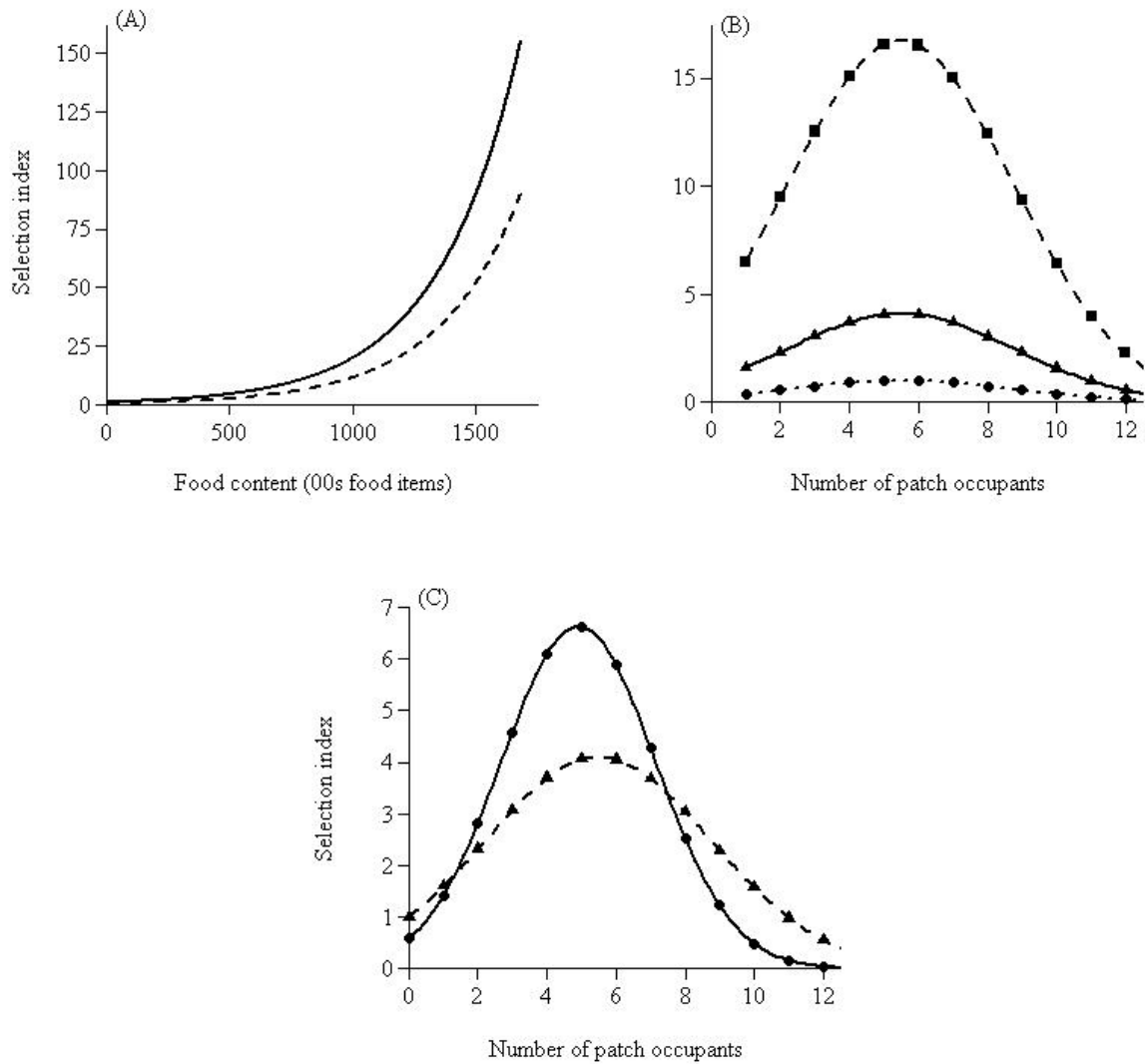


Figure 4.1. Baseline patch preference model. (A) shows the effect of patch food content on patch preference (as measured by the selection index) where patches have a high (dashed line) and low (solid line) handling time. (B) shows the effect of number of patch occupants on patch preference where the mean rank difference between the forager and the patch occupants is -1 (forager subordinate; dotted line and circles), 0 (solid line and triangles), and 1 (forager dominant, dashed line and squares). (C) shows the interactive effect between number of occupants and food handling time on patch selection index (high handling time = solid line and circles, low = dashed line and triangles).

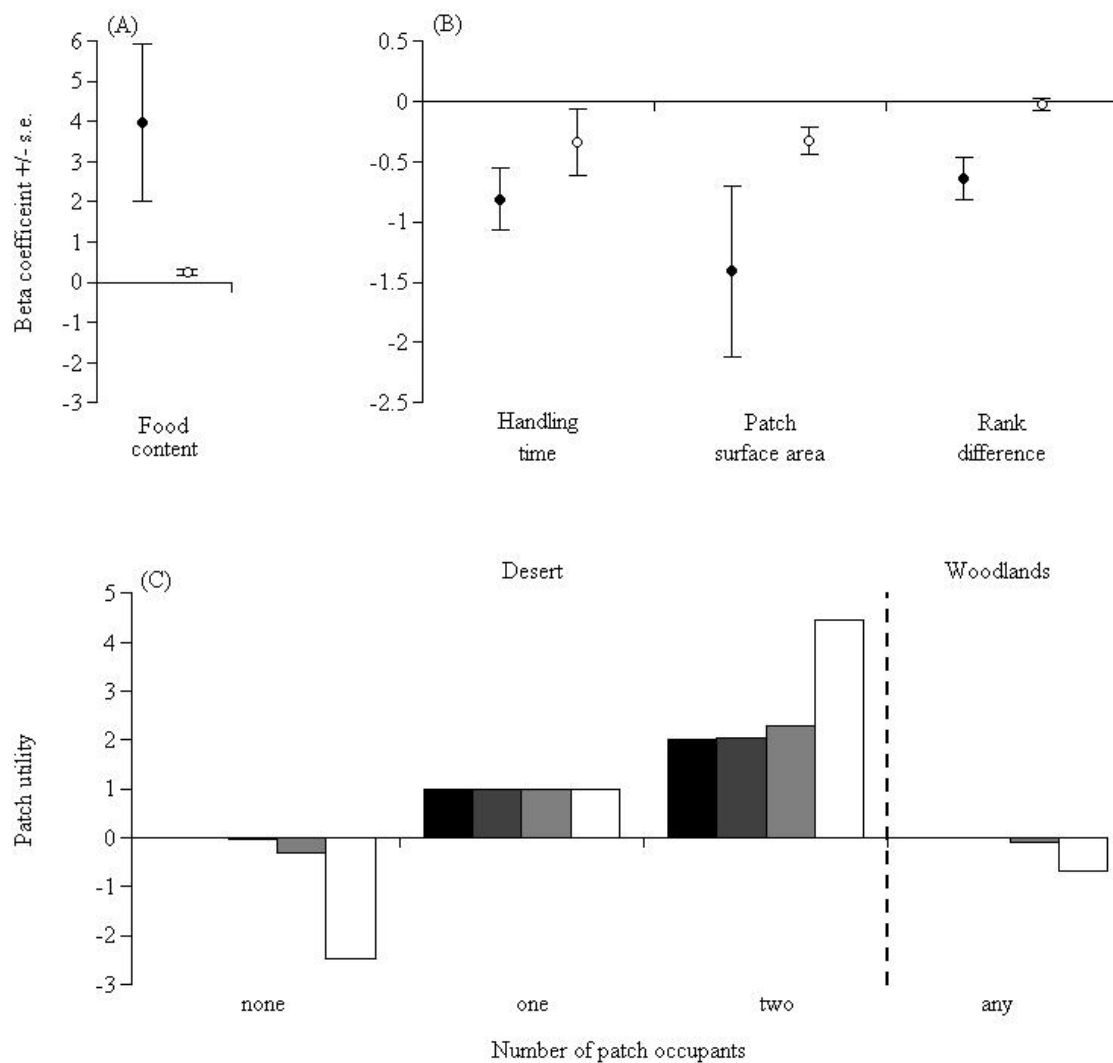


Figure 4.2. Comparing the desert and woodlands habitats' patch preference models. (A) compares the estimated beta coefficient ( $\pm$  unconditional standard error, s.e.) in equation 2 for patch food content in the desert (filled circles) and woodlands (open circles) patch preference models. (B) makes the same comparison for food-item handling time, patch size (as measured by surface area) and the mean rank difference between a forager and patch occupants. (C) shows the interactive effect of the number of occupants and patch size on patch utility (the natural logarithm of a patch's selection index – see equation 1) in the desert model and compares this to the effect of patch size on patch preference in the woodlands model where its effect is independent of the number of patch occupants. The bars, left to right in each group, represent the four patch sizes estimated in the desert: 0.4m<sup>2</sup>, 3.5m<sup>2</sup>, 28.1m<sup>2</sup> and 225m<sup>2</sup> (see Appendix S1 for scoring details).

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woodlands, where patch size had a moderately negative effect on patch preference independent of the number of patch occupants (Fig. 4.2C). Foragers in the desert were 11.9 times more likely to choose the smallest over the largest patch when unoccupied, but this relationship reversed when they contained two occupants. There was some indication that the influence of the number of occupants was a little stronger in the desert, however the errors associated with the linear and quadratic effects in the desert model were relatively large. The mean social capital and mean relatedness a forager had with patch occupants had no effect in either habitat, nor did the interaction between the number of patch occupants and food-item handling time.

In the socially advantaged and disadvantaged forager analyses (Table 4.2; see Tables S1.6 to S1.11 for the 95% confidence model sets) the final averaged models showed noticeable differences in the factors influencing these foragers' decisions (Fig. 4.3). The interaction between number of patch occupants and food-item handling time had a strong effect in high-ranked foragers but a negligible effect in low-ranked foragers, meaning that a high-handling-time patch containing five occupants was 86% more likely to be chosen by high- rather than low-ranked foragers (Fig. 4.3A). Instead, low-ranking foragers showed a much stronger effect of their mean social capital with patch occupants: they were 4.5 times more likely than high-ranked foragers to choose a patch containing individuals with whom they had contributed all grooming interactions, and so held a high amount of social capital (symmetry score = 0.5, Fig. 4.3B). Similarly, the mean rank difference with patch occupants had a marginally stronger effect in foragers with low social capital: they were 18% more likely than foragers with high social capital to choose a patch containing the lowest ranked occupant (Fig. 4.3C). Mean kinship with patch occupants had a negligible effect on the patch preferences when foragers were grouped either by rank or social capital. In contrast, comparing the patch preferences of individuals with many or few close kin in the social group, there was no difference in



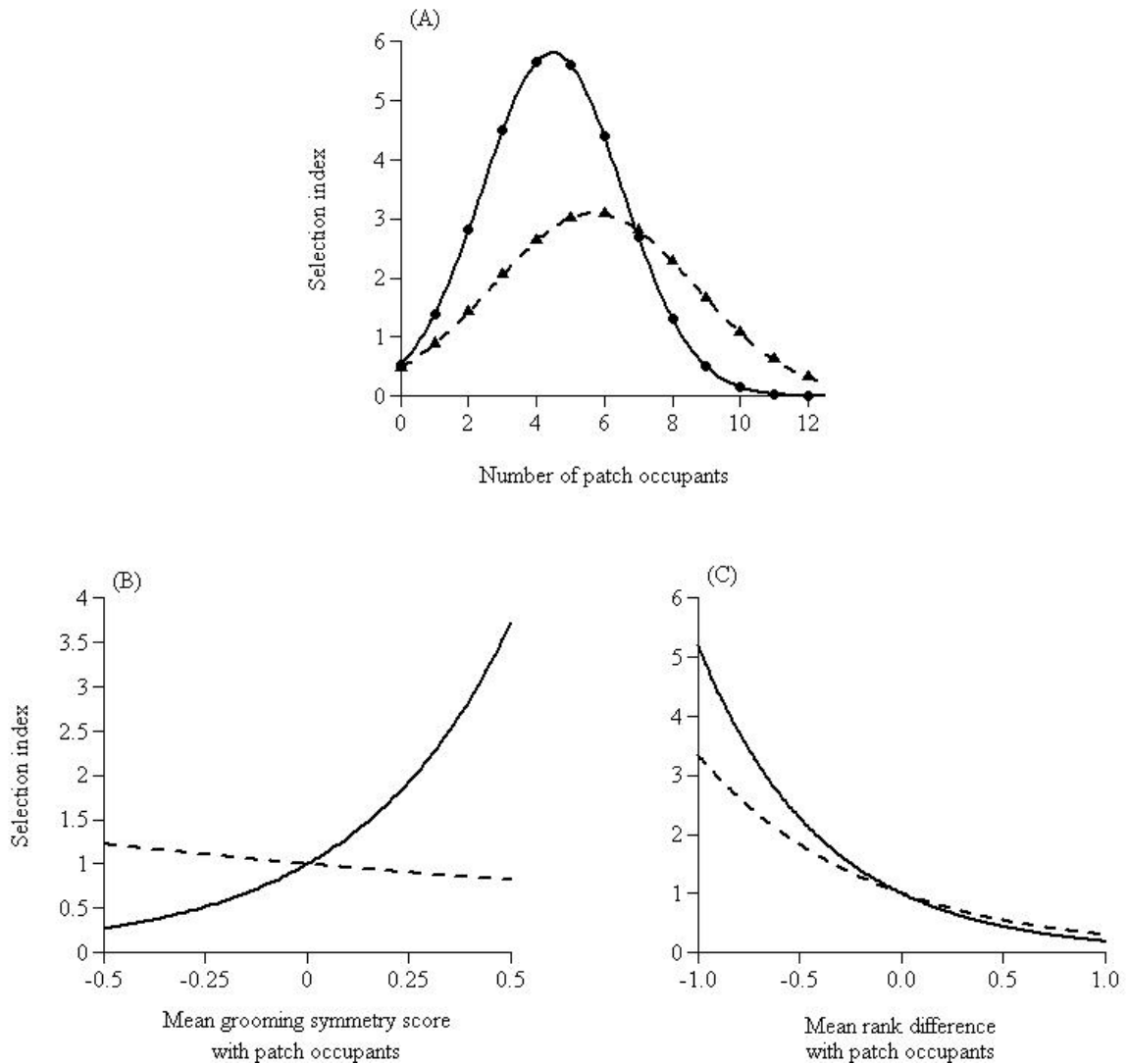


Figure 4.3. Comparing individual trait-specific patch preference models. (A) shows the effect of occupant number on the preference for high handling time patches in high (solid line and circles) and low (dashed line and triangles) ranked individuals. (B) shows the effect of social capital (as measured by a forager's mean grooming symmetry score with patch occupants) on patch preference in low (solid line) and high (dashed line) ranked foragers. (C) shows the effect of the mean rank difference between a forager and patch occupants on patch preference in foragers in with low (solid line) and high (dashed line) social capital.

the effect of the mean rank difference or mean social capital with patch occupants, but there was some indication of a difference in the effect of kinship: individuals with more close kin in the group showed a weak preference for patches containing such individuals, whilst individuals with fewer close kin in the group showed a strong aversion. Finally, there were also some differences in the effects of non-social factors and numbers of patch occupants. Patch preference in individuals with low social capital and high numbers of kin in the group showed a greater effect of food content and patch size and potentially increased faster at lower occupant numbers and declined faster at higher occupant numbers (as described by the greater effects of the linear and quadratic occupant variables), compared to individuals with high social capital and low numbers of close kin. No such differences occurred between individuals of high and low rank. The interactive effect of patch occupant number and patch size was similar across all socially advantaged and disadvantaged models.

## **Discussion**

My findings demonstrate how discrete choice models can be used to explore the variable influences of multiple factors in multiple contexts on animal decision-making. Each context-specific model allowed me to explore and compare the influence of multiple non-social and social factors on baboon foraging decisions. Using discrete choice models in a multi-context framework further allowed me to show that the influence of these factors is often contingent upon the habitat's characteristics and the forager's social traits. Previous work has shown that the drivers of foraging decisions can be numerous (e.g. Smith et al. 2001; Kazahari & Agetsuma 2008) and can vary between habitats (e.g. Johnson et al. 2006; Sargeant et al. 2006) and individuals (e.g. Lendvai et al. 2004; Kurvers et al. 2010b). However, this study demonstrates that a multi-factor, multi-context approach is likely to be invaluable in fully understanding and integrating the factors influencing

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animal decision-making within a particular system, and identifying common trends across systems. Below I discuss the use of discrete choice analysis in this approach and then the implications of the patterns of baboon foraging decisions in the analyses.

### Using Discrete Choice Models to Study Animal Decision-Making

My findings demonstrate how discrete choice models can be used to take a multi-factor, multi-context approach to the study of animal decision-making. Their primary advantage is that they allow the influence of multiple factors on animal decisions to be quantified within a single analytical model. Unlike other multivariate methods they allow two key elements of realism: multiple alternatives at each decision, rather than the two alternatives in binomial models, and changes in the identity of these alternatives between decisions, rather than remaining constant as in classic resource-selection functions (Manly et al. 2002). These two elements are likely to be closer approximations of realism not only in the foraging behaviour explored here but also in many other behaviours such as mate choice and fighting decisions. In addition, discrete choice models explicitly study the decision itself, in this example which patch the baboon used, rather than attempting to deduce it from an outcome such the foraging success of the baboon within the patch. There is a growing appreciation that an animal's decisions are not always optimal, either due to incorrect decisions by the animal (Giraldeau et al. 2002; Houston et al. 2007) or because our understanding of what is optimal is flawed (Dall et al. 2004; Freidin & Kacelnik 2011). Using discrete choice models to explicitly study the factors influencing decisions and comparing these to the factors determining the outcomes of these decisions may, therefore, provide new insights into how good animals are at making decisions, how good our understanding of optimality is and how these vary between habitats and individuals.

There are, however, some limitations to the use of discrete choice models. As a multivariate method they are at risk of overparameterisation, especially as researchers ask increasingly detailed questions requiring the inclusion of multiple explanatory variables. For example, in my baboon foraging analysis, the maximal model in each context required the estimation of thirteen parameters (twelve explanatory variables and the intercept). Ideally, rather than fitting one model per context, I would have simply fitted one model including interaction terms to explore how the factors influencing foraging decisions varied between the two habitats and between individuals' social traits. However, this led to a maximal model with 109 parameters (108 explanatory variables and the intercept) and convergence issues even though I had a relatively large dataset ( $n = 683$ ). Discrete choice models also require researchers to define what resources are 'available', or in this case what patches the baboon could perceive. As in most other habitat-use analyses, this is dependent on researchers judging what is biologically reasonable and so could leave the method open to being criticised as subjective. Previous studies using discrete choice models (Cooper & Millspaugh 1999; Cooper et al. 2007) and other habitat-use analyses (Manly et al. 2002; McLoughlin et al. 2006) have been able to make this judgment and provide valuable insights into animal behaviour and habitat use. Nevertheless, the development of a rigorous and standardised method for determining what makes a resource 'available' would benefit this method in the future.

### Baboon Foraging Decisions

Baboon foraging decisions were influenced by multiple non-social and social patch characteristics. The baseline results were consistent with previous studies showing that increased food handling time can reduce a forager's intake rate (Cresswell et al. 2001; Illius et al. 2002), and how, in social species, foraging success is also commonly characterised as having a humped relationship with foraging group size (Krause & Ruxton 2002; Beauchamp 2007; MacNulty et al.

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2011) and being influenced by co-foragers' rank (Milinski & Parker 1991). Previous studies have also linked smaller patch size to increased inter-individual aggression (Sirot 2000; Johnson et al. 2004). The finding of a preference for smaller patches suggests that, in some cases, increased aggression costs in smaller patches can be outweighed by the improved foraging efficiency of searching for food in a smaller area (as the models controlled for the amount of food).

Previous studies have suggested that high handling time increases interference competition (Sirot 2000; Cresswell et al. 2001; Folmer et al. 2010), predicting that, across the humped relationship between patch preference and occupant number I observed, foragers should show a lower preference for patches with high handling time. However, whilst I found this at low and high occupant numbers I found the opposite at intermediate numbers. Food stealing, i.e. kleptoparasitism, is common in many social foraging species (Giraldeau & Dubois 2008), including baboons (Cheney & Seyfarth 2008; King et al. 2009 and personal observations), and provides a potential tactic for foragers to avoid high handling times by stealing ready-processed food from subordinate animals. My results, therefore, suggest that kleptoparasitism makes high-handling time patches more profitable at intermediate numbers of patch occupants, but at lower numbers kleptoparasitism opportunities are too scarce, and at higher numbers its benefits are outweighed by feeding competition costs (Stillman et al. 1996; Sirot 2000). Beauchamp's (2008b) spatial producer-scrounger model shows how a similar mechanism can produce a similar relationship between forager density and the use of the scrounging tactic (joining another forager on a patch but not necessarily stealing food from them). Scrounging initially increased with forager density, as opportunities to scrounge became more common, but then levelled off or decreased at higher forager densities as the number of foragers exploiting each food discovery increased, decreasing each scrounger's share. This model and my results suggest that the shape of the relationship between foraging group size and individual forager success can be influenced by the opportunities

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for joining other's food discovery (scrounging), or actively stealing food from others (kleptoparasitism) that the underlying physical environment presents.

In addition to exploring how multiple factors influence foraging decisions, this study's comparisons between different habitats and individuals have highlighted the importance of considering multiple contexts when studying animal decision-making. Comparing the desert and woodland habitat models, the effect of all non-social patch characteristics was weaker in the relatively closed, low-visibility woodland. This supports previous studies' findings that a habitat's characteristics can constrain animals' ability to visually assess a patch's non-social characteristics (Cresswell et al. 2001; Fortin & Fortin 2009). More interestingly, this comparison also suggested that differences in the costs of social foraging between habitats may alter foraging decisions. The stronger negative effects of food-item handling time and co-forager rank in the desert are consistent with more intense interference competition (Milinski & Parker 1991; Sirot 2000; Folmer et al. 2010). This suggestion is further supported by the interactive effect of patch size and number of occupants in the desert. Here the smallest patches were preferred when unoccupied but once they contained more than two occupants the largest were preferred, suggesting strongly density-dependent interference competition (e.g. Rutten et al. 2010). There was no suggestion, however, that the benefits of social foraging similarly varied between the two habitats. Previous work has suggested that predation risk (Cowlshaw 1997) and the benefits of social information use (Valone & Templeton 2002; Dall et al. 2005) can be habitat-dependent. Yet if this were the case a difference between the habitats in the baboons' preferences for joining co-foragers in a food patch might have been expected, given that both safety from predators and the availability of social information increase with co-forager number (Quinn & Cresswell 2004; King & Cowlshaw 2007). The fact that that this was not observed may suggest that the proposed difference in interference competition between habitats overwhelmed any detectable variation in social foraging benefits. Indeed, previous

experimental studies reporting habitat-specific changes in the benefits of social foraging explicitly controlled for variation in interference competition (Giraldeau et al. 1994; Templeton & Giraldeau 1995; Rieucau & Giraldeau 2011). This highlights the importance of considering how behaviour varies between natural, as well as artificial or controlled, habitats. It also suggests that, in some cases, habitat-level variation in social foraging benefits may be relatively unimportant compared to the costs.

The factors influencing foraging decisions also varied with individuals' social traits, their rank in particular. Previous studies have shown that subordinate foragers can adjust their behaviour to maintain foraging gains in the face of dominant co-foragers (Bugnyar & Kotrschal 2004; Hewitson et al. 2007; Held et al. 2010). I found support for this mechanism, showing that high-ranked individuals preferred high handling-time patches at intermediate occupant numbers, presumably due to the greater number of kleptoparasitistic opportunities (Stillman et al. 1996; Sirot 2000; Cresswell et al. 2001). In contrast, low-ranking individuals preferred patches containing co-foragers with whom they had more social capital (higher grooming symmetry scores) and so were more likely to tolerate them, allowing greater foraging success (Fruteau et al. 2009; Tiddi et al. 2011). Silk et al. (2010b) suggested that the fitness costs imposed by low rank in baboons were offset by improved social relationships and my findings seem to indicate one possible mechanism through which this offsetting might occur. There was also some suggestion of a complementary effect since individuals with low social capital had a somewhat stronger preference for patches containing lower ranked occupants compared to individuals with high social capital. This difference was not, however, as marked as that between high- and low-ranked individuals' use of social capital. This may reflect the fact that whilst low-ranked individuals can compensate for their social position by investing more in social capital outside of foraging periods, comparable opportunities for individuals with low social capital to invest in rank do not exist since rank is not a tradeable

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commodity (indeed, female rank is maternally inherited, while male rank depends on competitive ability). To similarly compensate for their social disadvantage, individuals with low social capital might therefore be expected to place greater emphasis on patches' non-social characteristics and the number of co-foragers present when making foraging decisions, and this is exactly what I observed. Studies on the influence of social relationships on social foraging performance (Barrett et al. 1999; Fruteau et al. 2009) and individual fitness (Silk 2007a) have tended to focus on primates. However, there is emerging evidence that they can have positive effects on foraging performance (Beauchamp 2000b; Carter et al. 2009) and fitness (Cameron et al. 2009; Frère et al. 2010; Barocas et al. 2011) in other social systems. The suggested mechanism, by which foragers offset fitness costs of low rank by using their social relationships, may, therefore, be found in other primate and non-primate social systems.

Differences between foraging decisions made by individuals with high and low numbers of close kin were less clear. In general, the effect of kinship on social foraging behaviour in previous studies has been mixed (Ha et al. 2003; Tóth et al. 2009; Mathot & Giraldeau 2010a). Mathot and Giraldeau (2010a) suggest that one explanation for these mixed results may be that, whilst foragers outside a patch are expected to avoid imposing co-foraging costs on kin by joining patches containing non-kin, patch occupants are expected to prefer foragers who are kin joining the patch. They modelled both of these considerations within a producer-scrounger framework and predicted greater scrounging amongst kin. In support of this model, there was some evidence that individuals' preference for joining patches containing kin increased with the number of close kin they had in the troop. However, this model would also suggest that high ranked individuals, who have greater control over patch entry, should show a greater preference for avoiding kin, which they do not. There are two reasons I may have failed to find a strong effect of kinship on foraging decisions in this study. First, the effects of kinship on foraging baboons, and other social primates, may be low



as there is evidence that daily access to food is primarily negotiated through social capital (Barrett et al. 1999; Henzi et al. 2009; Fruteau et al. 2009), whilst kinship provides longer-term benefits such as social support (Cheney et al. 2010; Silk et al. 2010a) and reduced stress levels (Crockford et al. 2008). Second, like previous studies that failed to find a clear kinship effect on foraging at this site (King et al. 2009; 2011), I only considered adult patch occupants who have relatively low levels of relatedness compared to adults and juveniles (e.g. parent-offspring versus half-sibling relationships). To understand the role of kinship in social foraging it may, therefore, be important to consider all social group members.

In overview, multiple factors influence baboons' foraging decisions and the influence of these factors varies between habitats and individuals with differing social traits. This variation is consistent with baboons adjusting their decision-making in response to the differing foraging costs and benefits associated with these habitat and individual contexts. Many of these factors and contexts have been shown to influence social foraging behaviour in a similar manner across a broad range of social foraging systems including birds (Johnson et al. 2006; Folmer et al. 2010), ungulates (Fortin & Fortin 2009; Held et al. 2010), carnivores (Waite & Field 2007; Metz et al. 2011) and cetaceans (Sargeant et al. 2006). This suggests that the finding that baboon foraging decisions are influenced by multiple factors in a context-dependent fashion is unlikely to be exceptional. Instead, multi-factor, multi-context systems of social forager decision-making are likely to be widespread. Describing these systems will be important in furthering our understanding of social foraging behaviour. As I have demonstrated here, discrete choice models can provide a powerful tool to further this investigation.

## Chapter 5

# How do foragers decide when to leave a patch? A test of alternative models under natural and experimental conditions

A version of this chapter is in review as:

Marshall, H. H., Carter, A. J., Ashford, A., Rowcliffe, J. M. & Cowlshaw G. In review. How do foragers decide when to leave a patch? A test of alternative models under natural and experimental conditions. At *Journal of Animal Ecology*.

### Abstract

1. A forager's optimal patch-departure time can be predicted by the prescient marginal value theorem (pMVT), which assumes they have perfect knowledge of the environment, or by approaches such as Bayesian-updating and learning rules, which avoid this assumption by allowing foragers to use recent experiences to inform their decisions.
2. In understanding and predicting broader scale ecological patterns, individual-level mechanisms, such as patch-departure decisions, need to be fully elucidated. Unfortunately, there are few empirical studies that compare the performance of patch-departure models that assume perfect knowledge with those that do not, resulting in a limited understanding of how foragers decide when to leave a patch.
3. I tested the patch-departure rules predicted by fixed-rule, pMVT, Bayesian-updating and learning models against one another, using patch residency times recorded from 54 chacma baboons (*Papio*

*ursinus*) across two groups in natural (n = 6,594 patch visits) and field-experimental (n = 8,569) conditions.

4. I found greater support in the experiment for the model based on Bayesian-updating rules, but greater support for the model based on the pMVT in natural foraging conditions. This suggests that foragers may place more importance on recent experiences in predictable environments, like our experiment, where these experiences provide more reliable information about future opportunities.

5. Furthermore, the effect of a single recent foraging experience on patch residency times was uniformly weak across both conditions. This suggests that foragers' perception of their environment may incorporate many previous experiences, thus approximating the perfect knowledge assumed by the pMVT. Foragers may, therefore, optimise their patch-departure decisions in line with the pMVT through the adoption of rules similar to those predicted by Bayesian-updating.

## **Introduction**

There is a growing appreciation of the need to understand the individual-level mechanisms that drive broader scale ecological and evolutionary patterns (Evans 2012). Two such mechanisms which are being increasingly recognised as important are individuals' foraging behaviour and information use (Giraldeau & Caraco 2000; Danchin et al. 2004; Dall et al. 2005; Stephens et al. 2007). Decisions made by foragers, and particularly the rules governing patch-departure decisions, involve both these mechanisms, and are central to optimal foraging theory (Giraldeau & Caraco 2000; Stephens et al. 2007; Fawcett et al. 2013).

Early work on this topic tended to search for the departure rule that would result in a forager leaving a patch at the optimal time (Stephens & Krebs 1986), but did not tackle the question of how a forager would judge when it had reached this optimal departure point, often implicitly assuming

the forager had perfect knowledge of its environment (Iwasa et al. 1981; as highlighted by Green 1984; van Gils et al. 2003; Olsson & Brown 2006). Two well-recognised examples of this work include the use of simple fixed rules and the original, and prescient, version of the marginal value theorem (pMVT, Charnov 1976). Fixed-rule foragers, as the name suggests, leave patches at a fixed point, such as after a fixed amount of time since entering the patch has elapsed (e.g. Nolet et al. 2006; Olsson & Brown 2006). The pMVT predicts that foragers should leave a patch when the return they receive (the instantaneous intake rate) is reduced by patch depletion so that it is more profitable to accept the travel costs of leaving the patch in search of a new one. This threshold intake rate is known as the ‘marginal value’ and is set by the habitat’s long-term average intake rate, which is a function of the average patch quality and density. The pMVT assumes foragers have perfect knowledge (i.e. are prescient) of the habitat’s patch quality and density and so can judge when their intake rate has reached the marginal value, resulting in patch residency times being shorter in habitats where patches are closer together and better quality. In addition to perfect knowledge, the pMVT also assumes that foragers gain energy in a continuous flow, rather than as discrete units, and that there is no short-term variation in the marginal value (reviewed in Nonacs 2001). Consequently, it has been criticised as unrealistic (van Gils et al. 2003; McNamara, Green & Olsson 2006; Nonacs 2001), despite receiving some qualitative empirical support for its predictions (Nonacs 2001).

Further work on patch-departure decisions has addressed the fact that foragers are likely to have imperfect knowledge of their environment, and so will need to use their past foraging experiences to estimate the optimal patch departure time. Two such approaches which have received particular attention are Bayesian-updating (Oaten 1977; Green 1984) and learning-rule models (Kacelnik & Krebs 1985). In the case of Bayesian-updating, these models were developed in direct response to the above criticisms of the pMVT (e.g. Green 1984; reviewed in McNamara et

al. 2006). In these models, individuals make foraging decisions as an iterative process, using their foraging experiences to update their perception of the available food distribution (their “prior” knowledge), making decisions on the basis of this updated perception (their “posterior” knowledge), and then using the outcome of this decision to further update their perception, and so on. Learning-rule models (Kacelnik & Krebs 1985) appear to have developed separately to Bayesian models, but similarly describe foragers using information from past experiences in their current foraging decisions. They differ from Bayesian models, however, in that they describe past experiences accumulating in a moving average representing a perceived valuation of the environment (Kacelnik & Krebs 1985), rather than a perceived distribution of the relative occurrence of different patch qualities as in Bayesian models (Dall et al. 2005; McNamara et al. 2006). A learning-rule forager then makes a decision about whether to leave a patch or not by combining its moving average valuation of the environment up to the last time step with information gathered in the current time step (e.g. Beauchamp 2000a; Groß et al. 2008; Hamblin & Giraldeau 2009).

Compared to this considerable amount of theoretical work, empirical tests of these models’ predictions are relatively limited and have mainly focussed on the pMVT (reviewed in Nonacs 2001; but see Valone 2006). In those few cases where models of perfectly informed foragers have been empirically compared against either Bayesian or learning models (i.e. models of foragers with imperfect information), perfect-information models provided a relatively poor explanation of the foraging behaviour observed (Alonso et al. 1995; Amano et al. 2006; van Gils et al. 2003, but see Nolet et al. 2006). For example, Bayesian updating models explained foraging behaviour better than other models, including a prescient forager model, in red knots (*Calidris canutus*) (van Gils et al. 2003). I know of no empirical study, however, that has compared the performance of Bayesian, learning and perfect-information models, such as the pMVT, in the same analysis. Furthermore, there is evidence that a forager’s use of past experiences in its patch-departure decisions, within

either the Bayesian or learning framework, can be dependent on the characteristics of the foraging habitat (Biernaskie, Walker & Gegeer 2009; Devenport & Devenport 1994; Lima 1984; Valone 1991, 1992). However, most studies to date have only compared foraging behaviour between captive environments or differing configurations of artificial food patches (but see Alonso et al. 1995). Therefore, to fully understand how a forager uses previous experiences in its decision-making, a simultaneous comparison of perfect-information, Bayesian-updating and learning-rule models, ideally involving both natural and experimental conditions (in which the characteristics of the foraging habitat can be manipulated), would be extremely valuable.

The purpose of this chapter is, therefore, to empirically test whether patch departure models that assume foragers' knowledge of their environment is imperfect, such as the Bayesian-updating and learning rule approaches, provide a better description of patch-departure decisions than those that assume perfect knowledge. To do this, I consider which aspects of an individual's environment and its foraging experiences these different models predict will play a role in patch-departure decisions, and assess the explanatory power of these different factors in the patch residency times of wild chacma baboons (*Papio ursinus*) in both their natural foraging habitat and in a large-scale field experiment.

## **Materials and Methods**

### Study Site

Fieldwork was carried out at Tsaobis Leopard Park, Namibia (22°23'S, 15°45'E), from May to September 2010. The environment at Tsaobis predominantly consists of two habitats: open desert and riparian woodland. The open desert, hereafter 'desert', is characterised by alluvial plains and

steep-sided hills. Desert food patches mainly comprise small herbs and dwarf shrubs such as *Monechma cleomoides*, *Sesamum capense* and *Commiphora virgata*. The riparian woodland, hereafter ‘woodland’, is associated with the ephemeral Swakop River that bisects the site. Woodland food patches are large trees and bushes such as *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica* (see Chapter 3 and Cowlshaw & Davies 1997 for more detail). At Tsaobis, two troops of chacma baboons (total troop sizes = 41 and 33 in May 2010), hereafter the ‘large’ and ‘small’ troop, have been habituated to the presence of human observers at close proximity. The baboons at Tsaobis experience relatively low predation risk as their main predator, the leopard (*P. pardus*, Linnaeus 1758), occurs at low densities, while two other potential predators, lions (*Panthera leo*, Linnaeus 1758) and spotted hyenas (*Crocuta crocuta*, Erxleben 1777), are entirely absent (Cowlshaw 1994). We collected data from all adults and those juveniles over two years old ( $n = 32$  and  $22$ ), all of whom were individually recognisable (see Huchard et al. 2010 for details). Individuals younger than two were not individually recognisable and so were not included in this study.

### Data Collection

#### *Natural foraging behaviour*

Baboon behaviour was observed under natural conditions using focal follows (Altmann 1974b), and recorded on handheld Motorola MC35 (Illinois, U.S.A) and Hewlett-Packard iPAQ Personal Digital Assistants (Berkshire, U.K.) using a customised spreadsheet in SpreadCE version 2.03 (Bye Design Ltd 1999) and Cybertracker v3.237 (<http://cybertracker.org>), respectively. Focal animals were selected in a stratified manner to ensure even sampling from four three-hour time blocks (6 – 9 a.m., 9 a.m. – 12 p.m., 12 – 3 p.m. and 3 – 6 p.m.) across the field season, and no

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animal was sampled more than once per day. Focal follows lasted from twenty to thirty minutes (any less than twenty minutes were discarded). At all times we recorded the focal animal's activity (mainly foraging, resting, travelling or grooming) and the occurrence, partner identity and direction of any grooming or dominance interactions. We also recorded the duration of grooming bouts. During foraging we recorded when the focal animal entered and exited discrete food patches. Entry was defined as the focal moving into and eating an item from the patch (to rule out the possibility that they were simply passing by or through the patch), and exit defined as the focal subsequently moving out of the patch. Patches were defined as herbs, shrubs or trees with no other conspecific plant within one metre (closer conspecifics, which could potentially be reached by the forager without moving, were treated as part of the same patch), and made up the vast majority of the baboons' diet. At each patch entry we recorded the local habitat (woodland or desert), the number of other baboons already occupying the patch, the identity of any adult occupants, and three patch characteristics: the patch size, type, and food-item handling time. Patch size was scored on a scale of 1-6 in the woodland and 1-4 in the desert (see Tables 3.3. and 3.4 in Chapter 3), and subsequently converted into an estimate of surface area (m<sup>2</sup>) using patch sizes recorded during a one-off survey of 5,693 woodland patches and monthly phenological surveys of desert patches, respectively. See below for details of the surveys; for details of the surface area estimations, see Marshall et al. (2012a)/Chapter 4. Patch type was recorded by species for large trees and bushes in the woodland, and as non-specified 'herb/shrub' for smaller woodland and all desert patches. Food-item handling time was classed as high (bark, pods and roots) or low (leaves, berries and flowers). Overall, we recorded 1,481 focal hours ( $27 \pm 10$  hours, mean  $\pm$  s.d., per individual) containing 6,594 patch visits ( $112 \pm 71$  visits per individual) for my analyses.

Temporal variation in habitat quality was estimated by the monthly, habitat-specific, variation in both the mean number of food items per patch and the patch density. These calculations



were based on monthly phenological surveys in which we estimated the number of food items in randomly selected food patches. In the woodland, we monitored a representative sample of 110 patches selected from an earlier survey of 5,693 woodland patches (G. Cowlishaw, unpublished data); in the desert, we monitored 73 food patches that fell within eight randomly placed 50 m x 1 m transects. In both habitats, the monitored patches fell within the study troops' home ranges. Monthly estimates of patch density were calculated as the mean number of patches containing food per km<sup>2</sup>. In the woodland, this was calculated by randomly grouping the survey patches into 11 groups of 10, and calculating the proportion of these patches containing food in each group per month. Each group's proportion was then used to estimate a patch density (the number of the 5,693 woodland patches containing food divided by 9.9 km<sup>2</sup>, the extent of the woodland habitat in the study area) and the mean of these values taken as the woodland patch density, for any given month. In the desert, monthly estimates of patch density were calculated from the mean of the number of patches containing food in each transect divided by  $5 \times 10^{-5}$  (transect area of  $50\text{m}^2 = 5 \times 10^{-5} \text{ km}^2$ ).

### *Large-scale feeding experiments*

The foraging experiments were conducted in an open, flat and sandy area in each troop's home range. They involved a configuration of five artificial food patches of loose maize kernels arranged as shown in Figure 5.1. The baboons visiting each patch were recorded using Panasonic SDR-S15 (Kadoma Osaka, Japan) video cameras on tripods, and so patches were trapezoidal to maximise the use of their field of view. The five patches were a combination of sizes, two measuring 20 m<sup>2</sup> (patches B and C in Fig. 5.1) and three at 80 m<sup>2</sup> (patches A, D and E) for the small troop, producing a total per-animal feeding area of 8.5 m<sup>2</sup> (280 m<sup>2</sup> divided by 33 animals). We kept the total per-animal feeding area approximately constant by increasing these patch sizes to 27 m<sup>2</sup> and 96 m<sup>2</sup> for the large troop, producing a total per-animal feeding area of 8.3 m<sup>2</sup> (342 m<sup>2</sup> divided

by 41 animals). The experiment was run in two 14-day periods, alternating between troops. In the first period, patch food content ( $f$  in Fig. 5.1) was ‘low’ ( $11.4 \pm 0.3 \text{ g/m}^2$ , mean  $\pm$  s.d.) while inter-patch distance ( $d$ ) was ‘short’ (25 m) for the first 7 days and ‘long’ (50 m) for the second 7 days. In the second 14-day period, patch food content was increased by 50% to ‘high’ ( $17.1 \pm 0.4 \text{ g/m}^2$ ) while inter-patch distance was ‘long’ for the first 7 days and ‘short’ for the second 7 days. The experiments were therefore run over 28 days in total, involving four different food content – inter-patch distance combinations, for each troop. The amount of food per patch was measured using a standard level cup of maize kernels weighing  $222 \pm 1 \text{ g}$  (mean  $\pm$  s.d.,  $n = 20$ ).

Experimental food patches were marked out with large stones, painted white, and were evenly scattered with maize kernels before dawn each morning. Video cameras (one per patch, started simultaneously when the first baboon was sighted) were used to record all patch activity and trained observers (one per patch) recorded the identity of all individuals entering and exiting the patch. These patch entry and exit data were subsequently transcribed from the videos to create a dataset in which each row represented one patch visit and included: the forager ID, the patch ID, the patch residency time (s), the initial food density of the patch at the start of the experiment ( $\text{g/m}^2$ ), the patch depletion (indexed by the cumulative number of seconds any baboon had previously occupied the patch), the forager’s satiation (indexed by the cumulative number of seconds the focal baboon had foraged in any patch that day) and the number and identity of all other individuals in the patch. Video camera error on day 11 of the large troop’s experiment meant that data from all patches were not available on that day, resulting in unreliable depletion and satiation estimates. Data from this day were therefore excluded, leaving 8,569 patch visits ( $159 \pm 137$  per individual) in the final dataset for analysis.

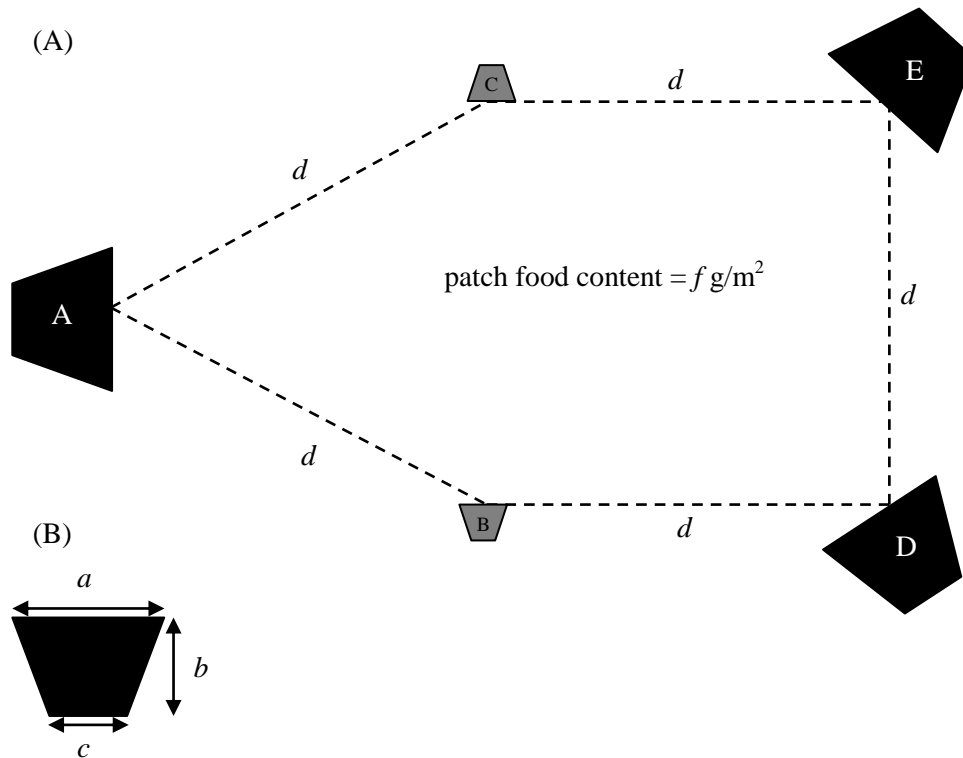


Figure 5.1. Schematic of the foraging-experiment's patch (A) layout and (B) dimensions. For each troop's patch food content,  $f$ , was varied between  $11.1 \pm 0.1$  grams/m<sup>2</sup> (low, first 14 day period) and  $16.7 \pm 0.1$  g/m<sup>2</sup> (high, second 14 day treatment) of loose dried maize kernels. Inter-patch distance ( $d$ ) was varied with each 14-day period. In the first period it was set at 25m (low) for the starting 7 days and 50m (high) for the remaining 7 days, and vice versa for the second period. Patch size was constant with troops. Large patches (A, D and E) were set at 80m<sup>2</sup> ( $a = 10$ m,  $b = 10$ m,  $c = 6$ m) for the small troop and 96m<sup>2</sup> (10, 12, 6) for the large troop. Small patches (C and D) were set at 20m<sup>2</sup> (5, 5, 3) for the small troop and 27m<sup>2</sup> (6, 6, 3) for the large troop.

### *Individual forager characteristics*

For each focal animal, I calculated its dominance rank, social (grooming) capital, and genetic relatedness to other animals in the troop. Dominance hierarchies were calculated from all dominance interactions recorded in focal follows and *ad libitum* (in both cases, outside of the experimental periods;  $n_{\text{large}} = 2391$ ,  $n_{\text{small}} = 1931$ ) using Matman 1.1.4 (Noldus Information Technology 2003). Hierarchies in both troops were strongly linear (Landau's corrected linearity index:  $h'_{\text{large}} = 0.71$ ,  $h'_{\text{small}} = 0.82$ ,  $p < 0.001$  in both) and subsequently standardised to vary between 0 (most subordinate) and 1 (most dominant) to control for the difference in troop sizes. Social

capital was calculated using a grooming symmetry measure as there is growing evidence, particularly in primates, that asymmetries in grooming interactions can be traded for foraging tolerance (e.g. Fruteau et al. 2009). This symmetry measure was calculated as the proportion of grooming time between two individuals that the focal animal was the groomer, minus 0.5 (to make balanced relationships 0), multiplied by the proportion of total focal time that the focal and partner were observed grooming together during focal follows. Finally, dyadic relatedness ( $r$ ) was estimated on the basis of 16 microsatellite loci using Wang's triadic estimator (Wang 2007; see Huchard et al. 2010 for further details). These data were then used in the analysis of natural and experimental foraging behaviour to calculate: (1) each forager's rank, mean social capital and mean relatedness with other troop members, as individual characteristics of the forager that were constant across patches, and (2) the mean rank difference, social capital and relatedness between the focal forager and other patch occupants, which were specific for each patch visit.

### Analysis

I formulated eight models describing the factors predicted to influence patch departure decisions, and so patch residency times, by the three types of patch-departure model (fixed-rule, including pMVT, Bayesian-updating, and learning rules: see Introduction). I then compared these models' performances against each other as explanations of the natural and experimental patch residency times we observed. These models comprised different combinations of three groups of variables that described, respectively, the forager's current foraging experience,  $\mathbf{c}$ , its recent foraging experience,  $t$ , and the broader habitat characteristics,  $\mathbf{h}$ . Here  $t$  is simply the time the forager spent in the previous patch, whilst  $\mathbf{c}$  and  $\mathbf{h}$  are vectors of variables that describe the current physical and social characteristics of both the patch and the forager, in the case of  $\mathbf{c}$ , and the

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foraging habitat's characteristics, in the case of  $\mathbf{h}$  (see below for details of the variables included in each vector).

The simplest patch-departure models assume that a forager's decision to leave a patch (and so the time it spends in it) is solely based on a rule fixed by some aspect of their environment. To explore this approach, my first three models predict patch residency time (PRT) simply from the forager's current experience, i.e.  $\text{PRT} = f(\mathbf{c})$  (model 1), recent experience,  $\text{PRT} = f(t)$  (m2) and habitat characteristics,  $\text{PRT} = f(\mathbf{h})$  (m3), respectively. Such fixed-rule models are often considered to represent the 'floor' on foraging performance (e.g. Olsson & Brown 2006), i.e., the poorest of performances, so these three models (m1-m3) are intended to act as a baseline against which the more sophisticated models, that are likely to achieve higher levels of performance, can be compared (see below). The prescient version of the marginal-value theorem (Charnov 1976), which assumes foragers are perfectly informed, predicts a forager should leave a patch when their intake rate in that patch falls below the habitat's long-term average, or 'marginal value'. In this case, my fourth model predicts PRT from a combination of the forager's current experience and the habitat characteristics:  $\text{PRT} = f(\mathbf{c} + \mathbf{h})$  (m4).

Bayesian-updating and learning-rule models suggest that foragers use their recent experiences to inform their patch-departure decisions. In learning models, foragers possess a valuation of their environment, a moving average of their foraging experiences up to the previous time step, and information about the foraging conditions in the current time step. Foraging decisions in the current time step are made by differentially weighting and combining these two elements (environmental valuation and current information) into a single value for the current patch or foraging tactic (Kacelnik & Krebs 1985; Beauchamp 2000a; Hamblin & Giraldeau 2009). This suggests that, in this study, PRT should be predicted by the previous foraging experience,

representing the forager's valuation of the environment, and the current foraging conditions, or  $PRT = f(\mathbf{c} + t)$  (m5), approximately describing the simplest learning rule, the linear operator (Kacelnik & Krebs 1985). Bayesian models, in contrast, suggest that foragers have a perception of the environment's distribution of food (rather than a simple valuation), which they update using their recent experiences, and then combine this information with current foraging experiences to make their patch-departure decisions (see Dall et al. 2005; McNamara et al. 2006), thus suggesting:  $PRT = f(\mathbf{c} + t + \mathbf{h})$  (m6). Finally, there is some evidence that the use of recent experiences may be contingent on habitat variability, as increases in variability may decrease the reliability of recent experiences in predicting the next experience, and so informing decisions (Lima 1984; Valone 1992). Therefore, my final two models develop m5 and m6 further by including an interaction between the forager's recent experience and habitat variability:

$$PRT = f(\mathbf{c} + t + \mathbf{h}_{sd} + t \times \mathbf{h}_{sd}) \text{ (m7)}$$

$$\text{and, } PRT = f(\mathbf{c} + t + \mathbf{h} + \mathbf{h}_{sd} + t \times \mathbf{h}_{sd}) \text{ (m8).}$$

Here,  $\mathbf{h}_{sd}$  is a vector of variables describing the standard deviation of the mean estimated habitat characteristics (see below for details).

The variables included in vectors  $\mathbf{c}$ ,  $\mathbf{h}$  and  $\mathbf{h}_{sd}$  were as follows. In models predicting natural PRTs, the forager's current experience,  $\mathbf{c}$ , was described by the patch size, food species and handling time. In models predicting experimental PRTs,  $\mathbf{c}$  comprised the patch's initial food density, estimated depletion and the focal forager's estimated satiation. Since the social environment can also influence a forager's current foraging experience,  $\mathbf{c}$  also included (for both natural and experimental PRT models) the focal forager's rank, mean social capital and mean relatedness to other troop members, and, on a patch-by-patch basis, their mean rank difference,

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social capital and relatedness to other patch occupants, plus the number of patch occupants present (linear and quadratic terms). The variables describing the foraging habitat characteristics,  $\mathbf{h}$ , reflected the average patch quality and density. In the natural PRT models, these were the monthly habitat-specific estimates of both food items per patch and food patches per km<sup>2</sup>; in the experimental PRT models, these were the mean initial weight of food per patch (g) and inter-patch distance (m). Finally, in the natural PRT models,  $\mathbf{h}_{sd}$  described the standard deviations around the estimates of both the mean number of food items per patch and patch density ( $\mathbf{h}_{sd}$  was not explored in the experimental PRT models, since the initial patch quality and density were fixed with zero variance).

Models 1 to 8 and a null model (containing no fixed effects) were estimated using generalised linear mixed models for the natural and experimental PRTs datasets. In both cases, all non-categorical explanatory variables were standardised to have a mean of zero and standard deviation of one. Natural models included focal follow number nested within focal animal ID, nested within troop as random effects. Experimental models included focal animal ID, patch ID and experiment day cross-classified with each other and nested within troop, as random effects. To account for overdispersion in the PRT data, all models also included an observation-level random effect and were fitted as Poisson lognormal mixed effects models using a log link function (Elston et al. 2001) in the package lmer in R (Bates et al. 2011; R Development Core Team 2011). I assessed these models' performance (nine models in the natural analyses, seven in the experimental analyses) using Akaike's model weights. These were calculated from AIC values, since in all models  $n/k > 40$ , where  $n$  is the number patch visits and  $k$  is the number of parameters in the maximal model (Burnham & Anderson 2002; Symonds & Moussalli 2011).

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## Results

The baboons visited food patches for a median of 30 seconds (inter-quartile range = 12 – 79 s,  $n = 6,594$ ) in natural foraging conditions and 52 seconds (16 – 157 s,  $n = 8,569$ ) in experimental foraging conditions.

Natural PRTs were best explained by the model containing factors predicted by the prescient marginal value theorem (Akaike's model weight  $w_i = 0.69$ , Table 5.1, see Table S2.1 for full details of the models) but also showed some support for the model containing factors predicted by a Bayesian-updating rule ( $w_i = 0.27$ ). In contrast, experimental PRTs were best explained by the model containing factors predicted by a Bayesian-updating rule above all other models ( $w_i = 0.98$ , Table 5.1, see Table S2.2 for full details of the models). In both conditions, the influence of the foraging habitat's characteristics on PRTs was consistent with the predictions of the prescient marginal value theorem (Table 5.2): the baboons spent less time in food patches when the environment was characterised by higher quality patches at higher densities. In both conditions, the model based on a Bayesian-updating rule also showed that baboons stayed longer in a patch when they had spent more time in the previous patch. The effect of this recent foraging experience was, however, relatively weak, especially in the natural observations (Table 5.2).



Table 5.1. Model performance in explaining patch residency times, under natural and experimental conditions. Models in bold make up the 95% confidence model set. AIC = Akaike's information criterion,  $\Delta\text{AIC}$  = difference between AIC score and lowest AIC score,  $w_i$  = Akaike's model weight. See Tables S2.1 and S2.2 for full details of the models.

<u>natural</u>					<u>experimental</u>				
no.	patch-departure rule from predictions of :	AIC	$\Delta\text{AIC}$	$w_i$	no.	patch-departure rule from predictions of :	AIC	$\Delta\text{AIC}$	$w_i$
<b>4</b>	<b>prescient marginal value theorem</b>	<b>28342.16</b>	<b>0.00</b>	<b>0.69</b>	<b>6</b>	<b>Bayesian updating</b>	<b>48410.75</b>	<b>0.00</b>	<b>0.98</b>
<b>6</b>	<b>Bayesian updating</b>	<b>28344.06</b>	<b>1.90</b>	<b>0.27</b>	5	learning-rule	48418.16	7.41	0.02
7	learning-rule dependent on habitat variability	28348.33	6.18	0.03	4	prescient marginal value theorem	48429.22	18.47	0.00
8	Bayesian updating dependent on habitat variability	28349.61	7.46	0.02	1	fixed rule based on current foraging condition	48436.57	25.82	0.00
1	fixed rule based on current foraging condition	28377.87	35.71	0.00	3	fixed rule based on habitat's patch configuration	49161.69	750.94	0.00
5	learning-rule	28379.16	37.01	0.00	2	fixed rule based on recent foraging experience	49174.14	763.39	0.00
3	fixed rule based on habitat's patch configuration	29323.18	981.0	0.00		null	49200.07	789.32	0.00
2	fixed rule based on recent foraging experience	29521.79	1179.64	0.00					
	null	29543.59	1201.43	0.00					

Table 5.2. The influence of previous foraging experience and foraging habitat characteristics (effect sizes,  $\beta \pm$  s.e.) on patch residency times (PRTs) in the best models (95% confidence set, see Table 5.1) under natural and experimental conditions

natural PRT models (model number)			experimental PRT models (model number)	
predictors	prescient marginal value theorem (m4)	Bayesian-updating (m6)	predictors	Bayesian-updating (m6)
time in previous patch (s)		$0.006 \pm 0.02$	time in previous patch (s)	$0.08 \pm 0.02$
mean number of food items per patch	$-0.11 \pm 0.03$	$-0.11 \pm 0.03$	mean weight of food per patch (g)	$-0.56 \pm 0.15$
mean number of food patches per km <sup>2</sup>	$-0.16 \pm 0.02$	$-0.16 \pm 0.03$	inter-patch distance (m)	$0.10 \pm 0.04$

## Discussion

The use of a patch-departure decision rule consistent with a Bayesian-updating process was strongly supported by the behaviour of the foragers on the experimental food patches. In contrast, foraging behaviour under natural conditions, whilst showing some support for the use of Bayesian-updating, showed greater support for a patch-departure rule based on the prescient marginal value theorem. Furthermore, in both environments my Bayesian-updating models also suggested that the influence of a single previous foraging experience was relatively weak. The discussion first focuses on why these differences in decision-making between the two environments might occur and what this might suggest about the animals' abilities to efficiently exploit different environments. I then consider what these results reveal about how foragers use their recent experiences in their patch-departure decisions and the implications of these findings for the modelling of foraging behaviour.

Previous work has suggested that differences in the weight a forager places on their most recent experiences between habitats may be due to these experiences providing more reliable indicators of future foraging rewards when environments are either more predictable (Valone 1991; Devenport & Devenport 1994; Fortin 2002; Vásquez et al. 2006; Eliassen et al. 2009) or less variable (Lima 1984; Valone 1992; Biernaskie et al. 2009). These alternative hypotheses may coincide, since less variable environments may also be more predictable – but not always, since some patterns of variation, such as seasonal habitat changes, can also be highly predictable (Eliassen et al. 2009). My findings are able to distinguish between these two hypotheses to some extent, and support the former. If environmental variability had influenced the baboons' use of recent experiences I would have expected more support for my models which explicitly incorporated it (models 7 and 8). Instead, the baboons incorporated their most recent experience into their patch-departure decisions to a greater extent in the more predictable, i.e. experimental, foraging environment (Table 5.2). This environment was likely to have been more predictable as the relative quality and position of each patch remained constant throughout, and their absolute quality and position only changed once (after 14 days) and three times (after 7, 14, and 21 days), respectively (see Fig. 5.1, and Methods). In contrast, natural foraging environments, such as at Tsaobis, where food patches consist of multiple plant species, with different plant parts, whose phenology varies considerably across the year (not only between species but also between individuals), are inherently much less predictable.

An ability to flexibly incorporate recent experience, contingent on its reliability, into decision-making should allow foragers to maximise the efficiency with which they exploit different environments (Valone & Brown 1989; Valone 1991; Devenport & Devenport 1994; Rodriguez-Gironés & Vásquez 1997; Koops & Abrahams 2003). Such an ability appears to be possessed by the foragers in this study. This flexibility may also be widely distributed across a variety of taxa,

and not limited solely to cognitively advanced animals such as baboons. A model by Holmgren & Olsson (2000) demonstrated that incorporating recent experiences during Bayesian foraging was possible using a simple three-neurone network. Furthermore, there is growing evidence, from a range of taxa, that the incorporation of recent experiences into foragers' decision-making can vary between environments (insects: Biernaskie et al. 2009, birds: Alonso et al. 1995; Valone 1991, non-primate mammals: Devenport & Devenport 1994; Vásquez et al. 2006).

The model of forager behaviour predicted by Bayesian-updating was consistently supported over the model predicted by learning rules. This was true for both natural and experimental environments. Both Bayesian-updating (Oaten 1977; Green 1984; McNamara et al. 2006) and learning rules (Kacelnik & Krebs 1985; Beauchamp 2000a; Hamblin & Giraldeau 2009) have been proposed as descriptions of how foragers incorporate past experiences into their decision-making. My results seem to suggest that the former is more accurate in this system. This difference in performance may be explained by the fact that learning rules, particularly the linear operator rule that my model represents, are often simpler than Bayesian-updating approaches and may be less responsive to environmental variability (Groß et al. 2008; Eliassen et al. 2009). There is, however, evidence that the best way for a forager to incorporate previous experiences into their foraging decisions can be dependent on the underlying resource distribution (Rodríguez-Gironés & Vásquez 1997; Olsson & Brown 2006; Eliassen et al. 2009). Thus, although this study favours the Bayesian-updating approach, another study in a different setting might not. Furthermore, in this study I built each of the candidate models from the general theoretical principles underlying each approach. However, within each approach, different methods for incorporating previous experiences have been proposed, e.g. the 'linear operator' versus 'relative payoff sum' methods for learning rules (Beauchamp 2000a; Hamblin & Giraldeau 2009), and the 'current value' versus 'potential value assessment' methods for Bayesian updating (Olsson & Holmgren 1998; van Gils et al. 2003).

Another study, which was able to test more specifically these different methods, might find a narrower gap in performance between the learning and Bayesian approaches.

The influence of the baboons' most recent experience on their patch-departure decisions, whilst generally important, was still relatively small, suggesting that, where foragers inform such decisions with their recent experiences, they do so incrementally (Beauchamp 2000a; Amano et al. 2006; Biernaskie et al. 2009; Hamblin & Giraldeau 2009). That is, it is not just the previous foraging experience that is important but the experiences before that, and so on. This is consistent with the concept, common across models of imperfectly-informed foragers, that an individual's estimate of the environment's distribution of resources (Bayesian-updating) or value (learning rules) is an aggregate of their past experiences, and that individuals are continually updating this estimate with each subsequent experience (Kacelnik & Krebs 1985; McNamara et al. 2006). If, as here, the influence of each of these experiences is low, then as an increasing number of previous experiences are remembered this perceived distribution or valuation will increasingly approximate the true distribution (Koops & Abrahams 2003), i.e. the perfect knowledge assumed by the prescient marginal value theorem (pMVT; Charnov 1976). The predicted effects of patch quality and density characteristics in the best supported models (Table 5.2) were consistent with the pMVT's prediction, suggesting that the baboons' perception of their environment did incorporate many past experiences and was a good approximation of perfect knowledge. Once again, there is reason to believe that this finding is not specific to baboons, since (1) a weak effect of a single recent experience on foraging decisions has been shown many times previously (Beauchamp 2000a; Amano et al. 2006; Biernaskie et al. 2009; Hamblin & Giraldeau 2009), and (2) there is evidence from other taxa that foragers can incorporate experiences over many days into their decision-making (birds: Valone 1991; non-primate mammals: Devenport & Devenport 1994; Vásquez et al. 2006). Furthermore, in theoretical comparisons, prescient (i.e. perfect-knowledge) foragers perform

best (Koops & Abrahams 2003; Olsson & Brown 2006; Eliassen et al. 2009), and so it would seem likely that there is widespread selection for the ability to retain and use as many experiences as possible in foraging decision-making.

The finding that the baboons' perception of their environment included many past experiences and approximated perfect knowledge has two implications. First, it may provide an extra explanation for why the pMVT model outperformed the Bayesian-updating model in the natural foraging conditions. Here, the baboons were assigning very little weight to each foraging experience, which, as I have argued, is expected in this more natural, unpredictable environment. The inclusion of the single previous foraging experience variable in the Bayesian-updating model would therefore have provided very little extra explanatory power over the pMVT model, where this variable is absent, whilst being penalised 2 AIC points for the inclusion of the extra parameter. The AIC score difference of 1.9 points between the two models supports this argument. Thus, the baboons may have been using previous experiences in the natural foraging habitat, but this was less detectable given the relatively low weight assigned to each foraging experience. Indeed, it is hard to imagine how the baboons would have acquired sufficient knowledge of their environment to follow the pMVT were it not for the gradual accumulation of information through a process like Bayesian-updating or learning. It has also been noted that, where foragers update their information about the environment in such a gradual manner, distinguishing an updating from a non-updating strategy may be difficult (Eliassen et al. 2009).

The second implication is more important. If a forager's perception of its environment approximates perfect knowledge, then, in theory, its behaviour should also approximate optimality (Koops & Abrahams 2003), within the scope of its informational or physiological constraints (Fawcett et al. 2013). The empirical support for this theoretical prediction suggests that the

assumption of such knowledge by the prescient marginal value theorem may not be so unrealistic. Indeed, the predictions of the pMVT have received widespread qualitative support (Nonacs 2001). Modelling any natural process requires researchers to trade-off model accuracy and simplicity (Evans 2012). The present study, and previous research, indicates that models of patch-departure decisions that consider how foragers incorporate past experiences into these decisions will usually provide more realism and accuracy than simpler models. However, my findings also suggest that when attempting to predict foraging behaviour, the prescient marginal value theorem may provide a simpler approach without sacrificing a great deal of accuracy.

## Chapter 6

# The influence of primate social traits on foraging behaviour and success is dependent on local environmental conditions

### Abstract

In complex social groups an individual's dominance rank, social bonds and kinship with other group members have been shown to influence their foraging behaviour. However, there is growing evidence that the particular effects of these social traits may be dependent on local environmental conditions. I investigated this by comparing the foraging behaviour of wild chacma baboons, *Papio ursinus*, under natural conditions and in a field experiment where food was relatively high quality and spatially-clumped. Data were collected from 55 animals across two troops, including over 1,000 agonistic foraging interactions and over 9,000 food patch visits in each condition. In both conditions, lower ranked individuals were more likely to use unoccupied patches and to mediate the agonism they experienced using their social capital. However, there were also important differences between conditions. In natural conditions, where agonism rates were lower, foraging success was mostly independent of foragers' social traits; but in experimental conditions, where agonism rates were higher, higher ranked individuals had greater foraging success. My results suggest that, under natural conditions, foragers were able to compensate for low rank, but in the experiment, where competition was high, these compensatory mechanisms were overwhelmed. These findings support previous studies, suggesting that natural variation in food distributions can lead to advantages for dominant foragers during some periods but not others. They also highlight that persistent spatial clumping of food resources, which can be a result of anthropogenic impacts,



may lead to low-ranked foragers experiencing persistently lower foraging successes, with implications for their fitness and long-term group stability.

## **Introduction**

Understanding the causes and consequences of individual variation is central to behavioural ecology. In complex social groups, three primary axes of variation are an individual's dominance rank, social relationships and kinship relationships with other group members (Earley & Dugatkin 2010; East & Hofer 2010; Gardner et al. 2010). All three of these social traits can influence an individual's behaviour, in particular their foraging behaviour, which has been especially well-studied since foraging performance plays such an important role in an individual's fitness (Sutherland 1996; Giraldeau & Caraco 2000; Waite & Field 2007).

Individuals who are dominant over others, have good quality social bonds or are closely related to other group members tend to show improved foraging performance. However, there are many different ways in which this improved performance can be manifested. Dominant individuals tend to be less susceptible to interference competition, and more able to initiate aggression either in the defence or theft of food resources (Stillman et al. 1996; Stillman et al. 1997; Smith et al. 2001; Di Bitetti & Janson 2001; Barrett et al. 2002; Liker & Barta 2002; McCormack et al. 2007). There is evidence, however, that social capital or kinship ties with co-foragers can ameliorate these effects (Ha et al. 2003; King et al. 2009; Carter et al. 2009; Cheney et al. 2010; Silk et al. 2010a). Through these two mechanisms (defence and theft), dominant animals tend to occupy the best quality patches (Goss-Custard et al. 1995b; Bautista et al. 1995; Holmgren 1999) and, in spatially-structured groups, to hold those preferred spatial positions, usually at the centre and front, that provide access to such patches (Hemelrijk 2000; Di Bitetti & Janson 2001; Hirsch 2007; 2010).

Although, again, there is evidence that social capital and kinship ties can be used to negotiate access to better patches or spatial positions (Barrett et al. 1999; King et al. 2008; Fruteau et al. 2009; Mathot & Giraldeau 2010a). Finally, individuals' social traits may influence their ability to make optimal foraging decisions. Classic models of patch-departure decisions, such as the marginal value theorem (Charnov 1976), predict that foragers will leave patches when their intake rate falls below a certain threshold such that their long-term intake rate is maximised. However, this rate-maximisation approach ignores other fitness-linked motivations for leaving a patch, such as social aggression. In theory, foragers who incorporate these considerations into their decision-making experience increased fitness compared to those who make decisions in line with the classic rate-maximisation model (Nonacs 2001). As the social aggression that a forager experiences is likely to be influenced by their social traits (see above), it seems likely that these traits might also influence a forager's optimal decision-making and so their ability to exploit their environment. It appears, however, that this possibility is yet to be explored.

There is growing evidence that the influence of social traits on individual behaviour may also be dependent on local environmental conditions (Stillman et al. 2002; Vahl et al. 2005; 2007; Tanner & Jackson 2012). There is a long-established view that dominance hierarchies, particularly in primate systems, only emerge when resources are clumped requiring group members to contest them (Van Schaik 1989; Isbell & Young 2002). More recently, there has been growing evidence that, in groups where dominance hierarchies exist, the influence of an individuals' rank on its foraging behaviour can be dependent on the local environment. Stillman et al. (1996) found that dominant oystercatchers (*Haematopus ostralegus*) were only less susceptible to interference competition where competitor densities were high. Stillman et al. (2002) also found that common crane (*Grus grus*) feeding aggression was best predicted by a model in which dominant individuals only engaged in aggressive behaviour in those environments where their intake fell below a certain

threshold. Similarly, Vahl et al. (2005) related the effect of rank directly to food distribution, showing that dominant ruddy turnstones (*Arenaria interpres*) only experienced greater intake rates where food resources were spatially clumped. An individual-based model by Rands et al. (2006) also showed that the difference between dominant and subordinate energy reserves was greater in food-scarce environments. Fewer studies have investigated the environment-dependent effects of social capital. Barrett et al. (2002) found that female baboons (*Papio ursinus*) made greater use of social capital to reduce aggression when feeding competition was higher. More recently, European shore crabs (*Carcinus maenus*) have been shown only to form aggregations, and stable social networks, when food resources were clumped (Tanner et al. 2011; Tanner & Jackson 2012). I am unaware, however, of any studies investigating how the influence of kinship on social foraging might depend on local environmental conditions.

The environment-dependent influences of rank, social capital and kinship on social foraging behaviour are likely to play a fundamental role in determining how fitness varies between individual group members in different environments. Understanding these influences is, therefore, likely to be important in our appreciation of how the costs and benefits of sociality vary between individuals in different environments, and thus how sociality evolves and is maintained over time. In addition, such knowledge will also help us to predict how social animals are likely to be influenced by future environmental change.

Here I explore the influences of social traits on chacma baboon foraging behaviour in two environments: a natural environment, where food resources occurred in discrete patches but varied spatially and temporally in both their quality and distribution; and in a field-experimental environment, where a high-quality food resource was available in few concentrated patches. Baboons live in stable social groups within which individuals vary in their dominance rank, social

capital and kinship (Cheney & Seyfarth 2008). Comparing between the natural and experimental environments, I explored how these three social traits influenced (1) the feeding-related agonism individuals' experienced and (2) how these patterns of agonism might influence further aspects of their foraging behaviour and success. In the first case, I explored how individuals differed in the rate of agonism they experienced and the proportion of this agonism that they initiated. In the second case, my analysis explored four measures (i-iv) of foraging behaviour. I explored (i) how individuals differed in their use of occupied food patches, given that the costs and benefits of foraging with others might be expected to vary with individuals' social traits and the surrounding environment (Giraldeau & Caraco 2000; Waite & Field 2007). I then explored how individuals' social traits influenced their foraging success as measured by their (ii) intake rate and (iii) the time they spent in a food patch. Finally, I explored (iv) how variation in the foraging agonism individuals experienced might influence their ability to exploit their environment. Foraging theory suggests that the optimal strategy for exploiting an environment involves leaving patches once their food content falls below a fixed threshold (Charnov 1976; Stephens & Krebs 1986), predicting a positive correlation between initial intake rate and patch residency time (once physical and social factors influencing differences in patch depletion rates are controlled for). Therefore, I measured the effect of the predictors of agonism in the first step, on the strength of this correlation and so the ability to efficiently exploit the environment.

## **Methods**

### Study Site

Fieldwork was carried out at Tsaobis Leopard Park, Namibia (22°23'S, 15°45'E), from May to September 2010. The environment at Tsaobis predominantly consists of two habitats: open desert

and riparian woodland. The open desert, hereafter ‘desert’, consists of alluvial plains and steep-sided hills mainly containing small herbs and dwarf shrubs such as *Monechma cleomoides*, *Sesamum capense* and *Commiphora virgata*. The riparian woodland, hereafter ‘woodland’, is associated with the ephemeral Swakop River that bisects the site and mainly contains large trees and bushes such as *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica* (see Chapter 3 and Cowlshaw & Davies 1997 for more details). At Tsaobis, two troops of chacma baboons (total troop sizes = 41 and 33 in May 2010), hereafter the ‘large’ and ‘small’ troop, have been habituated to the presence of human observers at close proximity. We collected data from all adults and those juveniles over two years old ( $n = 32$  and  $22$ ), all of whom were individually recognisable (see Huchard et al. 2010 for details). Younger animals were not individually recognisable and so were not included in this study.

### Data Collection

#### *Natural foraging behaviour*

Baboon behaviour was observed under natural conditions using focal follows (Altmann 1974b), and recorded on handheld Motorola MC35 and Hewlett-Packard iPAQ Personal Digital Assistants using a customised spreadsheet in SpreadCE version 2.03 (Bye Design Ltd 1999) and Cybertracker v3.237 (<http://cybertracker.org>), respectively. Focal animals were selected in a stratified manner to ensure even sampling from four three-hour time blocks (6 – 9am, 9am – 12pm, 12 – 3pm and 3 – 6pm) across the field season. No animal was sampled more than once per day. Focal follows lasted from 20 – 30 minutes (any less than 20 minutes were discarded). At all times we recorded the focal animal’s activity (mainly foraging, resting, travelling or grooming) and the occurrence, partner identity and direction of any grooming or agonistic interactions. We also

recorded the duration of grooming bouts and the context of agonistic interactions (e.g. access to food, water or a preferred grooming partner). During foraging we recorded when the focal animal entered and exited discrete food patches. Entry was defined as the focal moving into and eating an item from the patch (to rule out the possibility that they were simply passing by or through the patch), and exit defined as the focal moving out of the patch. Patches were defined as herbs, shrubs or trees with no other conspecific plant within one metre (closer conspecifics, which could potentially be reached by the forager without moving, were treated as part of the same patch). These made up the vast majority of the baboons' diet. At each patch entry we recorded the habitat (woodland or desert), the patch's size, type and food-item handling time, the number of other baboons already occupying the patch, the identity of any adult occupants and, where possible, the focal individual's initial intake rate (bites in the first ten seconds). Patch size was scored on a scale of 1-6 in the woodland and 1-4 in the desert, and subsequently converted into an estimate of surface area ( $\text{m}^2$ ) (for details of these conversions, see Marshall et al. 2012a/Chapter 4). Patch type was recorded by species for large trees and bushes in the woodland, and as non-specified 'herb/shrub' for smaller woodland and all desert patches. Food-item handling time was classed as high (bark, pods and roots) or low (leaves, berries and flowers). Overall, we recorded 624 hours of feeding behaviour ( $11 \pm 5$ , mean  $\pm$  s.d., hours per individual). For the analyses, this sample contained 1,355 agonistic interactions over food resources ( $25 \pm 11$  per individual), 2,970 intake rates ( $54 \pm 35$  per individual), 2,358 patch visits ( $43 \pm 28$  per individual) for the analysis of patch residency time and 9,965 patch visits ( $181 \pm 92$  per individual) for the analysis of the use of occupied or unoccupied patches.

For each habitat in each month, we estimated both the mean number of food items per patch, and the patch density for each habitat, using monthly phenological surveys of randomly selected food patches. In the woodland, these were a representative sample of 110 patches from an earlier

survey of 5,693 woodland patches (G. Cowlshaw, unpublished data). In the desert, these were 73 food patches that fell within eight 50 m x 1 m transects randomly placed at four localities within the study troops' home ranges. Patch density estimates were calculated as the mean number of patches containing food per km<sup>2</sup>. In the woodland, this was calculated by randomly grouping the survey patches into 11 groups of 10, calculating the proportion of patches in each group containing food, extrapolating these proportions to estimate, out of all 5,693 woodland patches, how many patches in the woodland contained food, and then dividing these estimates by 9.9 km<sup>2</sup> (the extent of woodland habitat) to produce estimated patch densities. The mean and standard deviation of the groups' estimated densities was calculated to obtain an estimate of woodland patch density for that month. In the desert, monthly estimates of patch density were calculated from the mean of the number of patches containing food in each transect divided by 5 x 10<sup>-5</sup> km<sup>2</sup> (the transect area, 50m<sup>2</sup>).

### *Large-Scale Foraging Experiment*

Foraging experiments were conducted in an open, flat and sandy area in each troop's home range. They involved a configuration of five artificial food patches of loose maize kernels arranged as shown in Figure 6.1. Baboons visiting each patch were recorded using Panasonic SDR-S15 video cameras on tripods and so patches were trapezoidal to maximise the use of their field of view. Patches measured 20 m<sup>2</sup> (patches B and C in Figure 6.1) and 80 m<sup>2</sup> (patches A, D and E) for the small troop and, to keep the per-animal feeding area constant, 27 m<sup>2</sup> and 96 m<sup>2</sup> for the large troop (large troop  $n$ /small troop  $n = 41/33 \approx$  a patch size increase of 25%). The experiment was run in two 14-day periods for each troop. In the first period, patch food content ( $f$  in Figure 6.1) was 'low' ( $11.4 \pm 0.3$  g/m<sup>2</sup>, mean  $\pm$  s.d.) while inter-patch distance ( $d$ ) was 'short' (25 m) for the first 7 days and 'long' (50 m) for the second 7 days. In the second 14-day period, patch food content was increased by 50% to 'high' ( $17.1 \pm 0.4$  g/m<sup>2</sup>) while inter-patch distance was 'long' for the first 7

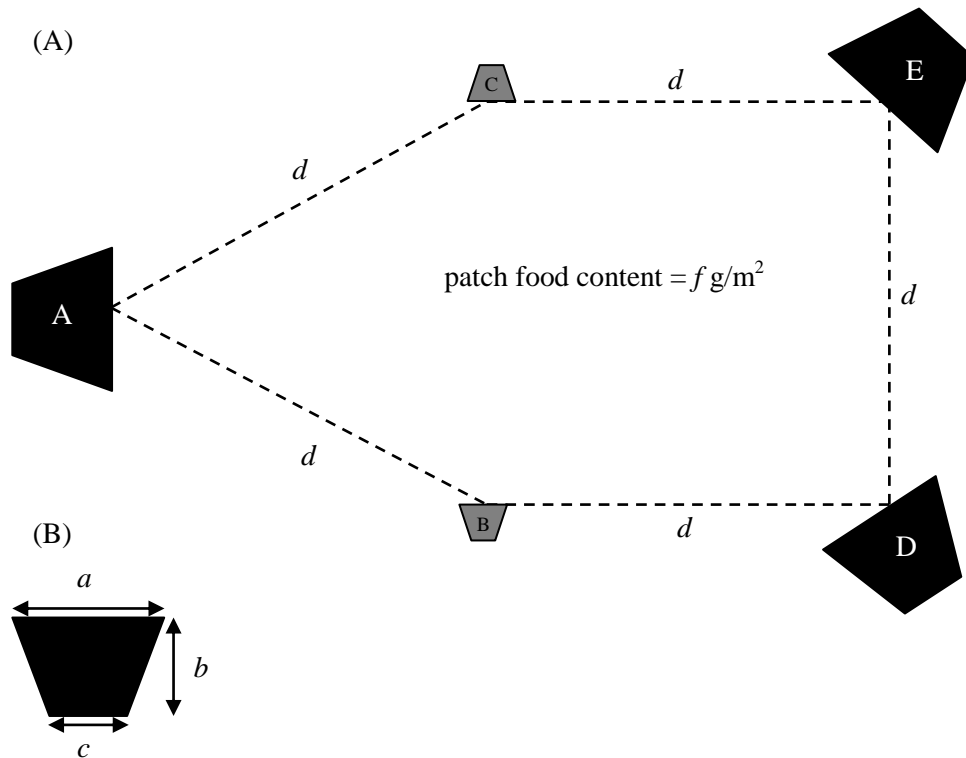


Figure 6.1. Schematic of the foraging-experiment's patch (A) layout and (B) dimensions. For each troop, patch food content,  $f$ , was varied between  $11.1 \pm 0.1 \text{ grams/m}^2$  (low, first 14 day period) and  $16.7 \pm 0.1 \text{ g/m}^2$  (high, second 14 day treatment) of loose dried maize kernels. Inter-patch distance ( $d$ ) was varied with each 14-day period. In the first period it was set at 25m (low) for the starting 7 days and 50m (high) for the remaining 7 days, and vice versa for the second period. Patch size was constant with troops. Large patches (A, D and E) were set at  $80\text{m}^2$  ( $a = 10\text{m}$ ,  $b = 10\text{m}$ ,  $c = 6\text{m}$ ) for the small troop and  $96\text{m}^2$  (10, 12, 6) for the large troop. Small patches (C and D) were set at  $20\text{m}^2$  (5, 5, 3) for the small troop and  $27\text{m}^2$  (6, 6, 3) for the large troop.

days and 'short' for the second 7 days. The experiments were therefore run over 28 days in total, involving four different food content – inter-patch distance combinations, for each troop.

Experimental food patches were marked out with large stones, painted white, and were evenly scattered with maize kernels before dawn each morning. Video cameras (one per patch, started simultaneously when the first baboon was sighted) were used to record all patch activity. Trained observers (one per patch) narrated the identity of all individuals entering and exiting the patch, and the actor and receiver in any agonistic interactions where at least one interactant was in



the patch or an 8m zone around it (also marked out with large white stones). Patch entry and exit data were subsequently transcribed from the videos to create a dataset in which each row represented one patch visit and included: the patch residency time (s), the initial food density of the patch at the start of the experiment ( $\text{g/m}^2$ ), the patch depletion (indexed by the cumulative number of seconds any baboon had previously occupied the patch), the forager's satiation (indexed by the cumulative number of seconds the focal baboon had foraged in any patch that day, as the baboons visited the experimental patches at the start of the day before natural foraging) and the number and identity of all other individuals in the patch. A random selection of these patch visits was then selected and the initial intake rate (bites in the first ten seconds) recorded. Video camera error on day 11 of the large troop's experiment meant data were not available from all patches on that day, resulting in unreliable depletion and satiation estimates. Data from this day were therefore excluded. The sample thus comprised a mean of  $9 \pm 7$  hours (mean  $\pm$  s.d.) of feeding behaviour per individual. For the analyses this contained 27,129 agonistic interactions ( $646 \pm 465$  per individual), 872 intake rates ( $16 \pm 9$  per individual), 730 patch residency times ( $15 \pm 8$  per individual) and 9,603 visits to occupied/unoccupied patches ( $178 \pm 144$  per individual) (the difference in intake rate and patch visit sample sizes being due the availability of the explanatory variables used in the analysis of each).

### *Individual Forager Characteristics*

For each focal animal, I calculated its dominance rank, social (grooming) capital, and genetic relatedness to other animals in the troop. Dominance hierarchies were calculated from dominance interactions recorded in the focal follows and *ad libitum* (in both cases, outside of the experimental periods;  $n_{\text{large}} = 2391$ ,  $n_{\text{small}} = 1931$ ) using Matman 1.1.4 (Noldus Information Technology 2003). Hierarchies in both troops were strongly linear (Landau's corrected linearity

index:  $h'_{\text{large}} = 0.71$ ,  $h'_{\text{small}} = 0.82$ ,  $p < 0.001$  in both) and subsequently standardised to between 0 (most subordinate) and 1 (most dominant) to control for the difference in troop sizes. Social capital was calculated using a grooming symmetry measure, as there is growing evidence, particularly in primates, that asymmetries in grooming interactions can be traded for tolerance at shared feeding sites (e.g. Fruteau et al. 2009). This measure was calculated as the proportion of grooming time between two individuals that the focal animal was the groomer minus 0.5 (to make balanced relationships 0), multiplied by the proportion of total focal time that the focal and partner were observed grooming together during focal follows. This measure, therefore, described the social capital held an individual held with a troop member by incorporating both the balance of the relationship and the time invested in it, such that a high score represented a relationship in which an individual had contributed a disproportionate and large amount of grooming time to another troop member. Finally, dyadic relatedness ( $r$ ) was estimated on the basis of 16 microsatellite loci using Wang's triadic estimator (Wang 2007; see Huchard et al. 2010) for further details. Social capital and relatedness were dyadic measures, and so were averaged across all possible dyads for each individual (involving all troop members >2 years of age) to obtain single individual scores.

### Analysis

The data analysis was performed in two stages, in line with my two research questions, testing how social traits predicted measures of individuals' (1) feeding-related agonism and (2) further foraging behaviour and success. Throughout I used generalised linear mixed models (GLMMs), fitted separately to data recorded under natural and experimental conditions. All models included the following fixed effects: individual rank, mean social capital and mean kinship, and all two-way interactions between these three traits, and, to control for the wider foraging habitat's

characteristics, mean patch food content and either patch density (natural conditions) or inter-patch distance (experimental conditions).

In the first stage of the analysis, I compared individual rates of food-related agonistic interactions in natural and experimental conditions using a Wilcoxon signed-rank test. I then explored the influence of social traits on rates of foraging agonism individuals experienced and the proportion of agonism they initiated. To do this, I separated each individual's agonistic interactions by habitat and month for the natural environment, and by food patch configuration (defined by patch quality and interpatch distance) for the experimental environment. I then calculated individual rates and proportions for each of these subsamples (8 habitat-month combinations and 4 patch configurations per individual) and analysed these data as response variables in GLMMs. Rates of agonism were overdispersed so, as the data were also continuous, I used a compound Poisson error structure with a log link. I analysed the proportion of agonism initiated using a binomial error structure and a logit link function. Individual ID, nested in troop ID were included in all models as random intercepts.

In the second stage of the analysis, I used GLMMs to explore how individual social traits influence foraging behaviour and performance, as measured by (i) the probability of using an occupied patch, (ii) initial intake rates, (iii) patch residency times and (iv) the correlation between intake rates and patch residency times (a measure of how efficiently a forager was exploiting the environment, see Introduction). To analyse the probability of foraging with others, patch visits were coded as with others (1) or alone (0) and models were fitted using a binomial error structure with a logit link function. Intakes rates and patch residency times were overdispersed and so analysed using an observation-level random effect and a Poisson-lognormal error structure with a log link function (Elston et al. 2001). As each data point in these datasets represented a single patch visit,

rather than an overall agonism measure for an individual (as in the first stage of the analysis), I included extra fixed effects to control for the physical and social attributes of the patch. Intake rate and patch residency time models included the number of patch occupants (linear and quadratic terms). Experimental models also included estimated forager satiation and, in the analysis of experimental patch residency times, the time the forager had spent in the previous patch as this can influence patch residency time (see Chapter 5). To control for the effects of physical food-patch characteristics, models of natural foraging behaviour included patch size ( $m^2$ ), species and food-part handling time (high/low), while experimental models included the patch's initial quality ( $g/m^2$ ) and estimated depletion. Finally, to test whether the foraging agonism an individual experienced influenced how efficiently they could exploit their environment – as measured by the positive correlation between initial intake rate and patch residency time (see Introduction) - I included initial intake rate, plus interactions between intake rate and the important variables identified by the agonism models, as fixed effects in the models of patch residency time. Models of natural foraging behaviour included focal follow number nested in focal animal ID nested in troop ID as random intercepts, and experimental foraging models included focal animal ID, patch ID and experiment day all nested in troop ID as random intercepts.

In both steps, all explanatory variables were standardised to have a mean of zero and standard deviation of one. Final models for each analysis were calculated using an information-theoretic approach. For each of the models the candidate model set consisted of all possible combinations of the fixed effects with the following conditions: the quadratic number-of-patch-occupants term was only fitted in models containing the linear term; interactions were only fitted in models containing both interaction variables as main effects; and the fixed effects included as controls in the second step were retained in all candidate models. Following Burnham and Anderson (2002), candidate models in the agonism analyses were evaluated using AICc because  $n/k$

$< 40$  in all cases (where  $n$  is the number of observations and  $k$  is the number of parameters in the maximal model) whereas candidate models in the foraging analyses were evaluated using AIC because  $n/k > 40$  in all cases. The maximum Akaike's model weight was relatively low in all analyses (maximum weight = 0.36) so I used all-subset model averaging to calculate a final model for each analysis (Symonds & Moussalli 2011). I interpreted the importance and influence of each fixed effect on the basis of their Akaike's weight, parameter estimate and confidence interval of this estimate.

All analyses were performed in R version 2.14.2 (R Development Core Team 2012) using the `cplm` package version 0.5-1 to fit compound Poisson models (Zhang 2012), the `lme4` package version 0.999375-42 to fit all other GLMMs (Bates et al. 2011) and the `MuMIn` package version 1.7.2 for model averaging (Barton 2012).

## Results

The rate of agonism experienced by baboons in natural foraging conditions (median = 0.036 interactions/minute, inter-quartile range = 0.026 – 0.049,  $n = 55$ ) was lower than in experimental conditions (1.42 interactions/minute, 0.85 – 1.82,  $n = 42$ ; Wilcoxon Signed rank  $W = 903$ ,  $p < 0.0001$ ,  $n = 56$ ). The proportion of agonistic interactions that individuals initiated ranged from 0 to 1, or 0.04 to 0.99, in natural and experimental conditions respectively. I found that dominant animals were involved in more agonism in natural conditions (Table 6.1, Figure 6.2A) but less in experimental conditions (Figure 6.2B). High social capital reduced agonism, but only for subordinate animals, and only consistently under natural conditions (Figure 6.2A). (There was evidence of a similar effect in the experimental conditions, Figure 6.2B, but the importance of both social capital and its interaction with rank was relatively low, and the confidence intervals were

Table 6.1. All-subset averaged models describing how individuals' rate of agonism and probability of initiating agonism in natural and experimental foraging conditions were influenced by their social traits and the habitats' patch configuration. See Appendix S3 for 95% confidence model sets.

Foraging conditions	Fixed effects	Rate of agonism (interactions/minute)				Probability of initiating agonism			
		Coefficient	Lower C.I.	Upper C.I.	Importance	Coefficient	Lower C.I.	Upper C.I.	Importance
Natural	(Intercept)	-3.29	-3.39	-3.19		-0.53	-0.75	-0.31	
	Rank	0.29	0.19	0.40	1.00	1.25	1.02	1.49	1.00
	Relatedness	-0.03	-0.13	0.07	0.48	0.10	-0.11	0.32	0.51
	Social bonds	-0.17	-0.31	-0.03	0.92	0.25	-0.05	0.54	1.00
	Rank x Relatedness	-0.06	-0.16	0.04	0.19	0.00	-0.24	0.25	0.13
	Rank x Social bonds	0.13	0.03	0.23	0.80	-0.70	-1.00	-0.39	1.00
	Relatedness x Social bonds	-0.01	-0.12	0.09	0.12	-0.12	-0.37	0.12	0.18
	Mean patch food content	-0.03	-0.13	0.07	0.30	0.12	-0.02	0.26	0.59
	Patch density	-0.14	-0.23	-0.05	0.97	0.05	-0.12	0.23	0.31
Experimental	(Intercept)	0.28	0.07	0.49		0.05	-0.22	0.33	
	Rank	-0.17	-0.32	-0.02	0.87	1.26	1.00	1.52	1.00
	Relatedness	-0.03	-0.20	0.14	0.38	0.19	-0.06	0.45	0.76
	Social bonds	-0.03	-0.26	0.19	0.66	-0.20	-0.52	0.12	1.00
	Rank x Relatedness	0.05	-0.09	0.19	0.10	0.27	0.02	0.52	0.59
	Rank x Social bonds	0.19	0.04	0.34	0.48	-0.46	-0.73	-0.18	0.97
	Relatedness x Social bonds	0.01	-0.15	0.16	0.06	0.11	-0.19	0.41	0.24
	Mean patch food content	-0.21	-0.30	-0.12	1.00	0.19	0.16	0.23	1.00
	Inter-patch distance	-0.07	-0.15	0.01	0.54	0.04	0.01	0.07	0.94

Table 6.1 note: Importance measured by Akaike's weight.

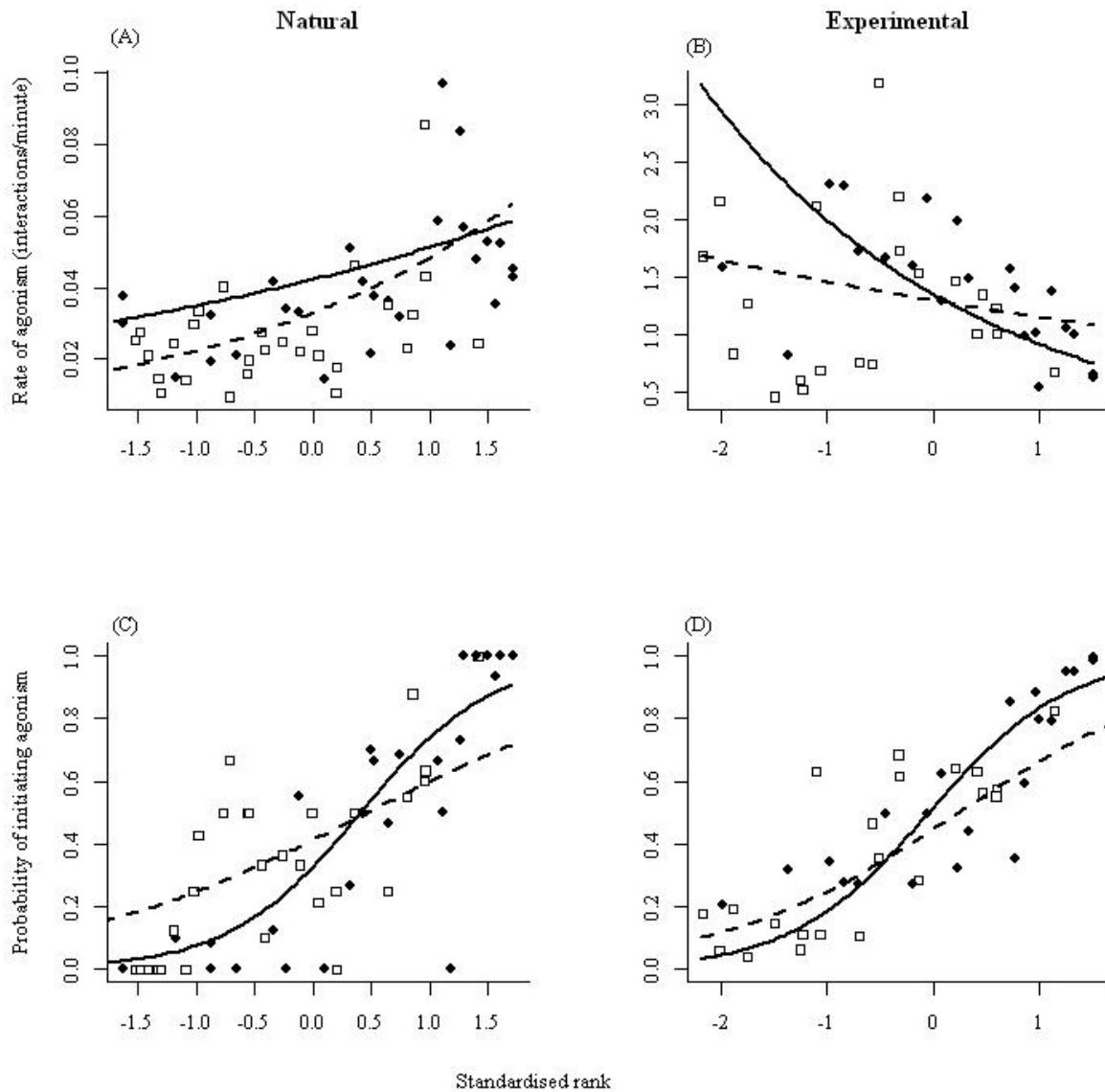


Figure 6.2. The effect of individual rank and social bonds on their rate of agonism (A and B) and probability of initiating agonism (C and D) in natural (A,C) and experimental (B,D) foraging conditions. In all plots the points are median values for each individual and the lines are the predicted relationships from each model (see table 6.1). Individuals are divided into those with social bonds higher (open squares and dashed line) and lower (closed circles and solid line) than the median.

large: Table 6.1). Higher-ranked animals were also more likely to initiate agonism (Figures 6.2C and 6.2D), although high social capital increased the probability of initiation for subordinate animals while reducing the probability for dominant animals. In addition to these social effects, individuals were involved in less agonism at higher patch densities in the natural environment and when patch food content was lower in the experiment. The probability of initiation also increased with patch food content and inter-patch distance in experimental conditions (Table 6.1). The fact that higher rates of initiation were not balanced by higher rates of receipt indicates that under these circumstances a greater proportion of agonistic interactions were being directed at individuals under the age of two (who were not individually recognisable) or at an unknown receiver (where agonism was directed over a distance and the intended receiver was unclear).

Baboons were less likely to enter occupied patches in natural conditions (median proportion of patches = 0.23, inter-quartile range = 0.17 – 0.33,  $n = 9,965$ ) but more likely to do so in experimental conditions (0.87, 0.79 – 0.92,  $n = 9,603$ ). Dominant animals (in both conditions) and animals with high social capital (in experimental conditions) were more likely to enter an occupied patch (Table 6.2, Figure 6.3). The use of occupied patches was also more frequent when patches were scarce (in natural conditions) and patch quality was low (in experimental conditions).

Baboons experienced median intake rates of 7 bites/10 seconds (inter-quartile range = 4 – 10,  $n = 2,970$ ) in natural conditions, and 4 bites/10 seconds (1 – 8,  $n = 872$ ) in experimental conditions. The corresponding patch residency times were 45 seconds (23 – 100,  $n = 2,358$ ) and 92 seconds (31 – 269,  $n = 730$ ), respectively. Whilst rank had little effect on either measure of foraging performance in natural conditions (Figures 6.4A and 6.4C), dominant animals were more likely to exhibit higher intake rates and longer patch residence times in the experiment (Figures 6.4B and 6.4D). Higher intake rates were also associated with more occupants and lower satiation in the



Table 6.2. All-subset averaged models describing how individuals' probabilities of using an occupied patch were influenced by their social traits and the habitats' patch configuration in natural and experimental foraging conditions. See Appendix S3 for 95% confidence model sets.

Foraging conditions	Fixed effects	Probability of foraging in an occupied patch			
		Coefficient	Lower C.I.	Upper C.I.	Importance
Natural	(Intercept)	0.22	-0.23	0.67	
	Rank	0.58	0.42	0.74	1.00
	Relatedness	0.12	-0.05	0.29	0.57
	Social bonds	0.02	-0.21	0.25	0.78
	Rank x Relatedness	0.00	-0.17	0.18	0.16
	Rank x Social bonds	0.13	-0.02	0.27	0.46
	Relatedness x Social bonds	-0.12	-0.26	0.03	0.25
	Mean patch food content	-0.04	-0.13	0.05	0.34
	Patch density	-0.48	-0.59	-0.37	1.00
Experimental	(Intercept)	2.27	0.42	4.11	
	Rank	0.40	0.20	0.61	1.00
	Relatedness	-0.07	-0.39	0.26	0.57
	Social bonds	0.40	0.10	0.70	0.99
	Rank x Relatedness	0.13	-0.06	0.31	0.28
	Rank x Social bonds	0.25	0.03	0.47	0.79
	Relatedness x Social bonds	0.06	-0.20	0.32	0.17
	Inter-patch distance	0.13	0.01	0.25	0.78
	Mean patch food content	-1.52	-2.41	-0.63	0.98
Satiation	0.02	-0.09	0.12	0.28	

Table 6.2 note: Models also included variables controlling for patches' physical characteristics (natural: patch size, species and handling time; experimental: patches' initial food density and estimated depletion), forager satiation and the wider foraging habitats' characteristics (natural: patch density and mean patch food content; experimental: inter-patch distance, mean patch food content). See Appendix S3 for full details.

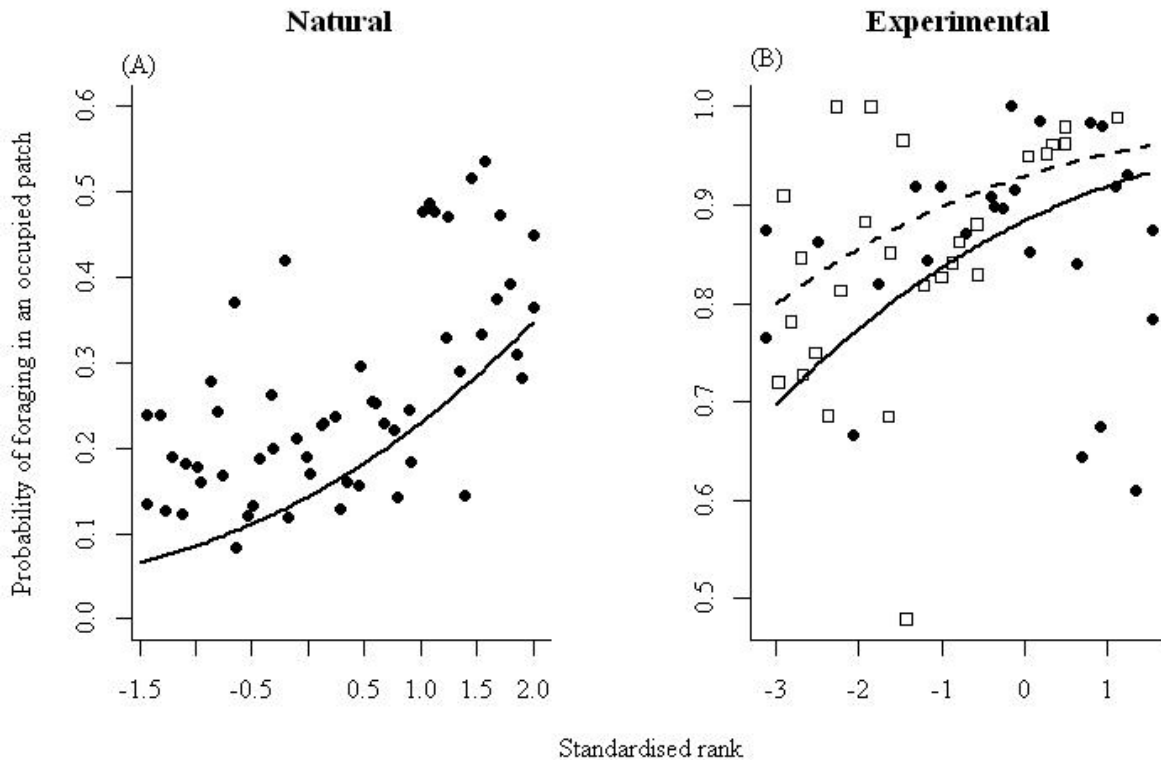


Figure 6.3. The effect of rank on the probability of using an occupied patch in (A) natural and (B) experimental foraging conditions. In both plots the points are the median values for each individual and the lines are the predicted relationships from each model (see table 6.2). In (B) the data is split into individuals with social bonds higher (dashed line and open squares) and lower (solid line and filled circles) than the median.

experiment (Table 6.3). Patch residency times had a convex relationship with number of patch occupants, peaking at nine occupants, in natural conditions but a simple positive relationship in the experiment (Table 6.3). This difference may arise because the maximum number of patch occupants in the experiment was seven (compared to 21 in natural conditions). Patch residency times were also shorter for animals with more social capital in both conditions (although in the experiment the confidence intervals crossed zero) (Table 6.3).

Finally, as optimal foraging theory predicts, individual patch residence times were longer in more profitable patches, i.e. where intake rates were higher, in natural conditions (Table 6.3, Figure 6.5A). This effect was independent of rank (i.e. there was no interaction between intake and rank).

Table 6.3. All-subset averaged models describing how individuals' initial intake rates and patch residency times in natural (this page) and experimental (next page) foraging conditions were influenced by their social traits, the number of patch occupants and (for patch residency times only) their initial intake rate. See Appendix S3 for 95% confidence model sets.

Foraging conditions	Fixed effects	Initial intake rate (bites/ten seconds)				Patch residency time (s)			
		Coefficient	Lower C.I.	Upper C.I.	Importance	Coefficient	Lower C.I.	Upper C.I.	Importance
Natural	(Intercept)	1.03	0.80	1.26		4.99	4.60	5.37	
	Rank	-0.05	-0.09	-0.01	0.91	0.01	-0.06	0.07	0.51
	Relatedness	0.04	0.00	0.09	0.94	0.09	0.02	0.15	0.74
	Social bonds	-0.03	-0.08	0.02	0.80	-0.12	-0.20	-0.05	0.99
	Rank x Relatedness	-0.01	-0.06	0.04	0.26	0.04	-0.04	0.11	0.15
	Rank x Social bonds	0.02	-0.02	0.06	0.27	-0.01	-0.07	0.06	0.14
	Relatedness x Social bonds	0.05	0.01	0.09	0.65	0.02	-0.05	0.08	0.22
	No. of patch occupants	0.01	-0.03	0.05	0.42	0.47	0.35	0.60	1.00
	No. of patch occupants <sup>2</sup>	0.02	-0.03	0.06	0.13	-0.28	-0.38	-0.18	1.00
	Initial intake rate					0.31	0.26	0.36	1.00
	x Rank					-0.01	-0.06	0.04	0.15
	x Social bonds					0.02	-0.03	0.06	0.34
	x Patch density					0.05	0.00	0.09	0.78

Table 6.3. continued

Foraging conditions	Fixed effects	Initial intake rate (bites/ten seconds)				Patch residency time (s)			
		Coefficient	Lower C.I.	Upper C.I.	Importance	Coefficient	Lower C.I.	Upper C.I.	Importance
Experimental	(Intercept)	1.33	0.86	1.81		4.61	4.41	4.80	
	Rank	0.29	0.17	0.42	1.00	0.35	0.21	0.48	1.00
	Relatedness	0.03	-0.15	0.21	0.89	0.09	-0.04	0.22	0.93
	Social bonds	-0.06	-0.22	0.10	0.57	-0.09	-0.22	0.03	0.92
	Rank x Relatedness	-0.11	-0.21	-0.01	0.65	-0.09	-0.19	0.01	0.59
	Rank x Social bonds	0.02	-0.11	0.16	0.17	0.00	-0.11	0.12	0.26
	Relatedness x Social bonds	0.11	-0.03	0.25	0.29	0.08	-0.03	0.18	0.45
	No. of patch occupants	0.18	0.05	0.30	1.00	0.36	0.17	0.55	1.00
	No. of patch occupants <sup>2</sup>	-0.03	-0.22	0.16	0.28	0.00	-0.32	0.31	0.27
	Satiation	-0.27	-0.37	-0.18	1.00	0.08	-0.06	0.22	0.40
	Initial intake rate					0.00	-0.13	0.13	0.97
	x Rank					0.19	0.04	0.34	0.90
	x Social bonds					0.12	-0.02	0.26	0.57
	x Inter-patch distance					-0.06	-0.17	0.04	0.40
	x Mean patch food content					-0.10	-0.22	0.02	0.56

Table 6.3.note: Models also included variables controlling for patches' physical characteristics (natural: patch size, species and handling time; experimental: patches' initial food density and estimated depletion), forager satiation and the wider foraging habitats' characteristics (natural: patch density and mean patch food content; experimental: inter-patch distance, mean patch food content and – patch residency times only – time in previous patch). See Appendix S3 for full details.

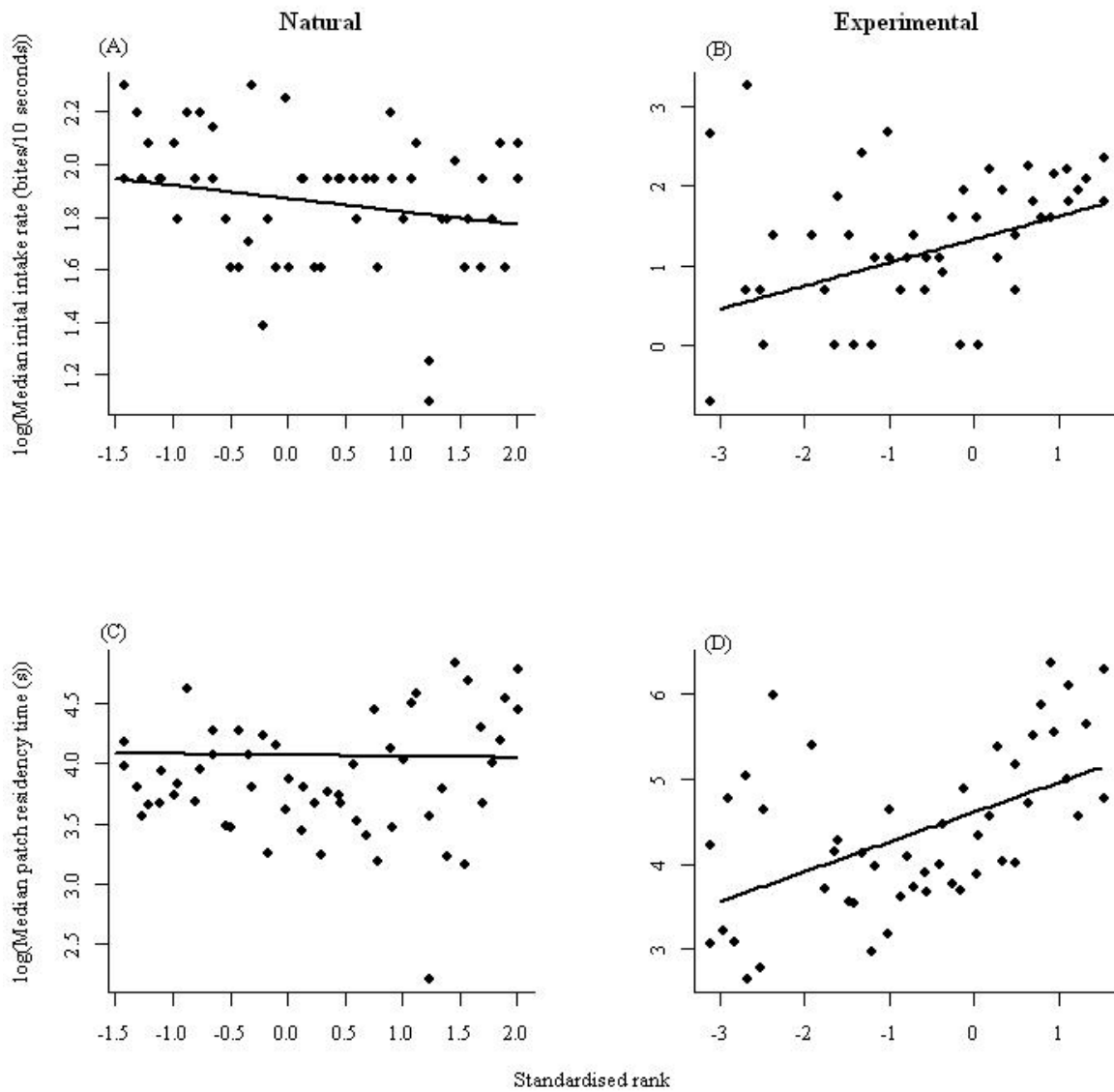


Figure 6.4. The effect of individual rank on initial intake rates (A and B) and patch residency times (C and D) in natural (A,C) and experimental (B,D) foraging environments. In all plots the points are median values for each individual and lines are the relationship estimated by each model (see table 2). y-axis values are log-transformed.

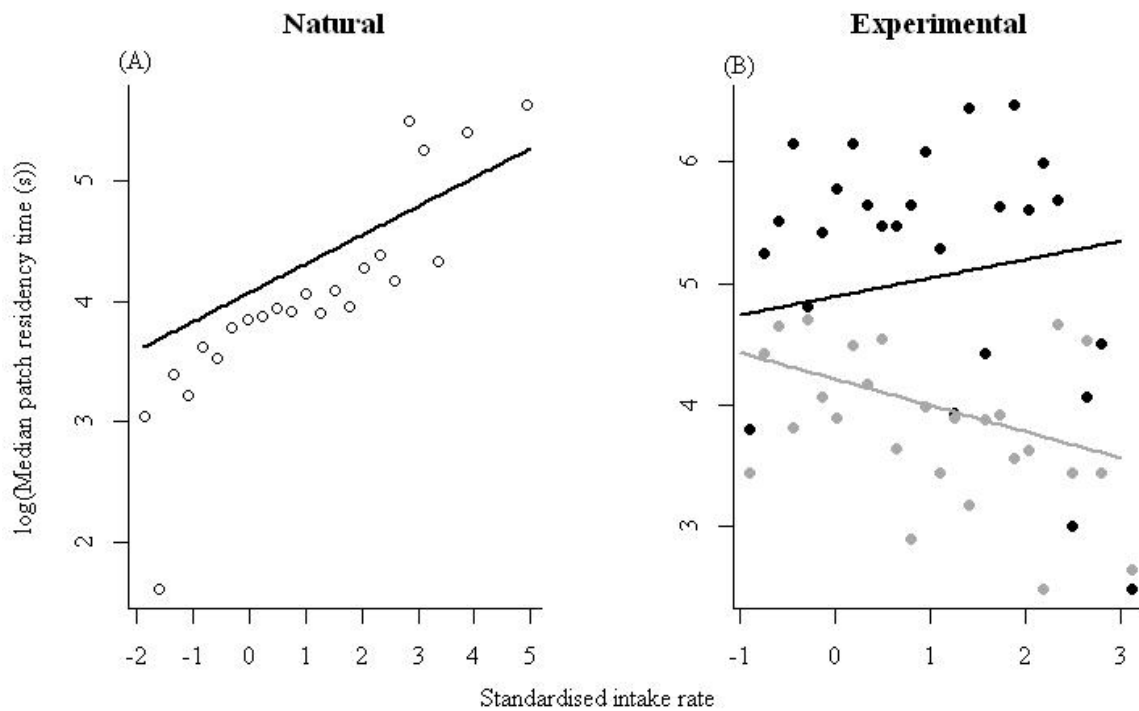


Figure 6.5. The relationship between initial intake rate and patch residency time in (A) natural and (B) experimental foraging conditions. In all plots the points are the median patch residency times recorded for each intake rates and the lines are the relationships estimated by the models (see table 6.3). In (B) the data is split into individuals whose rank is higher (black) and lower (grey) than the median. The relationship in (A) is independent of individual rank (see table 6.3.).

In contrast, in experimental conditions, the size of this effect was dependent on rank such that whilst the most dominant animal spent longer in more profitable patches, the most subordinate animal spent less time in these patches (Figure 6.5B)

## Discussion

Under natural conditions, individuals' foraging success was largely independent of their social traits (rank, social bonds and kinship). Higher ranked individuals were, however, more likely

to use a patch occupied by others and experienced higher rates of food-related agonism which they were more likely to initiate. This agonism pattern was mediated by social capital, such that, amongst low-ranked individuals, those with high social capital experienced less agonism but were more likely to initiate it. Under experimental conditions, where the overall rate of food-related agonism was higher, individuals' foraging success and ability to exploit the environment increased with rank. Higher-ranked individuals were still more likely to use an unoccupied patch and initiate agonism. However, they experienced a lower (rather than higher) rate of agonism and this pattern was only weakly mediated by their social capital. I first discuss how the results contribute to current debate about the role of social bonds and kinship within social foraging group. I then consider the implications of the differing effects of individuals' social traits on their foraging behaviour between the natural and experimental conditions.

The influence of social bonds and kinship on foraging behaviour within social groups is still debated. I found a consistent role for social bonds, but little or no role for kinship. Despite an expectation that kinship with co-foragers should have a positive influence on foraging behaviour, the evidence for its effect is mixed (King et al. 2009; Tóth et al. 2009; Mathot & Giraldeau 2010a). In some cases, the absence of a kinship effect has been attributed to data only being available from adult group members, between whom levels of relatedness are relatively low compared to parent-offspring dyads that would be present if data from juveniles were available (King et al. 2009; 2011). However, these findings refute this suggestion, as I included data on juvenile foraging behaviour and still failed to find a role for kinship. Instead, it supports the argument that social bonds, rather than kinship ties, play a more important role in negotiating foraging tolerance between group members. Studies investigating the function of social bonds have been largely confined to primates (but see Beauchamp 2000b; Carter et al. 2009). These studies have tended to suggest that the function of social bonds is either to negotiate foraging tolerance through the exchange of social

bond imbalances (Barrett et al. 1999; Fruteau et al. 2009; Tiddi et al. 2011), or to buffer individuals from the physiological stress associated with social aggression (Crockford et al. 2008; Silk et al. 2010a). These findings support a previous study (Barrett et al. 2002) in potentially reconciling these two perspectives, since the finding that social bonds mediate agonism during foraging could also explain the stress-relieving effects of social bonds (Shutt et al. 2007; Crockford et al. 2008; Wittig et al. 2008). Additionally, since this role of social capital is in compensation for a foragers' low rank, and so does not result in a direct correlation between social bond strength and foraging behaviour across all individuals, it may explain why the role of social bonds in mediating foraging success is sometimes challenged (e.g. Silk et al. 2010b).

Under natural foraging conditions, higher-ranked individuals initiated more agonism and were more likely to forage with others, yet, contrary to expectations (Smith et al. 2001; Stillman et al. 2002; Beauchamp 2008a; Rieucou & Giraldeau 2011), this did not mean they enjoyed greater foraging success. This suggests that low-ranked foragers were able to mitigate for their poor social position and maintain similar foraging successes to their higher-ranked counterparts. Mitigation tactics by subordinate foragers have been shown elsewhere (Bugnyar & Kotrschal 2004; Held et al. 2010), and my results indicate two mechanisms through which this may have occurred. First, there is growing evidence that social bonds can be used to negotiate foraging tolerance (Beauchamp 2000b; Carter et al. 2009; Fruteau et al. 2009) and social support (Cheney et al. 2010), and may be particularly used by low-ranked individuals (Silk et al. 2010b; Marshall et al. 2012a/Chapter 4). My results support this, suggesting that strong social bonds allowed low-ranked foragers to initiate more, and receive less, agonism, potentially allowing them access to more foraging opportunities. Second, by choosing to forage in unoccupied patches, low-ranked foragers will have benefited from lower foraging competition, potentially compensating for costs such as increased predation risk (Hirsch 2007; Morrell & Romey 2008) and loss of social information about foraging opportunities



(Valone & Templeton 2002; Rieucou & Giraldeau 2011). These findings suggest that low-ranked individuals used peripheral patches more often. This pattern is commonly observed in social foraging groups but is generally seen as a process driven by dominant individuals (Tregenza et al. 1996; Holmgren 1999; Hirsch 2007; Smallegange & van der Meer 2009). My results suggest that it can also be an active compensatory tactic employed by subordinate foragers. In patchy environments, such as the natural conditions in this study, dominance hierarchies are expected to lead to differences in overall foraging performance (Barta & Giraldeau 1998; Isbell & Young 2002). My findings highlight that this may not necessarily be the case if subordinates accept other costs (such as higher predation risk) in order to maintain comparable foraging performances (Liker & Barta 2002).

These mitigation mechanisms are, however, expected to have limits. Studies showing that social capital can be used to negotiate foraging tolerance have also shown that this negotiating ability is limited by the amount of time and effort individuals invest in socialising (Barrett et al. 1999; Fruteau et al. 2009). Similarly, there is evidence that differences in foraging success between spatially central and peripheral foragers may be dependent on the distribution of food resources (Hall & Fedigan 1997; Hirsch 2010). In our experiment, agonism was more frequent, so requiring foragers to have more social capital to negotiate tolerance from others, and resources were concentrated in a localised area. It appears these conditions may have exceeded the mitigation measures' limits since high-ranked foragers experienced greater foraging success and ability to exploit the environment (i.e. a stronger correlation between intake rate and patch residency time). Low-ranked foragers still used their social capital to mediate the proportion of agonism they received and still foraged in unoccupied patches more often. However, the mediatory effect of their social capital on the rate of agonism they received was weak and these rates were higher (rather than lower as observed in natural conditions). This is consistent with previous findings that low-

ranked foragers disproportionately bear the costs of increased competition (Stillman et al. 1996; Liker & Barta 2002; McCormack et al. 2007; King et al. 2009). It has also been suggested that the ability of social foragers to leave food patches at the optimal time, and so most efficiently exploit their environment, is influenced by the level of social aggression (Nonacs 2001). This appears to be the case in the experiment, as high-ranked foragers experienced lower rates of agonism and were able to more efficiently exploit the environment (as shown by their stronger correlation between initial intake rate and patch residency time).

Increased foraging success with rank has been linked to increased resource clumping and/or competition in other social foraging systems including primates (Barrett et al. 2002; King et al. 2009) and birds (Stillman et al. 1996; 2002; Vahl et al. 2005; Johnson et al. 2006). Mechanisms allowing foragers to offset the costs of low rank in certain environments are, therefore, likely to be common. In some cases seasonal variation in resource distribution and foraging competition leads to advantages for high-ranked foragers during higher-competition periods (Barrett et al. 2002; Stillman et al. 2002), which may contribute to the overall higher levels of fitness commonly observed in dominant individuals (East & Hofer 2010). However, anthropogenic effects on the environment can lead to persistent (rather than seasonal) clumping of resources and can produce extreme spatial concentrations of food resources, similar to conditions in the experiment (Bronikowski & Altmann 1996; Shochat et al. 2006). In this case, low-ranked foragers may have persistently lower foraging success forcing them to devote more time to foraging, and less time to resting and socialising (Dunbar 1992; Dunbar et al. 2009) with implications for their ability to maintain social bonds and efficiently digest and thermoregulate (Hill et al. 2004; Lehmann et al. 2007; Korstjens et al. 2010). Under natural conditions, environmental variation (such as seasonal change) may mean that low-ranked individuals only experience these costs some of the time. However, where food distributions remain concentrated over longer periods, low-ranked individuals

may have to persistently bear these costs with implications for their fitness and, ultimately, the profitability of remaining a member of the social group.

## Chapter 7

# Environmental and rank effects on foraging time budgets emerge from individual foraging decisions

### Abstract

The amount of time a social animal must spend foraging will determine the time remaining for activities such as resting and socialising, with implications for individual fitness and social group cohesion. Previous studies of social animals' time budgets have tended to focus on group-level variation, despite an appreciation that understanding how individual-level mechanisms produce this variation is important in anticipating how time budgets are likely to vary in novel environmental conditions. Using data from wild chacma baboons (*Papio ursinus*), I develop and validate an individual-based model of social foraging behaviour predicting monthly variation in daily foraging time. Exploring the predictions of the model in more extreme environmental conditions (defined by food patch density, quality, and variance), I show that foraging time can be an important constraint in social species, and that, under environmental degradation, these constraints are likely to appear rapidly. I also show that rank-related differences between individuals in foraging time may only appear in certain environments, but may exacerbate the effects of environmental degradation where they do occur. These findings highlight the importance of incorporating individual-level behaviour in social species conservation and management, and demonstrate how individual-based modelling can be used to achieve this.

## Introduction

The amount of time an animal is able to allocate to different activities can have important fitness consequences (Dunbar 1992; Dunbar et al. 2009). In social species, the activities making up an individual's time budget are generally categorised as feeding, travelling, resting and socialising (Pollard & Blumstein 2008; Dunbar et al. 2009). Foraging time – time spent feeding plus travelling between food sources – is a key component of this time budget, as an individual must devote enough time to gather sufficient resources to survive and reproduce (Dunbar et al. 2009). Where time available for other activities, primarily resting and socialising, is restricted this can have short-term effects, such as impaired digestion (Korstjens & Dunbar 2007; Pollard & Blumstein 2008) and an inability to maintain social affiliations with other group members (Wittemyer et al. 2007; Lehmann et al. 2007; Henzi et al. 2009), respectively. These effects can also have implications at the group level, influencing group size and ranging patterns (Dunbar 1992; Chapman et al. 1995; Pollard & Blumstein 2008; Dunbar et al. 2009; Grove 2012), and at the species level, restricting their geographic ranges (Korstjens et al. 2010; Lehmann et al. 2010).

The distribution and availability of food within an environment will clearly play a key role in determining social individuals' foraging behaviour, and so the amount of time they must spend foraging. Groups spend more time foraging in environments with reduced food availability or quality (Hill & Dunbar 2002; Alberts et al. 2005; Hamel & Cote 2008). Similarly, where food resources are more concentrated into fewer food patches (or 'clumped'), competition at these patches is more intense. This means that individuals have to move on to other patches sooner, investing a greater amount of time in travelling (Chapman et al. 1995; Gillespie & Chapman 2001; Wittemyer et al. 2007). However, while these patterns are the result of individual-level decisions about how to allocate time, surprisingly few studies have investigated how these foraging time

budgets differ between individuals. Reduced foraging time has been shown in males (Revilla & Palomares 2002; Prates & Bicca-Marques 2008; Masi et al. 2009), older animals (Shi et al. 2003; Sueur et al. 2011a) and higher ranked individuals (Altmann & Muruthi 1988; Hamel & Cote 2008). However, the consistency of these effects is clearly variable, since other studies have failed to find these patterns (Alberts et al. 1996; Ramos-Fernandez et al. 2004; Aivaz & Ruckstuhl 2011). Furthermore, I know of no study which has explored how individual-level differences in foraging time might differ between different environments. Part of the problem may be that most time-budget studies have only explored patterns rather than the mechanisms underlying them

The importance of an individual-based, mechanistic approach to the study of broader-scale patterns is becoming increasingly apparent in the study of ecology and evolution (Sutherland 1996; Evans 2012). In the context of individual foraging time budgets, individual-based mechanistic models have been used to investigate why males tend to spend less time active and foraging and more time resting. Reasons suggested for this pattern have included sex differences in energy requirements and digestion efficiency (due to differing body sizes), predation risk and reproductive strategies (reviewed in Ruckstuhl & Neuhaus 2002; Bowyer 2004; Ruckstuhl 2007; Main 2008). Individual-based modelling has been used to show that it is likely to be a combination of these mechanisms that leads to these time budget differences (Conradt & Roper 2000; Ruckstuhl & Kokko 2002). The importance of this mechanistic approach to the study of foraging time budgets is further highlighted by growing evidence that patterns of social foraging behaviour can often be habitat-dependent (Vahl et al. 2005; Marshall et al. 2012a/Chapter 4; Tanner & Jackson 2012). For example, an individual-based model of common crane (*Grus grus*) feeding behaviour showed that differences in individual aggression rates between environments were likely to be caused by dominants only engaging in aggressive behaviour in poor environments, where their intake rate fell below a threshold (Stillman et al. 2002). Therefore, gaining a better understanding of the

mechanisms driving individual foraging time budgets, rather than their patterns of variation, is likely to allow the prediction of foraging time budgets in different environments with greater confidence and accuracy, and thus allow us to better anticipate the potential impacts of environmental change (see review in Marshall et al. 2012b/Chapter 2).

In this chapter I develop an individual-based, mechanistic model describing how foraging time budgets might emerge from individual foraging decisions in a social forager. I parameterise and validate the model using behavioural and environmental data collected from a wild population of chacma baboons (*Papio ursinus*). I then use the predictions of this validated model to explore how environmental differences, specifically differences in the configuration of food patches (density, quality, and variance), might lead to variation in (1) the time individuals spend foraging and (2) rank-related differences between individuals in the time spent foraging.

## **Methods**

### Field Data Collection

#### *Study Site*

Fieldwork was carried out at Tsaobis Leopard Park, Namibia (22°23'S, 15°45'E), from June to November 2009. The environment at Tsaobis predominantly consists of two habitats: open desert and riparian woodland. The open desert, hereafter 'desert', consists of alluvial plains and steep-sided hills mainly containing small herbs and dwarf shrubs such as *Monechma cleomoides*, *Sesamum capense* and *Commiphora virgata*. The riparian woodland, hereafter 'woodland', is associated with the ephemeral Swakop River that bisects the site and mainly contains large trees

and bushes such as *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica* (see Chapter 3 and Cowlshaw & Davies 1997 for more details). At Tsaobis, two troops of chacma baboons (total troop sizes = 44 and 32 in June 2009), hereafter the ‘large’ and ‘small’ troop, have been habituated to the presence of human observers at close proximity. To control for potential differences between age/sex classes in body size and reproductive strategy, I restrict the behavioural data presented in this chapter to that collected from adult females (n = 14 and 10), all of whom were individually recognisable (see Huchard et al. 2010 for details).

### *Behavioural Data*

Adult female behaviour was observed using focal follows (Altmann 1974b), and recorded on handheld Motorola MC35 and Hewlett-Packard iPAQ Personal Digital Assistants using a customised spreadsheet in SpreadCE version 2.03 (Bye Design Ltd 1999) and Cybertracker v3.237 (<http://cybertracker.org>), respectively. Two separate focal follow protocols were used to record baboons’ (a) time budgets and (b) foraging behaviour. Under both protocols, focal animals were selected in a stratified manner to ensure even sampling from four three-hour time blocks (6 – 9 am, 9 am – 12 pm, 12 – 3 pm and 3 – 6 pm) across the field season. No animal was sampled more than once per day in each protocol.

Time budgets focal follows lasted from 20 minutes to one hour (any less than 20 minutes were discarded). The focal animal’s activity was recorded at all times and classed as either ‘foraging’ (feeding or travelling) or ‘not foraging’ (resting, travelling, grooming or drinking). In total, we recorded 1,156 hours of time budget focal follows with a mean  $\pm$  s.d. of  $48 \pm 5$  hours per adult female.



Foraging behaviour focals consisted of following the focal over two consecutive food-patch visits. A food patch was defined as a shrub, herb or tree with no other conspecific plants within one metre (closer conspecifics, which could potentially be reached by the forager without moving, were treated as part of the same patch). Patch entry was defined as the focal moving into and eating an item from the patch (to rule out the possibility that they were simply passing through the patch), and exit defined as the focal moving out of the patch. At the first patch we recorded, where possible, the focal animal's intake rate (number of bites in the first 10 seconds) and at each patch entry we recorded the habitat, i.e. desert or woodlands, the patch was in. We also recorded the time and distance travelled between leaving the first patch and entering the second. In total, we recorded 617 foraging behaviour focal follows with a mean  $\pm$  s.d. of  $26 \pm 5$  per adult female.

During both focal protocols and *ad libitum* we recorded the occurrence, partner identity and direction of any agonistic interactions (total number of interactions per troop:  $n_{\text{large}} = 1655$ ,  $n_{\text{small}} = 1316$ ). These were used to calculate each adult females' dominance rank using Matman 1.1.4 (Noldus Information Technology 2003). Hierarchies in both troops were strongly linear ( $r$  (Landau's corrected linearity index:  $h'_{\text{large}} = 0.84$ ,  $h'_{\text{small}} = 1$ ,  $p < 0.001$  in both) and subsequently standardised to between 0 (most subordinate) and 1 (most dominant) to control for the difference in the number of adult females in each troop.

### *Environmental Data*

Food-patch configurations comprised monthly estimates of food-patch densities, and the mean and variance of the number of food items in each patch. These configurations were quantified each month for both habitats using monthly phenological surveys of randomly selected food patches. In the woodland, these were a representative sample of 110 patches from an earlier survey

of 5,693 woodland patches (G. Cowlshaw, unpublished data). In the desert, these were 132 food patches that fell within eight 50 m x 1 m transects randomly placed at four localities within the study troops' home ranges. Monthly estimates of patch density were calculated as the mean number of patches containing food per km<sup>2</sup>. In the woodland, this was calculated by randomly grouping the survey patches into 11 groups of 10, and calculating the proportion of patches in each group containing food each month. For each group, the proportion was then extrapolated to estimate, out of all 5,693 woodland patches, how many patches in the woodland contained food, and this estimate was then divided by 9.9 km<sup>2</sup> (the extent of the woodland habitat) to produce an estimate of patch density. The mean of the 11 groups' estimated densities was then calculated to obtain an estimate of woodland patch density for each month. In the desert, monthly estimates of patch density were calculated from the mean of the number of patches containing food in each transect divided by  $5 \times 10^{-5}$  km<sup>2</sup> (the transect area, 50m<sup>2</sup>) across the eight transects. Monthly estimates of the mean and variance in patch quality were based on the number of food items in patches containing food.

### The Individual-Based Model

I built an individual-based model in Netlogo version 5.0 (Wilensky 1999) using its extension for R (Thiele & Grimm 2010; R Development Core Team 2012). I describe the model below following the ODD (Overview, Design concepts, Detail) protocol (Grimm et al. 2006; Grimm et al. 2010).

#### *Purpose*

The model's purpose is to describe how the time that social individuals must spend foraging is influenced by environmental changes in the underlying food patch configuration.

Table 7.1. The state variables that define the global model environment and the patches and agents within it.

Entities	State variables	Description
Global	Patch density	Number of patches per m <sup>2</sup>
	Mean patch quality	Mean number of food items in each patch
	Variance of patch quality	Variance in number of food items in each patch
Patches	Location	Central x-y coordinates
	Food	Number of food items in each patch
Agents	Location	x-y coordinates
	State	Current behaviour
	Energy	Amount of energy (kJ) the agent has collected
	Rank	Social rank scaled between 1 (most dominant) and 0 (most subordinate)
	Body weight	In grams
	Travel speed	In metres per second

### *Entities, State Variables and Scales*

The model world is a 4 x 4 toroidal grid within which two entities are defined: patches and agents. The model world is defined by three variables describing the patch configuration: patch density, mean patch quality and patch quality variance. Sixteen patches are located at each point on the grid and contain an amount of food. Twelve agents (reflecting the mean number of adult females in the study troops) are located either on or between these patches and possess a state, energy, social rank, body weight and travel speed. The model runs in discrete time for 4,320 time

steps per simulation. One time step is equivalent to ten seconds, so one simulation is equivalent to twelve hours of daylight. The equivalent area that the model grid covers varies since the distance between each model patch is determined by the world's patch density and agents' travel speed (see 'Travel to Patch' in 'Input Data and Sub-Models' below). Table 7.1 provides further details of each of the variables listed here.

### *Process Overview and Scheduling*

The process followed by each agent in each time step is illustrated in Figure 7.1. Details of the sub-models named within this process are given in 'Input Data and Sub-Models' below. At the start of the procedure, agents choose whether to forage or not, depending on whether they possess more energy than a threshold value. Non-foraging can be seen as analogous to other time budget activities, i.e. resting, grooming and drinking. If agents do choose to forage (they possess less energy than the threshold) then they do one of three foraging activities depending on their state: choose patch, travel to patch or exploit patch. Agents can choose and either travel to or exploit a patch in the same time step, depending on whether they are located on their chosen patch or not. Similarly, if they start the time step in the travel state but have now arrived at their chosen patch (i.e. they travelled to it in the last time step) then they switch to exploiting the patch. Once agents are exploiting a patch they decide whether to leave it at the end of the time step (i.e. whether to choose a new patch in the next time step or not). If they are leaving a depleted patch (i.e. food = 0) then the patch is replenished but the departing agent cannot choose this patch in the next time step. Note that agents cannot travel to a patch and exploit it in the same time step.

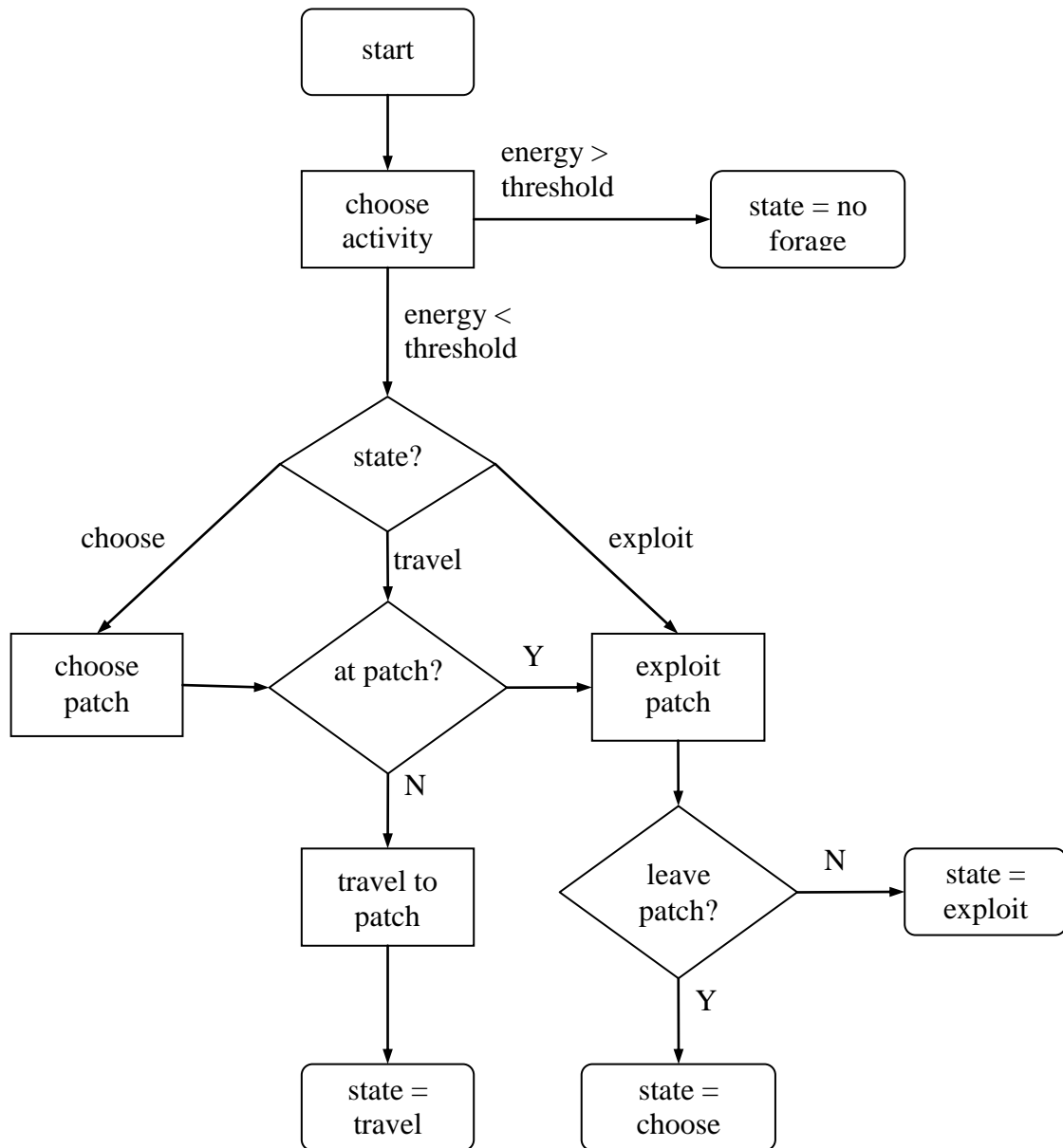


Figure 7.1. The process run by each model agent in each time step. The details of this process and the sub-models named within the figure are given in the ‘Process Overview and Scheduling’ and ‘Input Data and Sub-Models’ sections in the Methods.

### *Design Concepts*

*Emergence:* The number of time steps each agent spends foraging, or not, emerges as a result of the foraging decisions each agent makes in each time step (Fig. 7.1).

*Adaptation:* When choosing a patch, agents select the patch with the greatest utility (see ‘Choose Patch’ in ‘Input Data and Sub-Models’).

*Sensing:* Agents can sense the amount of food and both the number and rank of foraging agents in the patch they are located in and the eight neighbouring patches on the grid.

*Interaction:* Agents interact indirectly, through exploitation of common food resources, and directly, through aggressive encounters forcing subordinates to leave a patch (see ‘Leave Patch’ in ‘Input Data and Sub-Models’).

*Stochasticity:* The amount of food in each patch is randomly drawn from a negative binomial distribution and the energy intake rate of foraging agents is randomly drawn from a normal distribution in each time step (see ‘Exploit Patch’ in ‘Input Data and Sub-Models’).

*Objectives:* Agents aim to reach an energy threshold which will allow them to stop foraging and engage in other activities.

*Observation:* The number of time steps each agent spends foraging in each model run is recorded omnisciently.

### *Initialisation*

The model is initialised by setting the amount of food in each patch. This is drawn randomly from a negative binomial distribution described by the global environment’s patch quality mean and variance (see Table 7.1). The distance between each patch is varied by incorporating the global environment’s patch density in the calculation of the maximum travel distance across the model

world an agent can travel in one time step (see ‘Travel to Patch’ in ‘Sub-models’ below). Agents start at random locations throughout the model world with zero energy and in the ‘choose’ state. They are each assigned a unique social rank from a linear hierarchy between 0 (most subordinate) and 1 (most dominant).

### *Input Data and Sub-Models*

The model includes five sub-models which describe how a model agent chooses whether to forage or not, and then which patch they choose, how they travel to and exploit this patch and when to leave it. Each of these sub-models, and the data from the baboon study system used to parameterise them, is described here under the headings given for each in Figure 7.1.

*Choose Activity.* Agents forage until they have gathered enough resources to fulfil their daily energetic needs, after which they stop foraging. I estimated agents’ daily energy needs by calculating their field metabolic rate (FMR). This describes the amount of energy an animal needs to perform their basal metabolic functions plus other daily activities such as locomotion, thermoregulation and digestion (Nagy 1987; Nagy et al. 1999). Agents’ FMR is calculated using Nagy et al.’s (1999) general equation for mammals.

$$\text{FMR(kJ/day)} = 4.82(\text{body weight})^{0.734} \quad (7.1)$$

Adult female baboon body weight was estimated from data collected during previous live capture events at Tsaobis (see Huchard et al. 2010 for details), yielding an estimate of  $14,200 \pm 1,850$  g (n = 22). This generates an FMR of 5,381 kJ/day.

*Choose Patch.* Agents are able to sense nine patches at any one time: the patch at the grid position they are located at, plus the patches in the eight neighbouring grid positions. Agents in the state ‘choose’ calculate the utility of each these patches and choose the one with the highest value (although the patch they were previously located at is excluded from their next choice). Utility is calculated using an equation estimated in a previous study of patch choice in this baboon system (Marshall et al. 2012a/Chapter 4):

$$\text{Utility} = 3 \times 10^{-5}(\text{food}) + 0.515(\text{occ}) - 0.047(\text{occ}^2) - 1.406(\text{rank diff}) \quad (7.2)$$

Here, ‘food’ is the number of food items, ‘occ’ is the number of other foraging agents (or patch occupants) and ‘rank diff’ is the mean social rank difference between the focal agent and the other foraging agents in the patch. Utility is a general measure of ‘satisfaction’ (Cooper & Millspaugh 1999) and as such can be seen as a measure of the net payoff an agent perceives each patch will return, incorporating the simple foraging return of the patch as well as other costs and benefits of social foraging such as feeding competition and protection from predators.

*Travel to Patch.* Agents in the state ‘travel’ move towards their chosen patch. If the distance to this patch is less than the maximum travel distance then they move this distance, otherwise they move the maximum distance. This is calculated as a proportion of the distance between each patch that an agent can travel in each time step (given that each time step represents ten seconds), and is calculated from the global environment’s patch density and the agents’ travel speed as:

$$\text{maximum travel distance} = \frac{\text{travel speed} \times 10}{(1/\text{patch density})^{0.5}} \quad (7.3)$$



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Thus, as patch density increases, the proportion of the distance between patches that agents can travel in each time step also increases. Travel speed was estimated as the mean travel speed foraging baboons were observed travelling at between two food patches in the foraging behaviour focal follows (see ‘Behavioural Data’ above), yielding an estimate of  $0.81 \pm 0.61$  m/s (mean  $\pm$  s.d.,  $n = 536$ ).

*Exploit Patch.* Agents in the state ‘exploit’ remove food items from the patch they are exploiting and convert these into energy. Analysis of the baboon intake rates recorded here and in a previous chapter showed that they are independent of food-patch quality (Chapter 6, Appendix S4). Therefore, the number of food items that agents removed from a patch in a time step was drawn from a normal distribution, truncated at zero, described by the intake rates (bites per 10 second) recorded in the foraging behaviour focal follows (mean = 7.80, s.d. = 3.72,  $n = 301$ ). The amount of energy gained by agents was calculated from estimates of the weight of each food item and the food’s energy content. Accurate estimates of the weight of each ingested food item were not available from this study system, therefore I used the estimated mean intake rate of 0.03 g/sec from another baboon system (Sellers et al. 2007) to estimate the weight of each ingested food item as 0.038 g (0.03 g/sec divided by 0.78 items/sec). Assuming agents assimilated 40% of the energy available in each food item (Nagy & Milton 1979; Dasilva 1992), and using previous estimates of food energy content in this study system (Cowlshaw 1997), yielded an assimilated energy content of each food item of  $0.31 \pm 0.07$  kJ (mean  $\pm$  s.d.,  $n = 9$  plant part types). The amount of energy an agent received in a time step was thus calculated by randomly drawing from a normal distribution, truncated at zero, described by this mean and standard deviation, and then multiplying by the number of food items it had removed from the patch.

*Leave Patch.* At the end of each time step, agents in the ‘exploit’ state decide whether to leave the patch they are exploiting or remain in it. Agents leave the patch if it has been depleted (food = 0). In addition, since aggression between co-foragers can play an important role in social foraging dynamics (Barrett et al. 2002; Stillman et al. 2002; Giraldeau & Dubois 2008), agents also leave if they are forced to by aggression from a dominant agent exploiting the same patch (assuming all aggressive encounters result in the subordinate leaving the patch). The rate at which a foraging agent is involved in aggressive interactions (as initiator or receiver), and the probability of them being the receiver in those interactions, is described as a function of rank by two equations derived in Chapter 6.

$$\text{agg rate} = \frac{\exp(-3.78 + 0.97 \times \text{rank})}{6} \quad (7.4)$$

$$P(\text{receive}) = \frac{1}{1 + \exp(-2.61 + 4.17 \times \text{rank})} \quad (7.5)$$

Equation 7.4 includes a denominator of six since it was calculated as a rate per minute in Chapter 6 (here one time step is analogous to ten seconds). It is also likely to provide a conservative estimate of the rate of aggression between foragers as it was calculated using the total time an individual spent foraging rather than the time an individual spent foraging with others.

### Model Simulations and Analysis

There were two stages to my model simulation and analysis: (1) a comparison of model predictions to observed data and (2) exploration of the model’s predictions outside the observed data range. In the first stage I ran the model under the five monthly patch configurations I estimated for both woodland and desert habitats (Table 7.2). For each month-habitat combination I ran the

Table 7.2. The patch configuration parameters estimated for each of the habitats at the study site over the five study months.

Month	Proportion of patch visits in the desert habitat	Desert			Woodland		
		Patch density (per m <sup>2</sup> )	Mean number of food items	Variance in number of food items	Patch density (per m <sup>2</sup> )	Mean number of food items	Variance in number of food items
July	0.96	0.16	50	5615	2.90E-4	1384	5952782
August	0.75	0.13	34	1339	3.10E-4	712	1785483
September	0.34	0.12	24	1004	3.80E-4	10748	2338882871
October	0.16	0.10	24	758	4.20E-4	2780	32504632
November	0.33	0.11	62	6934	3.70E-4	4899	175988588

model 30 times and calculated the mean proportion of time steps each agent spent foraging across these 30 replicates. For each month I then weighted each habitat's estimates by the proportion of patch visits observed in that habitat during that month to produce a predicted overall proportion of time spent foraging for each individual in each month. I then calculated corresponding values from the observed data by grouping the time budget focal follows into five monthly blocks and calculating the proportion of focal time each individual spent foraging. I compared the model predictions against the observed data by plotting the mean predicted and observed proportion of time spent foraging in each month. I also estimated the monthly effect of rank on the proportion of time spent foraging in the predicted and observed data and plotted these. The monthly effect of rank was estimated by fitting a generalised linear model to the predicted and observed datasets separately. Each model used a quasibinomial error structure and logit link function, and included the proportion of time individuals spent foraging as the response variable and the month, individuals'/agents' social rank, and the interaction between the two, as explanatory variables. The significance of the estimated effects of the two terms including rank was assessed by removing the

interaction and then the main effect from the model and comparing the full and reduced model at each step using F tests.

Once I was satisfied that the model's predictions matched the observations, I explored the model's predicted foraging time budgets over a wider range of patch configurations. This patch configuration parameter space was based on an expanded range of the observed patch configuration parameters (Table 7.2) and was defined as (variable, range): patch density,  $10^{-7}$  to  $10^2$ ; mean patch quality,  $10^0$  to  $10^7$ ; variance of patch quality,  $10^3$  to  $10^{11}$ . As in the first stage I repeated each combination of these parameters 30 times and calculated the mean proportion of time each agent spent foraging and the rank effect on the proportion of time spent foraging as before. I then explored these predictions using level plots. In these plots I explored the effect of rank by calculating the predicted difference in the proportion of time spent foraging between the highest and lowest ranked agent. All analyses of the model predictions and observed data were conducted in R (R Development Core Team 2012).

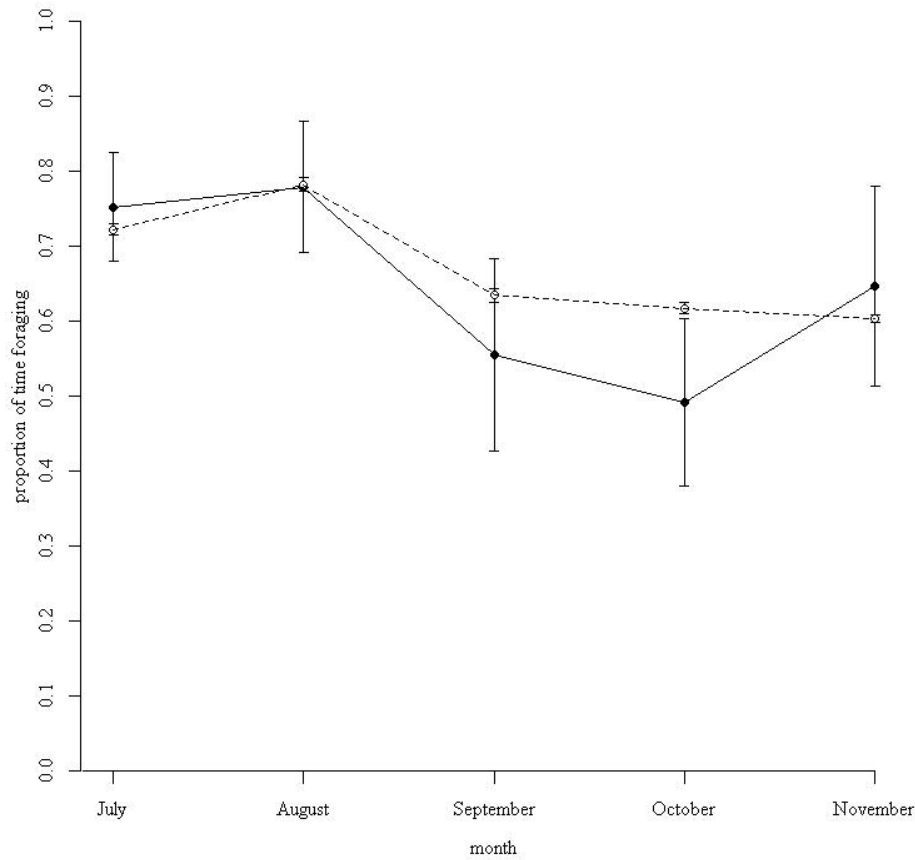


Figure 7.2. Mean proportion of time spent foraging in each study month by observed baboons (closed circles, solid line) and by model agents (open circles, dashed line). Error bars are 1 s.d.

## Results

### Comparing Model Predictions with Observations

Across the five observed monthly patch configurations (Table 7.2) we observed baboons foraging for a mean  $\pm$  s.d. of  $64.5 \pm 12.4$  % of focal time, compared to the model's prediction of  $67.2 \pm 7.7$  %. There was also good agreement between the monthly observed and predicted proportions of time spent foraging (Fig. 7.2). Mann-Whitney tests comparing the observed and predicted proportion of time spent foraging by individuals ( $n = 24$ ) and agents ( $n = 12$ ), respectively, in each month

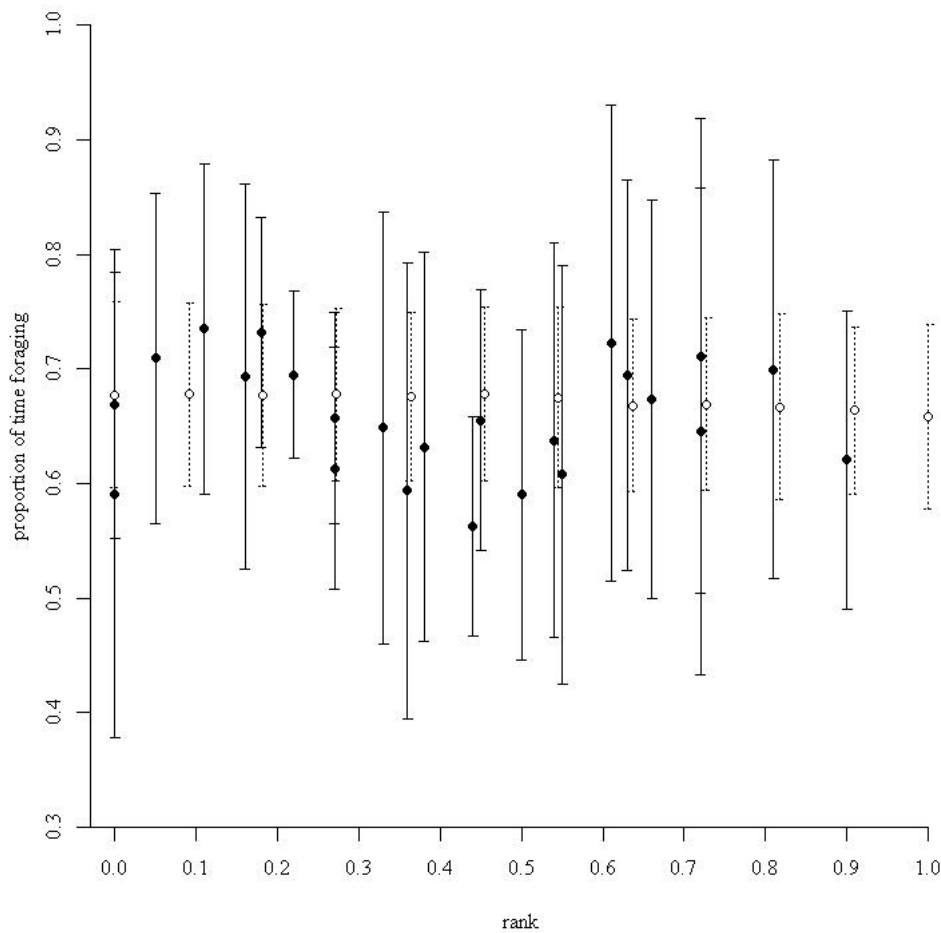


Figure 7.3. Change in mean proportion of time spent foraging with the social rank of the baboon (closed circles) and model agents (open circles). Error bars are 1 s.d. of mean across the study months.

showed that these were not significantly different ( $p > 0.05$ ), except for the October pairing ( $W = 48$ ,  $p = 8 \times 10^{-4}$ ). In our observations, rank had no influence on the amount of time a baboon spent foraging as a main effect ( $F_{114,115} = 0.25$ ,  $p = 0.62$ ) or in interaction with month ( $F_{110,114} = 2.27$ ,  $p = 0.07$ ). In the model predictions, rank did have a weak, but significant, influence on the amount of time an agent spent foraging as a main effect ( $\beta \pm \text{s.e.} = -0.09$ ,  $F_{54,55} = 76.8$ ,  $p < 0.001$ ), but not in interaction with month ( $F_{50,54} = 1.39$ ,  $p = 0.25$ ). However, plotting the observed and predicted data (Fig. 7.3) showed that the observed data contained greater variation within and between individuals. Such variation was likely to have masked the weak effect of rank predicted by the model (see Discussion for sources of individual variation that the model did not incorporate).

### Exploring Model Predictions

The mean time that agents spent foraging was influenced by all three patch configuration variables: patch density, mean patch quality and variance in patch quality (Fig. 7.4). In general, the time they spent foraging was lowest at higher patch qualities and variances (lighter areas in the top right of the panels in Fig. 7.4) and this effect was more marked at higher patch densities (e.g. Fig. 7.4A compared to Fig. 7.4F). Past a certain point, however, when patch quality and variance had all exceeded their intermediate values, further increases in the model environment's quality did not lead to further decreases in time spent foraging. Here the agents' intake rate imposed a minimum foraging time required to meet their energy needs (light grey shading = 50-55% time foraging, minimum = 51.4%). However, once decreases in the model environment's quality meant this minimum foraging time was exceeded, the time agents spent foraging very quickly increased (moving right to left in Figure 7.4's panels, the rapid change from light to dark shading). This led to patch configurations where agents had to spend all of their time foraging (black shading) and so rarely met their daily energetic needs.

Agents' rank had little influence on the time they spent foraging under most patch configurations (Fig. 7.5). At patch densities equal to or greater than  $10^{-4}$  patches/m<sup>2</sup> (panels A-F in Fig. 7.5) the maximum decrease in foraging time between the lowest and highest ranked agent was only 6.9%. However, once patch densities decreased further the effect of rank became increasingly pronounced at high patch quality means and variances (darker areas in the top right of panels G-I in Fig. 7.5). Here the maximum decrease in foraging time between the lowest- and highest-ranked agent increased markedly with each order of magnitude decrease in patch density: 14.4% ( $10^{-5}$  patches/m<sup>2</sup>, Fig. 7.5G), 28.6% ( $10^{-6}$ , Fig. 7.5H), 39.3% ( $10^{-7}$ , Fig. 7.5I).

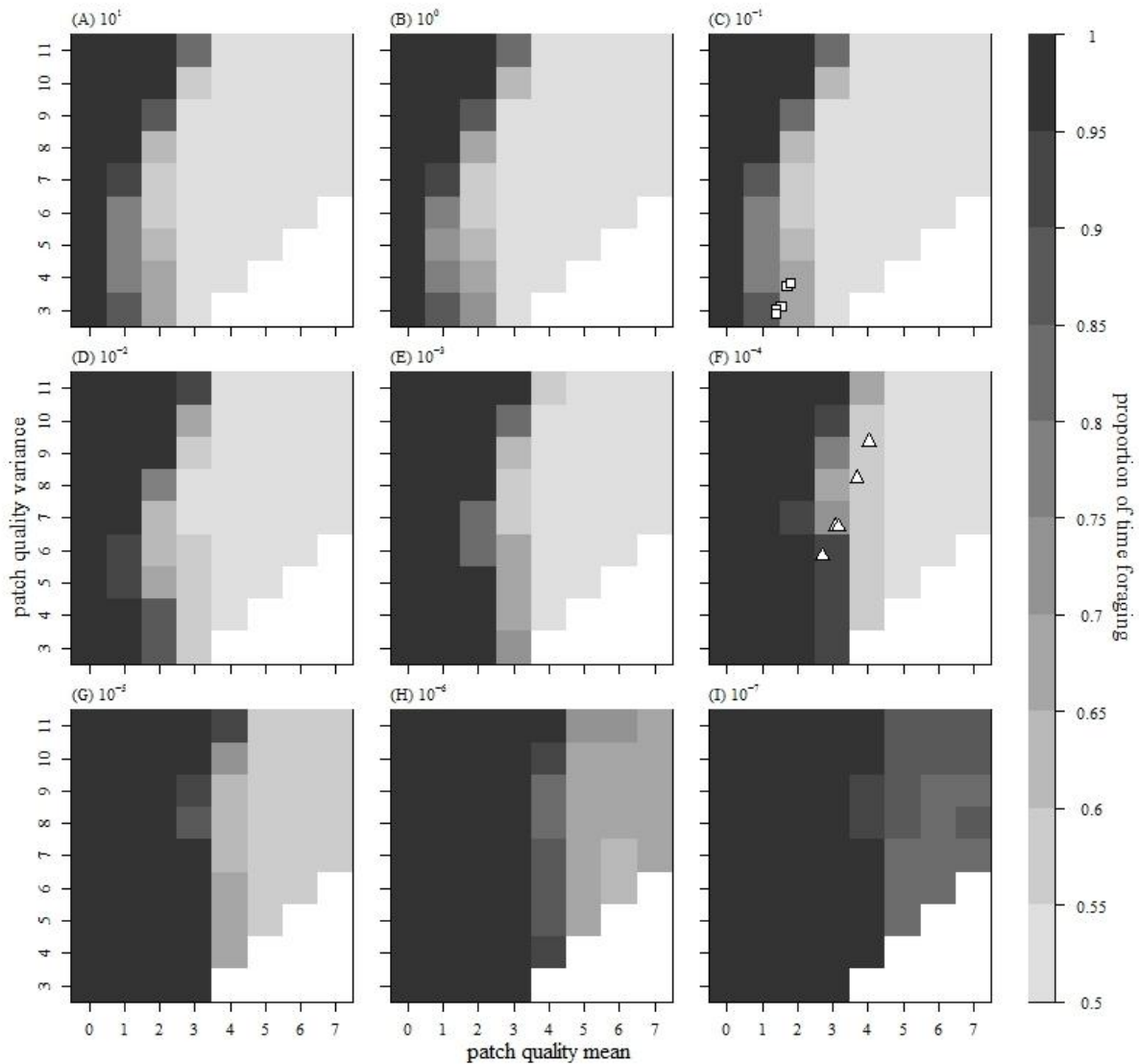


Figure 7.4. Predicted mean proportion of time spent foraging by model agents under different patch configurations. Patch quality mean and variance are plotted on a  $\log_{10}$  scale. Patch density decreases an order of magnitude between each panel, starting at 10 patches/m<sup>2</sup> in panel A and finishing at 10<sup>-7</sup> patches/m<sup>2</sup> in panel I. The white squares (desert habitat) and white triangles (woodland) show the observed patch configurations between July and November 2009 in Table 7.2 (patch densities approximated to nearest order of magnitude). The negative binomial distribution is not defined where the mean patch quality exceeds the variance and so the model was not run under these conditions (the white areas in the bottom right of each panel).



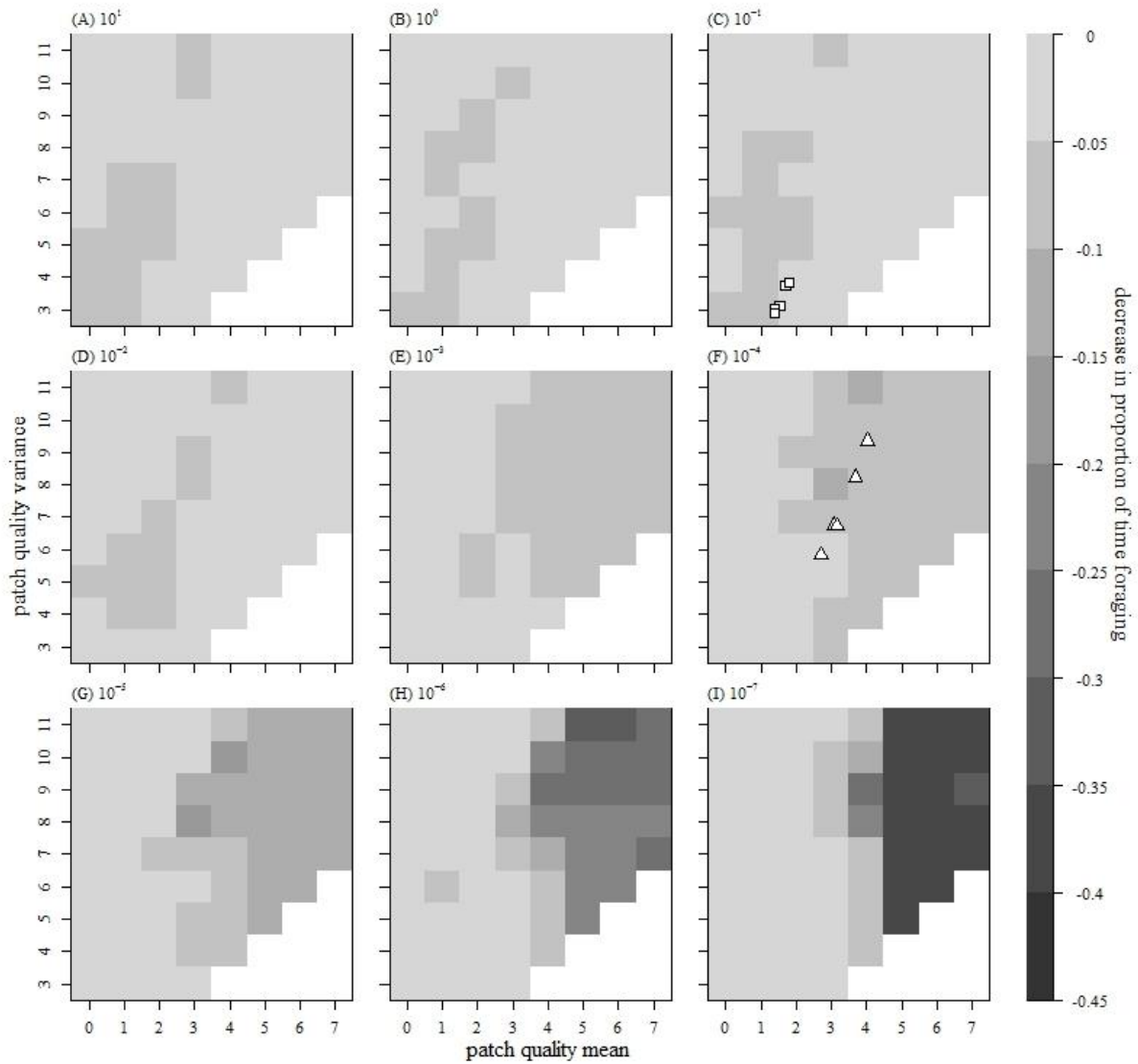


Figure 7.5. Predicted decrease in the proportion of time spent foraging between the lowest and highest ranked agent under different patch configurations. Patch quality mean and variance are plotted on a  $\log_{10}$  scale. Patch density decreases an order of magnitude between each panel, starting at 10 patches/ $\text{m}^2$  in panel A and finishing at  $10^{-7}$  patches/ $\text{m}^2$  in panel I. The white squares (desert habitat) and white triangles (woodland) show the observed patch configurations between July and November 2009 in Table 7.2 (patch densities approximated to nearest order of magnitude). The negative binomial distribution is not defined where the mean patch quality exceeds the variance and so the model was not run under these conditions (the white areas in the bottom right of each panel).

## Discussion

The model presented in this chapter used individual-based rules about how to forage and was able to predict observed variation in baboon foraging time budgets to a reasonable degree of accuracy. Exploring these model predictions revealed a distinct divide between patch configurations where individuals had to spend all their time foraging and configurations where they did not. These predictions also showed that, as in our observations, the effect of individual social rank on time spent foraging was generally weak and inconsistent. However, at particularly low patch densities (beyond our range of observation) a consistently strong and negative effect of rank emerged at high patch qualities.

Exploring how higher-level patterns and processes emerge from individual-level mechanisms is a field of research whose importance is being increasingly appreciated (Sutherland 1996; Evans 2012), and within which individual-based modelling is being increasingly recognised as a powerful tool (Grimm & Railsback 2005; Sueur et al. 2011b; Blumstein 2012; Evans 2012). This study supports this approach, showing how empirically-derived individual foraging rules can be used to inform an individual-based model whose emergent properties can predict observed variation in foraging time budgets. There were, however, discrepancies between the model predictions and observations, most notably in the mean foraging time in October. One explanation for this might be the high availability of young *Prosopis glandulosa* leaves in October (median number per patch = 2,800, inter-quartile range = 1,200 – 4,800, n = 23; all other months: 350, 40 – 1125, 80). Compared to other foods available at Tsaobis, these food items have relatively high energy content (Cowlshaw 1997) and, as young leaves, are likely to be more nutritious and digestible (Milton 1979; Chapman & Chapman 2002). This would have meant that the baboons' energy intake per unit time during this period was higher than usual allowing them to spend less

time foraging than predicted by the model, which did not include differences in food type. This also supports the growing appreciation that differing food types can have an important influence on individual foraging behaviour (Illius et al. 2002; Simpson et al. 2010; Houston et al. 2011), and that their consideration may also be important in the understanding of broader scale patterns and processes (Simpson et al. 2010).

The effect of rank on the time individuals spent foraging was weak or non-existent in our observations and corresponding model predictions. This finding is contrary to the few previous studies which have investigated the effect of rank on the time individuals spend foraging, which report a consistently negative effect (Altmann & Muruthi 1988; Pelletier & Festa-Bianchet 2004; Hamel & Cote 2008). Once rank was accounted for in the results there was still a great deal of unexplained individual variation in the observed time spent foraging, and the extent of this variation was much greater than that observed in the model predictions. This suggests that, in this system, other sources of individual variation, not included in the model, have a greater influence than rank in determining the time an individual spends foraging. One possibility is social bonds, given previous studies in this system that have indicated baboons may use their social relationships with other troop members to mitigate the effects of rank on their foraging behaviour (Marshall et al. 2012a/Chapter 4). Other potential sources of individual variation known to influence individual time budgets, include body size (Ruckstuhl 2007; Main 2008; Aivaz & Ruckstuhl 2011; Sueur et al. 2011a) and reproductive state (Barrett et al. 2006; Main 2008). It is worth noting, however, that the patch configurations under which the model predicts rank will have a strong effect on the time an individual spends foraging is consistent with our understanding of how dominance hierarchies form (discussed below) and that these patch configurations are considerably different from those observed at the study site . This suggests that the model's predictions are robust, and that the

weakly negative effect, predicted under the observed patch configurations, may represent the real influence of rank in this system once other sources of individual variation are removed.

The model predicted a distinct separation between suitable patch configurations, where foragers were able to gather enough energy, and unsuitable configurations, where they were unable to do this. It also predicted that the patch configurations observed in the desert and woodland study habitats were close to being unsuitable. This prediction is consistent with the observation the Tsaobis study population is near the edge of chacma baboons' geographic which does not extend into the Namib Desert, approximately 50 km west of the study site (see Figure 3.1), especially as there is evidence that primate geographic ranges are limited by time budget constraints (Korstjens et al. 2011). It is also supported by anecdotal evidence from 2007 (before the study period) when a drought at the study site drastically reduced the food availability at the study site and led to the death of around a quarter of the Tsaobis baboon population. During this period the fewer of the baboons' usual food trees and shrubs produced food (e.g. pods and berries), and those that did produced less. This suggests a reduction in both patch density and quality, corresponding to conditions represented in the left-hand half of panels G to I in Figure 7.4 where the model predicts individuals need to spend all their time foraging and often are not able to gather enough energy. The model's predictions seem to, therefore, provide some evidence that constraints on foraging time may have been a contributory factor in the high death rate of 2007 and highlight that they are likely to be an important consideration when exploring how environmental change might influence baboon populations.

More broadly, the model's prediction of foraging time budgets influencing habitat suitability is consistent with the growing appreciation that time budgets may play an important role in constraining which habitats a social species can occupy (Korstjens et al. 2010; Bettridge et al.

2010; Lehmann et al. 2010; Grove 2012). Importantly, the model also suggests that the switch from a suitable to unsuitable habitat may be rapid once a patch configuration requires individuals to devote more time to foraging than the minimum set by their foraging efficiency. The implication of this is that the effects of environmental change on social species' time budgets may not be apparent until the environment is already marginal, at which point they become apparent very rapidly. It is possible, however, that the model may have overestimated the rate at which a change to the environment influences foraging time budgets at this boundary. There is evidence that, in the face of environmental change, individuals can alter their foraging behaviour (Valone 1991; Devenport & Devenport 1994; Johnson et al. 2006; Biernaskie et al. 2009), particularly in primates (Alberts et al. 2005; Marshall et al. 2012a/Chapter 4). The behavioural rules in my model were fixed but behavioural flexibility might mitigate the effect that environmental change has on the time individuals are required to spend foraging. Alternatively, it is possible that the observed behavioural response to environmental change may be even more extreme than that predicted here. I considered a habitat as suitable if a forager is able to spend enough time foraging to meet their energetic needs, but time spent resting and socialising is also important for social individuals' fitness (Silk 2007b; Pollard & Blumstein 2008; Dunbar et al. 2009; Lehmann & Dunbar 2009). If social animals are required to sacrifice such time to meet their foraging demands, it is possible that the effects of environmental change will manifest even more rapidly. These findings support the growing recognition that non-linear responses to environmental change have important implications for conservation and management (Swift & Hannon 2010). They also support the long-standing, but under-utilised, argument for the importance in conservation and management of considering behavioural responses to environmental change (Sutherland & Gosling 2000; Stillman et al. 2003; Lehmann et al. 2010).

Compared to the effect of patch density and mean patch quality on the model's predictions, the variance in patch quality was less important. There was, however, evidence that, in the patch configurations near the boundary between suitable and unsuitable habitats, the time individuals spent foraging was lower at intermediate variance values. This corresponded to a situation where the amount of food in each patch is drawn from a negative binomial distribution which concentrates most of the resources in an intermediate number of patches. Intermediate levels of food availability and competition have been found to promote larger foraging group sizes in previous empirical and theoretical studies of social foraging, possibly by attracting individuals to aggregate at food sources but not in such numbers that the food source is depleted too quickly (Symington 1988; Wilson & Richards 2000; Ramos-Fernández et al. 2006). Group sizes are often limited by time constraints, especially the need to spend more time foraging (Dunbar 1992; Pollard & Blumstein 2008; Dunbar et al. 2009; Grove 2012). My model, therefore, suggests that in marginal habitats these larger group sizes might also be able to form at intermediate patch quality variances due to more relaxed time constraints. At the very least this result highlights the importance of considering the variation in food availability across patches, especially where the environment's suitability is marginal.

Dominance hierarchies are predicted to form in social groups, particularly primates, when food resources are clumped in a few high-quality and defensible patches (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Isbell & Young 2002). Similarly, other studies have shown that feeding aggression (which dominant foragers were more likely to use in my model) may only be advantageous in foraging environments with clumped food distributions (Sirot 2000; Vahl et al. 2005; Tanner & Jackson 2012). My model corroborates these studies, indicating that dominant individuals only gain a foraging time advantage when patch density is low and quality is high (all patches in the model being potentially and equally defensible). Under these conditions, the low patch density would have resulted in subordinate animals incurring high time and energy travel

costs every time they were excluded from a patch, while the high patch quality would have allowed dominant animals to extract more resources from each patch and thus incur fewer travel costs before they met their energetic requirements. This difference in travel costs between dominant and subordinate individuals would provide dominant animals with more opportunities to invest time in activities such as resting and socialising, and the fitness benefits these activities can provide (Silk 2007b; Dunbar et al. 2009; Korstjens et al. 2010). It is also likely that the effect of rank may have been underestimated in some configurations as, in addition to underestimating the rate of aggression, the model contained no restriction on subordinates moving away from dominants to less contested patches. In reality, subordinates moving away from their social group also incur costs such as increased predation risk (Quinn & Cresswell 2004; Hirsch 2007; Morrell & Romey 2008), which encourages them to stay closer to dominants. The introduction of such constraints on group dispersion in this model would almost certainly have increased the range of patch configurations over which rank effects were predicted. In addition, although these rank effects are likely to provide benefits to dominant individuals, they also create conflict between group members about the timing of foraging activity. In the short term, this conflict can lead to groups being less behaviourally synchronised and cohesive (Conradt & Roper 2000; Conradt & Roper 2005; Sueur et al. 2011b). In the longer term this may impair a group's ability to make collective decisions and, where a group is forced to split into sub-groups, entail costs such as increased predation risk (Krause & Ruxton 2002; Sueur et al. 2011b). Such effects may further constrain the range of suitable patch configurations the model predicts for such social foragers.

This chapter has demonstrated that an individual based model, using social foraging rules derived from empirical data, can predict observed variation in individual foraging time under changes in the environment's food availability and distribution. Under more extreme environmental degradation scenarios, this model predicts that foraging time will become an increasingly important

limiting factor on social animals, whose constraints are expected to appear rapidly. More broadly, this study has highlighted how individual based modelling can be a powerful tool in exploring variation in ecological patterns and processes, and how these models' predictions can provide important insights for species' conservation and management.



## Chapter 8

### Discussion

The importance of understanding how individual-level behaviour scales up to influence higher level processes such as population dynamics, with implications for conservation and management, has been appreciated for a considerable time (Sutherland 1996; Goss-Custard & Sutherland 1997; Caro 1999; Gosling & Sutherland 2000). This is especially the case for social species, in which an individual's survival and reproductive success can be heavily dependent not only on their own behaviour but also on the behaviour of other group members (Courchamp et al. 1999a; Krause & Ruxton 2002; Silk 2007b). Despite this, the understanding of how variation in individual behaviour scales up to higher-level patterns and processes is still limited (Stillman & Goss-Custard 2010; Caro & Sherman 2011; Evans 2012), particularly in social species (Blumstein 2010; Chapter 2). In this thesis I have attempted to address some of these gaps in our knowledge by exploring the drivers of individual baboons' foraging behaviour (Chapters 4 to 6), and how this behaviour scales up to produce emergent patterns in the amount of time that individuals allocate to different activities (Chapter 7). So far I have discussed the implications of each of these chapters' findings separately. In this final chapter I discuss the common themes that unite these analyses under the following headings: (i) flexibility in social foraging behaviour, (ii) the lack of a kinship effect, and (iii) the importance of studying behaviour under natural conditions. I finish by considering the implications of this thesis' findings for conservation and management, with a particular focus on social species.

## **Flexibility in Social Foraging Behaviour**

Early work in foraging theory tended to think of foraging behaviour as being the product of individuals applying fixed rules about where to feed and what to feed on (e.g. the ideal free distribution, Fretwell & Lucas 1969, and the Marginal Value Theorem, Charnov 1976). More recently, there has been a growing appreciation that individuals can flexibly adjust their foraging behaviour to suit changes in their physical (e.g. Devenport & Devenport 1994; Sargeant et al. 2006; Biernaskie et al. 2009) or social environment (e.g. Bugnyar & Kotrschal 2004; Hewitson et al. 2007; Held et al. 2010). In this thesis I have shown that baboons can adjust their foraging behaviour in response to changes in both types of environment. In Chapter 4, I showed how individuals' decisions about which patch to forage in were influenced by both physical (e.g. patch food availability) and social (e.g. number of patch occupants) factors, and that their relative influence was dependent on the habitat the baboon was in and their social traits. Similarly, in Chapter 5, I found evidence that the way baboons made patch-departure decisions depended on environmental conditions, namely habitat predictability. Finally, in Chapter 6, I showed that the aggression a foraging baboon experienced and their likelihood of using an unoccupied patch was dependent on social factors, namely their rank and social capital with other troop members, but that the influence of these factors on baboons' foraging performance varied between environments. Here I discuss the implications of individuals flexibly adjusting their foraging behaviour in response to different habitats and social positions in turn.

### Flexibility between Different Habitats

The finding that baboons can adjust their foraging decision-making to suit changes in the habitat's level of interference competition (Chapter 4) and predictability of food resources (Chapter

5) is consistent with the suggestion that baboons possess a high level of behavioural flexibility (Whiten et al. 1991; Alberts et al. 2005; Cheney & Seyfarth 2008). This flexible foraging behaviour is likely to allow baboons to efficiently exploit a wide range of habitats, contributing to their widespread distribution across sub-Saharan Africa and ability to occupy habitats ranging from semi-desert, such as at this study's field site, to rainforests (Estes 1991). Behavioural flexibility is also recognised as an important attribute for successful invasive species (Sol 2002), and so may explain why baboons have been successful at 'invading' African cities (e.g. Hoffman & O'Riain 2010).

Flexible foraging behaviour in the face of habitat change is not, however, restricted to baboons, or even primates, but has also been observed in other mammals (Devenport & Devenport 1994; Vásquez et al. 2006; Sargeant et al. 2006), birds (Valone 1991; Alonso et al. 1995; Johnson et al. 2006) and insects (Biernaskie et al. 2009). It appears, therefore, that flexible foraging behaviour may be a phenomenon found in many species. This should allow species' to maximise their ability to exploit their environment and, although the existence of such flexibility is predicted by foraging theory (Giraldeau & Caraco 2000; Stephens et al. 2007), its practical implications appear to have been largely ignored (but see Lehmann et al. 2010). One implication is that, without recording foraging behaviour under natural conditions (rather than in captivity), the applicability of a study's finding to the natural world may be unknown (see discussion below). Another is that, if individuals can adjust their foraging behaviour to cope with changes in the environment, this may mask the effects of a changing environment until these coping mechanisms are overwhelmed. An example of this is provided by Chapter 6, where individual differences in foraging success were only observed in the high-competition experimental environment. Similarly, behavioural flexibility has been linked with apes' ability to continue to occupy a changing habitat (Lehmann et al. 2010). Once these behavioural coping mechanisms are overwhelmed, the deleterious effects of environmental change may appear rapidly, and potentially before any mitigation measures have time to take effect.

I discuss further implications of this, and the thesis's other findings, for conservation and management in the final section of this chapter.

### Flexibility between Different Social Positions

I also found evidence that baboons adjust their foraging behaviour to suit their social position. Individuals with low rank appeared to compensate for this disadvantage by preferring patches containing co-foragers with whom they held greater social capital (i.e. with whom they had contributed a relatively large amount of the grooming in the dyadic social bond; Chapter 4) and using this social capital to negotiate foraging tolerance and so receive less foraging aggression (Chapter 6). The concept that social foragers, primates in particular, can trade their social capital in a biological marketplace for commodities such as foraging tolerance is becoming well established (Noë & Hammerstein 1995; Barrett et al. 1999; Fruteau et al. 2009). However, these chapters are the first studies, to my knowledge, to show that individuals might trade their social capital selectively depending on their dominance rank. They also suggest a mechanism for the recent finding that good social bonds (albeit measured as total bond strength rather than individuals' relative contribution as in this study) can compensate for the effects of low rank on longevity in baboons (Silk et al. 2010b): low-ranked individuals who are able to negotiate greater tolerance at foraging sites would be expected to receive fitness benefits through improved foraging success (Fruteau et al. 2009; Tiddi et al. 2011) and the health benefits of reduced stress as a result of lower levels of aggression (Crockford et al. 2008).

More broadly, these findings beg the question as to whether the mitigation of rank effects by certain aspects of individuals' social bonds, such as their social capital, is restricted to primates, or whether it is found in other social taxa. Research into the proximate function of social bonds has

generally been limited to primate systems (but see Beauchamp 2000b; Carter et al. 2009), despite complex social networks being identified in a broad range of taxa from insects to mammals (Connor et al. 1999; Croft et al. 2004; Wittemyer et al. 2005; Hill et al. 2008; Naug 2009). Nevertheless, social bonds are now increasingly associated with fitness effects in non-primate systems (feral horses, *Equus* sp., Cameron et al. 2009; bottlenose dolphins, *Tursiops* spp., Frère et al. 2010; rock hyraxes, *Procavia capensis*, Barocas et al. 2011; forked fungus beetles, *Bolitotherus cornutus*, Formica et al. 2012) as well as in primates (e.g. yellow baboons, *Papio cynocephalus*, Silk et al. 2003; Assamese macaques, *Macaca assamensis*, Schülke et al. 2010; reviewed in Silk 2007a). Similarly, dominance hierarchies are a common feature of many social systems (East & Hofer 2010). This suggests that the potential for individuals to use social bonds to compensate for low rank may be relatively common, and, given the apparent fitness benefits, should be selected for. If this were the case, it would suggest a mechanism that could mitigate the feeding competition costs of group-living for low-ranking individuals, increasing the maximum group size a given environment could support. The fact that stable and structured social groups are found in many taxa, at sizes at least as large as those observed in primates (e.g. elephants, cetaceans, birds), would seem to support this hypothesis. However, the maximum size a group can expand to, and remain profitable for all group members, is not just determined by feeding competition costs, but also other factors such as the benefits from reduced predation risk (Courchamp et al. 1999a; Krause & Ruxton 2002). These factors, particularly predation risk, are likely to vary considerably and explain much of the between (and within) taxon variance in group size. Furthermore, although the opportunity for individuals to use their social bonds to offset the effects of rank may exist in many social taxa, they may not always be able to take advantage of this opportunity. Managing and maintaining long-term social bonds requires specialised cognitive ability, which primates have been selected for (Dunbar 1998a; Dunbar & Shultz 2007; Cheney & Seyfarth 2008). In contradiction to the above hypothesis, this suggests that the use of social bonds to offset rank may be restricted to primates, and be an

evolutionary advantage of their specialised cognitive abilities. In this case, the fact that these cognitive abilities have not evolved in other taxa would indicate that the advantages of social bonds in these taxa are not large enough to justify the investment in the larger brain sizes required to maintain them, but are large enough in primates (Dunbar 1998a; Dunbar & Shultz 2007; Lehmann & Dunbar 2009). Future work might attempt to distinguish between these two hypotheses, i.e. that social bonds do or do not offset low rank in non-primate taxa, by exploring the proximate function of social bonds in such systems and examining how this function might vary across individuals of differing rank within social groups. One possibility may be a middle ground between these two hypotheses, where the ability to use social bonds to offset rank effects extends outside of primates, but only to more traditionally cognitively ‘advanced’ taxa, such as elephants and cetaceans. In support of this, these ‘advanced’ taxa tend to form more stable and discrete social groups, which provide the opportunity for the longer-term interactions that social bonds need, whilst other taxa, such as birds, fish and insects, tend to form looser aggregations.

### **The Lack of a Kinship Effect**

A consistent finding of this thesis was the effect of a baboon’s rank and social bonds (Chapters 4 and 6) on its foraging behaviour. This emphasises the point made in Chapter 2 about the importance of considering these social relationships in the study of foraging behaviour and its emergent properties. Notable in these findings, however, is the consistent lack of an effect of kinship. On the face of it, this is surprising as, in a social group where many individuals will be closely related, kinship might be expected to have a large effect on behaviour. In Chapter 4, I suggested that the lack of a kinship effect on foraging decisions was due to data only being available on adult foragers and co-foragers, and the level of kinship being relatively low between adults compared to between adults and juveniles (their offspring). This explanation was also

proposed in previous studies on adult baboons in the same system (King et al. 2009; 2011). However, the lack of a kinship effect in Chapter 6, which incorporated data on adults and juveniles, appears to refute this explanation.

Generally, despite the expectations of kin selection (Hamilton 1964), the evidence for the effect of kinship on social foraging behaviour is surprisingly unclear (reviewed in Mathot & Giraldeau 2010a and Chapter 2). In an attempt to resolve this debate, Mathot & Giraldeau (2010a) recently developed a model which predicted that inclusive fitness benefits should mean that foragers should favour joining and being joined by kin. They empirically validated this model by showing that the rate of joining other group members on food patches was higher in groups of captive zebra finches (*Taeniopygia guttata*) that contained full-siblings compared to groups that did not. In reality, however, individuals' kinship with other foraging group members tends to vary considerably (including in the present study system). This suggests that the effect of kinship on social foraging behaviour may only be apparent at particularly high levels of co-forager relatedness and/or may be non-linear (e.g. increasing more quickly in size past a certain threshold level of relatedness). This may explain the lack of a kinship effect on foraging behaviour found in this thesis, and the inconsistent effects found in other studies on natural foraging groups (McCormack et al. 2007; King et al. 2009; Tóth et al. 2009). To investigate this possibility, future empirical foraging behaviour studies would need to manipulate the kinship between foraging group members across a gradient (e.g. ranging from a group composed wholly of full sibs and/or offspring on the one hand, to no relatives on the other). It might prove most tractable to start this investigation by manipulating the kinship between a pair of foragers before moving on to larger foraging groups with differing levels of dyadic relatedness. Despite the importance of data on natural behaviour (see next section), it is likely this manipulation would need to be in a captive setting, since the manipulation of wild social groups in this way is unlikely to be logistically or ethically feasible. As

this would also require the use (and so housing) of multiple groups, a smaller study taxon than primates, such as small mammals, birds or fish, would probably be most appropriate.

## **The Importance of Studying Behaviour under Natural Conditions**

In Chapters 5 and 6 I showed how the drivers of social foraging behaviour and success differed markedly between the natural foraging conditions and the large-scale feeding experiment. I also showed in Chapter 7 that the time budgets patterns that emerge from these social foraging behaviours may be dependent on the underlying environment. These two points, in combination with the evidence of behavioural flexibility (Chapters 4 and 6, see above), highlight the importance in studies of social foraging, and wider behavioural studies, of recording animal behaviour in the natural environment.

Many behavioural studies use animal subjects under some level of captivity from ‘free-ranging’ (i.e. in a large semi-natural enclosure) to fully captive (i.e. in a cage in a laboratory). This appears to have been particularly the case in social foraging studies, where researchers need to record and manipulate detailed behaviours to test and develop relatively complex theories, resulting in many studies using captive bird populations (Giraldeau & Beauchamp 1999; Valone & Templeton 2002). This approach has undoubtedly provided the social foraging field with many important advances. However, this thesis highlights that studies of animal behaviour in artificial environments may have limited application in the natural world. This does, however, create something of a paradox: if exploring foraging behaviour requires the recording and manipulation of behaviours that is only possible in a controlled environment, but by placing animals in this controlled environment we alter their behaviour, how do we explore the drivers social foraging (or any other) behaviour in the natural world?



I propose that future studies should attempt to address this problem by using one or more of the following three approaches. First, where possible, natural behaviours should be recorded either as the primary source of data or to complement and validate (potentially more detailed) data from artificial settings. For example, in Chapters 5 and 6 I showed how behavioural data from natural and artificial settings can be productively used in tandem. In addition, the technology available to researchers for collecting data is expanding rapidly, e.g. placing collars on animals for the automated collection of behavioural and positional data (reviewed in Cagnacci et al. 2010; Tomkiewicz et al. 2010, see King et al. 2012 for a recent example). This is likely to make recording detailed natural behaviours increasingly possible in the future, potentially negating the need for data collection in a controlled environment in some cases. Second, field experiments may provide a good compromise between natural and laboratory conditions, as they allow control over key variables whilst remaining within a natural-world setting. Previous studies have used field experiments to provide valuable insight into social behaviours (Seyfarth et al. 1980; Cheney et al. 1996; King et al. 2008; Fruteau et al. 2009; Carter et al. 2012; see Cheney & Seyfarth 2008 for a review of playback experiments). However, as Chapters 5 and 6 show, when discussing their results, it should perhaps be acknowledged that they may produce extremes of behaviour. Third, in some cases the level of control and manipulation a study requires may only be feasible in a captive environment (e.g. the need to control a foraging group's composition to explore the effects of kinship, as discussed in the previous section). Here, researchers should design their study to minimise the possibility of altering their subjects' behaviour. The collection of complementary natural data on some basic behaviours to validate the captive behaviours they observe might be one way to achieve this. They might also do this by careful selection of their study taxa. For instance, whilst a primate or mammal probably has some perception of its captive situation, do fish or insects? This is perhaps itself a question for

future research, the answer to which should help to further the study of complex individual behaviours.

## **The Importance of Individual Behaviour in Conservation and Management**

Despite repeated calls for behavioural ecologists to use their findings to inform management and conservation (Gosling & Sutherland 2000; Caro 2007), examples of this are still relatively rare (Stillman et al. 2003; Durell et al. 2006; Lehmann et al. 2010). By understanding the underlying individual-level behavioural mechanisms, predictions about higher-level patterns in novel environments, such as those potentially caused by anthropogenic environmental change, can be made with greater confidence (Evans 2012). This thesis has provided an example of the power of this approach by using its findings about individual-level baboon foraging behaviour (Chapters 4 to 6) to accurately predict the observed monthly variation in the amount of time the baboons spent foraging, and then making predictions about how this foraging time is likely to vary with environmental change (Chapter 7). In this section, I discuss the implications of this study's findings for the conservation and management of social species. I then consider why the divide between behavioural ecology and conservation has only been bridged on relatively few occasions, and how future studies might go about doing this more successfully in the future.

The number and strength of social bonds an individual can maintain with other group members is partly constrained by the time available for socialising (Lehmann et al. 2007). There is a growing appreciation that these social bonds affect individuals' fitness (Silk 2007a,b; Cameron et al. 2009; Barocas et al. 2011) and are important in maintaining overall group cohesion, and so long-term group persistence (Dunbar 1992; Lehmann et al. 2007; Lehmann & Dunbar 2009). In this thesis, I have found evidence that social capital may achieve this, at least in subordinate animals, by

ameliorating the detrimental effects of low rank on foraging performance (Chapters 4 to 6). I have also shown that the time available for activities other than foraging (i.e. resting and socialising) is dependent on the underlying environment, and, using an individual-based model of social foraging behaviour, have shown that this remaining time is predicted to decline to zero in deteriorating environments (i.e. social species would be highly unlikely to persist in these extremely poor environments, Chapter 7). The conservation implications of these findings are clear since, as social bonds influence individual fitness and therefore group persistence, restrictions on the time available to maintain these social bonds is likely to be detrimental. Non-social species, which do not have this requirement, may be able to occupy habitats that require them to spend almost the entire day foraging (with some remaining time to rest). In social species, however, this requirement to spend time socialising may lower the critical foraging time limit, constraining the range of habitats suitable for them and potentially making them more susceptible to environmental change. Recently, there has been increasing awareness of the importance of time budgets in constraining social group size, determining biogeographic patterns, and predicting the effects of climate change on social species (Pollard & Blumstein 2008; Dunbar et al. 2009; Korstjens et al. 2010; Lehmann et al. 2010). This study's findings further emphasise this importance, and contribute to the increasing awareness that social species may differ in their susceptibility to environmental change compared to non-social species (reviewed in Blumstein 2012).

Ecological patterns and processes at the population (or higher) level tend to be most relevant for conservation and management, yet the understanding of how individual behaviours scale-up to these levels has remained elusive (Sutherland 1996; Sutherland & Gosling 2000; Stillman & Goss-Custard 2010). It seems likely, therefore, that one reason why relatively few behavioural studies have explored their implications for conservation and management is that there is a perception that behavioural ecology cannot make a meaningful contribution. Equally, researchers interested in

answering questions relevant to conservation science may perceive that the recording and analysis of individual-level behaviour cannot make a meaningful contribution, and so do not invest the relatively large amount of time, money and effort required (compared to collecting data at the population level). This thesis contributes to the growing literature (Korstjens et al. 2010; Stillman & Goss-Custard 2010; Lehmann et al. 2010), demonstrating that these perceived hurdles to integrating behaviour and conservation – linking behaviour with population-level patterns, and the investment required to record individual behaviour – are beginning to be addressed.

In this particular context, the primary contributions of this thesis are twofold. In the first case, Chapter 7 showed how individual-based modelling could be used to describe how individuals' foraging behaviour produced patterns in their overall time budgets, and how these patterns were likely to vary under different environmental conditions. Individual-based modelling is being increasingly advocated as a powerful tool in linking individual-level behaviours with higher level patterns (Chapter 2 and Grimm & Railsback 2005), particularly in the context of understanding the impacts of environmental change (Evans 2012). Future studies that use this approach may, therefore, continue to further the understanding of how behaviour influences population-level patterns, and thus contribute to the development of better predictive models for conservation and management decisions. In the second case, this thesis has demonstrated throughout how techniques such as generalised linear mixed modelling and individual-based modelling can be used – and combined – to effectively analyse data on individual behaviours. These techniques have traditionally been considered as advanced and computationally intense, however they are becoming increasingly accessible to ecologists (Grimm & Railsback 2005; Bolker et al. 2009), reducing the investment required in the analysis of individual behaviours. Technologies for collecting individual behavioural data (e.g. handheld computers and video cameras, as used in this study, and automated collars as discussed above) are also becoming increasingly available, reducing the investment

required to collect such data. Combining these modelling approaches and technologies is, therefore, likely to reduce the investment that individual-level behavioural data requires, making its use more attractive to future studies interested in informing conservation and management.

## **Conclusion**

Baboon social foraging behaviour is driven by many social and non-social factors, whose influence is dependent on both the characteristics of the foraging habitat and the social traits of the forager (Chapters 4 to 6). Despite this complexity, information about the drivers of these foraging behaviours can be used to predict seasonal variation in individual time budgets, and so how these time budgets are likely to change and constrain social species' habitat use in the face of more extreme anthropogenic environmental change in the future (Chapters 7). These findings highlight the importance of understanding the mechanisms linking individual behaviours, such as social foraging behaviour, with higher-level patterns, such as time budgets (as argued in Chapter 2). More broadly, they also emphasise the importance of considering the implications of studies on individual-level behaviour for conservation and management. Despite repeated calls over the last two decades for behavioural ecologists to consider the implications of their findings for conservation and management, examples of this are limited, potentially due to difficulties in understanding how variation in individual-behaviour leads to changes in higher-level patterns. I hope this study has provided an example of how this understanding can be improved, and gone some way to promoting further links between behaviour and conservation.

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## **Appendix S1**

### **Supporting Information for Chapter 4**

#### **Estimating Patch Food Content**

To estimate the food content of patches recorded in choice sets, data from monthly phenological surveys was used to predict food content from patch size and quality scores using linear mixed-effect models (Table S1.1). Where possible specific models for each patch-species/food-item combination observed in the choice sets were calculated, however in some cases the sample size in the environmental data was too small and data was pooled to create general species or food-item models. Patch ID was included as a random effect in all models and food-item type was included in general patch-species models and vice versa. In all models the response variable was log-transformed to normalize the residuals.

#### **Estimating Patch Size**

To estimate the sizes of patches recorded in choice sets, data from phenological surveys was used to predict patches' surface area from their size score using linear models (Table S1.2). A previous survey of 3,444 large bushes and trees in the woodland habitat allowed models for each species to be estimated. Data from our monthly environmental surveys was used to estimate a model across all herbs and shrubs. In all models the response variable was log-transformed to normalize the residuals.

Table S1.1: Linear mixed-effect models predicting patch food content from food-item density and patch size scores.

Response (log-transformed)	Intercept	Fixed effects		Random effects		
		Food-item density score	Size score	Patch ID	Food-item type	Patch species
<u>Woodland habitat: large bushes and trees</u>						
<i>Prosopis glandulosa</i> new shoots	1.60 (1.00)	1.10 (0.21)	-0.02 (0.17)	Y		
<i>Prosopis glandulosa</i> flowers						
<i>P. glandulosa</i> pods						
All <i>P. glandulosa</i> items	1.21 (1.15)	1.13 (0.21)	-0.05 (0.16)	Y	Y	
<i>Faidherbia albida</i> flowers	1.87 (0.44)	0.88 (0.07)	0.23 (0.82)	Y		
<i>F. albida</i> pods	0.30 (0.57)	0.96 (0.09)	0.25 (0.09)	Y		
All <i>F. albida</i> items	1.06 (0.70)	0.92 (0.06)	0.24 (0.06)	Y	Y	
<i>Salvadora persica</i> berries	3.16 (0.81)	1.12 (0.14)	-0.12 (0.23)	Y		
<i>Acacia erioloba</i> flowers						
<i>A. erioloba</i> pods	1.78 (1.26)	0.53 (0.20)	0.08 (0.31)	Y		
<i>A. tortilis</i> flowers						
<i>A. tortilis</i> pods						
All flowers	1.89 (0.56)	0.85 (0.07)	0.18 (0.09)	Y		Y
All pods	2.28 (0.67)	1.03 (0.10)	-0.21 (0.14)	Y		Y
<u>All herbs and shrubs</u>						
All flowers	-1.67 (0.58)	1.59 (0.16)	0.39 (0.26)	Y		Y
All pods	0.36 (0.86)	0.81 (0.13)	0.31 (0.38)	Y		Y
All food items	-1.51 (0.51)	1.44 (0.12)	0.60 (0.21)	Y	Y	Y

Note: All response variables were log-transformed to normalize residuals. Estimates ( $\pm$ s.e.) predict the log-transformed number of food items. Sample sizes refer to the number of cases recorded in the phenological surveys.

Table S1.2. Linear models predicting patch surface area from size score. Parameters ( $\pm$ s.e.) are for log-transformed models and sample sizes indicate number of records in the environmental surveys.

Surface area, log(m <sup>2</sup> ), of:	Intercept	Size score	<i>n</i>	<i>r</i> <sup>2</sup>
<i>Faidherbia albida</i>	4.70 (0.04)	0.35 (0.01)	600	0.74
<i>Prosopis glandulosa</i>	4.91 (0.02)	0.23 (0.01)	1326	0.65
<i>Salvadora persica</i>	4.29 (0.03)	0.37 (0.01)	1173	0.66
<i>Acacia erioloba</i>	4.41 (0.06)	0.28 (0.01)	185	0.75
<i>Acacia tortilis</i>	4.67 (0.05)	0.26 (0.01)	160	0.78
Herbs and shrubs	-2.91 (0.17)	2.08 (0.11)	137	0.74

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## Patch preference models 95% confidence sets

The baseline, habitat- and individual trait-specific models of patch preference in table 4.2 of Chapter 4 are averages of the full-model set. Tables S1.3 to S1.11 present the 95% confidence set from which each final model was averaged. The 95% confidence set is the set of candidate models which, when ordered from smallest to largest AIC score (or equivalent, e.g. AICc), have a cumulative Akaike's weight of 0.95. A model's Akaike's weight can be interpreted as the probability that it is the best model within the model set and so the 95% confidence set can be interpreted as having a 95% probability of including the best model from the candidate set. A model's Akaike's weight is calculated as the exponential of the difference between its and the top-ranked model's AIC (or equivalent) score multiplied by minus 0.5, and then divided by the sum of this value across all models in the model set. So, where there are  $R$  models in the model set, and  $\Delta$  is the difference in AIC scores (or equivalent) of the top ranked and  $i$ th model, then the  $i$ th model's Akaike's weight is (see Burnham and Anderson, 2002 for more details Akaike's weights and confidence sets):

$$\frac{\exp(-\Delta_i / 2)}{\sum_{r=1}^R \exp(-\Delta_r / 2)}$$

Table S1.3. Baseline patch preference model 95% confidence set.

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ x size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ x invest	$\beta_9$ occ <sup>2</sup> x invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
16	0.18 (0.06)	-0.55 (0.15)	-0.34 (0.09)	0.84 (0.14)	-0.08 (0.02)			0.77 (0.26)	-0.09 (0.04)	-0.16 (0.05)			0.30	0.30
48	0.18 (0.06)	-0.54 (0.15)	-0.33 (0.09)	0.79 (0.15)	-0.07 (0.02)			0.79 (0.26)	-0.09 (0.04)	-0.15 (0.05)		-0.06 (0.05)	0.22	0.53
40	0.18 (0.06)	-0.55 (0.15)	-0.34 (0.09)	0.85 (0.14)	-0.08 (0.02)			0.77 (0.26)	-0.09 (0.04)	-0.17 (0.05)	0.040 (0.05)		0.16	0.68
64	0.18 (0.06)	-0.55 (0.15)	-0.33 (0.09)	0.80 (0.15)	-0.07 (0.02)			0.79 (0.26)	-0.09 (0.04)	-0.16 (0.05)	0.05 (0.05)	-0.07 (0.05)	0.13	0.81
18	0.180 (0.06)	-0.53 (0.15)	-0.35 (0.11)	0.87 (0.17)	-0.09 (0.03)	-0.03 (0.09)	0.01 (0.02)	0.85 (0.29)	-0.11 (0.05)	-0.16 (0.05)			0.05	0.86
50	0.18 (0.06)	-0.53 (0.15)	-0.35 (0.11)	0.81 (0.17)	-0.09 (0.03)	-0.03 (0.09)	0.01 (0.02)	0.87 (0.29)	-0.11 (0.05)	-0.16 (0.05)		-0.06 (0.05)	0.04	0.90
42	0.18 (0.06)	-0.53 (0.15)	-0.34 (0.11)	0.88 (0.17)	-0.09 (0.03)	-0.03 (0.09)	0.01 (0.02)	0.85 (0.29)	-0.11 (0.05)	-0.17 (0.05)	0.04 (0.05)		0.03	0.93
66	0.180 (0.06)	-0.53 (0.15)	-0.345 (0.11)	0.82 (0.17)	-0.09 (0.03)	-0.03 (0.09)	0.01 (0.02)	0.87 (0.29)	-0.11 (0.05)	-0.16 (0.05)	0.04 (0.05)	-0.07 (0.05)	0.02	0.95

Note: Coefficient estimates  $\beta_n$  ( $\pm$ s.e.). Notations: food = patch food content, investment = handling time required by patch type, size = patch surface area, occ = number of patch occupants, rank = mean rank difference between focal forager and patch occupants; symmetry = mean symmetry of grooming bond between focal foragers and patch occupants; kinship = mean relatedness coefficient between focal forager and patch occupants,  $w_i$  = Akaike's model weight. See table 1 in main text for full model set fitted.

Table S1.4. Desert habitat patch preference model 95% confidence set. See Table S1.3 note for notations.

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ x size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ x invest	$\beta_9$ occ <sup>2</sup> x invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
13	3.95 (1.91)	-0.85 (0.19)	-1.32 (0.67)	1.65 (0.51)		2.63 (1.04)				-0.64 (0.17)			0.24	0.24
37	4.09 (1.94)	-0.85 (0.19)	-1.4 (0.68)	1.59 (0.51)		2.67 (1.04)				-0.65 (0.17)	-0.11 (0.09)		0.17	0.41
17	3.94 (1.91)	-0.74 (0.28)	-1.36 (0.67)	1.54 (0.54)		2.47 (1.06)		0.52 (0.91)		-0.63 (0.17)			0.10	0.51
45	3.99 (1.93)	-0.85 (0.19)	-1.35 (0.68)	1.67 (0.52)		2.63 (1.05)				-0.65 (0.18)		0.03 (0.11)	0.09	0.60
14	3.85 (1.98)	-0.85 (0.19)	-1.53 (0.73)	1.73 (0.8)	0.05 (0.69)	1.92 (1.87)	1.03 (2.13)			-0.63 (0.17)			0.07	0.67
61	4.21 (1.98)	-0.85 (0.19)	-1.46 (0.71)	1.63 (0.52)		2.67 (1.05)				-0.68 (0.18)	-0.12 (0.10)	0.06 (0.11)	0.07	0.74
41	4.08 (1.94)	-0.76 (0.28)	-1.43 (0.69)	1.51 (0.54)		2.54 (1.07)		0.43 (0.94)		-0.64 (0.17)	-0.11 (0.09)		0.07	0.81
38	3.95 (2.01)	-0.85 (0.19)	-1.63 (0.75)	1.62 (0.84)	0.08 (0.73)	1.84 (1.97)	1.20 (2.32)			-0.64 (0.17)	-0.11 (0.09)		0.05	0.86
49	3.98 (1.93)	-0.74 (0.28)	-1.39 (0.68)	1.56 (0.55)		2.47 (1.07)		0.51 (0.91)		-0.64 (0.18)		0.02 (0.11)	0.04	0.90
46	3.9 (1.99)	-0.86 (0.19)	-1.61 (0.75)	1.74 (0.81)	0.09 (0.71)	1.78 (1.92)	1.20 (2.21)			-0.65 (0.17)		0.06 (0.11)	0.03	0.93
65	4.19 (1.98)	-0.77 (0.28)	-1.48 (0.71)	1.55 (0.55)		2.55 (1.08)		0.39 (0.94)		-0.66 (0.18)	-0.12 (0.10)	0.05 (0.11)	0.03	0.96

Table S1.5. Woodlands habitat patch preference model 95% confidence set. See Table S1.3 note for notations.

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ size	$\beta_7$ x occ <sup>2</sup> size	$\beta_8$ occ invest	$\beta_9$ x occ <sup>2</sup> invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
4	0.25 (0.08)	-0.29 (0.26)	-0.33 (0.11)	1.23 (0.18)	-0.12 (0.02)								0.146	0.146
8	0.25 (0.08)	-0.41 (0.28)	-0.34 (0.11)	1.09 (0.19)	-0.11 (0.03)			0.59 (0.36)	-0.07 (0.06)				0.096	0.242
28	0.24 (0.08)	-0.29 (0.26)	-0.33 (0.11)	1.17 (0.18)	-0.12 (0.02)							-0.07 (0.07)	0.093	0.335
12	0.24 (0.08)	-0.28 (0.26)	-0.33 (0.11)	1.23 (0.18)	-0.12 (0.02)					-0.06 (0.06)			0.074	0.410
32	0.24 (0.08)	-0.41 (0.28)	-0.34 (0.11)	1.03 (0.20)	-0.10 (0.03)			0.60 (0.35)	-0.07 (0.06)			-0.08 (0.07)	0.063	0.473
16	0.24 (0.08)	-0.41 (0.28)	-0.35 (0.11)	1.08 (0.19)	-0.11 (0.03)			0.63 (0.36)	-0.07 (0.06)	-0.07 (0.07)			0.062	0.535
20	0.25 (0.08)	-0.29 (0.26)	-0.32 (0.11)	1.23 (0.18)	-0.12 (0.02)						0.04 (0.06)		0.060	0.595
44	0.24 (0.08)	-0.28 (0.26)	-0.34 (0.11)	1.18 (0.18)	-0.12 (0.02)					-0.05 (0.07)		-0.07 (0.07)	0.045	0.639
52	0.24 (0.08)	-0.29 (0.26)	-0.32 (0.11)	1.17 (0.18)	-0.12 (0.02)						0.04 (0.06)	-0.08 (0.07)	0.041	0.680
48	0.24 (0.08)	-0.42 (0.28)	-0.35 (0.11)	1.03 (0.20)	-0.10 (0.03)			0.63 (0.36)	-0.07 (0.06)	-0.07 (0.07)		-0.07 (0.07)	0.037	0.717
36	0.24 (0.08)	-0.28 (0.26)	-0.33 (0.11)	1.24 (0.18)	-0.12 (0.02)					-0.07 (0.07)	0.06 (0.07)		0.037	0.754
24	0.25	-0.41	-0.33	1.10	-0.11			0.58	-0.07		0.03		0.036	0.791



Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ x size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ x invest	$\beta_9$ occ <sup>2</sup> x invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
40	(0.08) 0.24	(0.28) -0.41	(0.11) -0.35	(0.19) 1.09	(0.03) -0.11			(0.36) 0.63	(0.06) -0.07		(0.06) 0.05		0.029	0.819
56	(0.08) 0.24	(0.28) -0.41	(0.11) -0.34	(0.19) 1.03	(0.03) -0.10			(0.35) 0.59	(0.06) -0.07		(0.07) 0.04	-0.08	0.026	0.845
60	(0.08) 0.24	(0.26) -0.29	(0.11) -0.33	(0.18) 1.18	(0.02) -0.12					-0.07	0.06	-0.08	0.025	0.870
64	(0.08) 0.24	(0.28) -0.42	(0.11) -0.35	(0.20) 1.03	(0.03) -0.10			(0.35) 0.63	(0.06) -0.07	(0.07) -0.09	(0.07) 0.06	(0.07) -0.08	0.019	0.889
6	(0.08) 0.25	(0.26) -0.29	(0.12) -0.33	(0.25) 1.23	(0.04) -0.13	0.00	0.00						0.018	0.907
10	(0.08) 0.25	(0.28) -0.39	(0.12) -0.33	(0.26) 1.15	(0.04) -0.13	-0.05	0.01	0.67	-0.09				0.013	0.919
30	(0.08) 0.24	(0.26) -0.29	(0.12) -0.34	(0.26) 1.15	(0.04) -0.12	0.01	0.00					-0.08	0.011	0.931

Table S1.6. High-ranked foragers' patch preference model 95% confidence set. See Table S1.3 note for notations.

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ size	$\beta_7$ occ <sup>2</sup> size	$\beta_8$ occ invest	$\beta_9$ occ <sup>2</sup> invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
16	0.19 (0.10)	-0.62 (0.22)	-0.29 (0.13)	0.89 (0.21)	-0.08 (0.03)			0.90 (0.36)	-0.11 (0.06)	-0.14 (0.08)			0.167	0.167
40	0.19 (0.10)	-0.63 (0.22)	-0.30 (0.13)	0.87 (0.22)	-0.08 (0.03)			0.88 (0.36)	-0.10 (0.06)	-0.13 (0.08)	-0.07 (0.06)		0.102	0.269
8	0.18 (0.10)	-0.62 (0.22)	-0.25 (0.13)	1.00 (0.21)	-0.09 (0.03)			0.83 (0.37)	-0.11 (0.06)				0.085	0.353
48	0.19 (0.10)	-0.62 (0.22)	-0.28 (0.13)	0.85 (0.22)	-0.07 (0.03)			0.91 (0.36)	-0.11 (0.06)	-0.12 (0.08)		-0.05 (0.07)	0.075	0.429
24	0.19 (0.10)	-0.63 (0.22)	-0.27 (0.13)	0.97 (0.21)	-0.09 (0.03)			0.81 (0.37)	-0.10 (0.06)		-0.08 (0.06)		0.067	0.495
32	0.18 (0.09)	-0.62 (0.22)	-0.25 (0.13)	0.91 (0.22)	-0.08 (0.03)			0.86 (0.37)	-0.11 (0.06)			-0.08 (0.06)	0.063	0.558
18	0.19 (0.09)	-0.58 (0.22)	-0.32 (0.15)	1.01 (0.24)	-0.13 (0.05)	-0.10 (0.12)	0.03 (0.02)	1.12 (0.40)	-0.16 (0.07)	-0.15 (0.08)			0.050	0.609
64	0.19 (0.10)	-0.63 (0.22)	-0.29 (0.13)	0.85 (0.23)	-0.07 (0.04)			0.88 (0.36)	-0.10 (0.06)	-0.12 (0.08)	-0.06 (0.07)	-0.03 (0.07)	0.039	0.648
42	0.19 (0.09)	-0.58 (0.22)	-0.35 (0.15)	0.98 (0.25)	-0.13 (0.05)	-0.09 (0.12)	0.03 (0.02)	1.11 (0.40)	-0.16 (0.07)	-0.14 (0.08)	-0.08 (0.06)		0.039	0.687
56	0.18 (0.09)	-0.63 (0.22)	-0.26 (0.13)	0.90 (0.22)	-0.08 (0.03)			0.83 (0.37)	-0.11 (0.06)		-0.06 (0.07)	-0.06 (0.07)	0.035	0.722
4	0.19 (0.10)	-0.63 (0.21)	-0.22 (0.13)	1.20 (0.18)	-0.12 (0.03)								0.030	0.752
12	0.20	-0.61	-0.24	1.14	-0.11					-0.09			0.027	0.779

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ x size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ x invest	$\beta_9$ occ <sup>2</sup> x invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
	(0.10)	(0.21)	(0.13)	(0.19)	(0.03)					(0.07)				
20	0.20 (0.10)	-0.63 (0.21)	-0.24 (0.13)	1.17 (0.19)	-0.11 (0.03)						-0.08 (0.06)		0.025	0.804
50	0.18 (0.09)	-0.58 (0.22)	-0.32 (0.15)	0.95 (0.26)	-0.12 (0.05)	-0.09 (0.12)	0.03 (0.02)	1.12 (0.40)	-0.16 (0.07)	-0.14 (0.08)		-0.05 (0.07)	0.022	0.826
26	0.18 (0.09)	-0.59 (0.22)	-0.32 (0.15)	1.04 (0.24)	-0.14 (0.05)	-0.05 (0.12)	0.02 (0.02)	0.98 (0.39)	-0.15 (0.07)		-0.09 (0.06)		0.019	0.845
28	0.19 (0.10)	-0.63 (0.21)	-0.22 (0.13)	1.13 (0.20)	-0.11 (0.03)							-0.07 (0.06)	0.019	0.864
10	0.18 (0.09)	-0.59 (0.22)	-0.29 (0.15)	1.07 (0.24)	-0.13 (0.05)	-0.06 (0.12)	0.02 (0.02)	0.98 (0.40)	-0.15 (0.07)				0.019	0.883
36	0.20 (0.10)	-0.62 (0.21)	-0.25 (0.13)	1.11 (0.19)	-0.11 (0.03)					-0.08 (0.07)	-0.07 (0.06)		0.018	0.901
34	0.17 (0.09)	-0.58 (0.22)	-0.30 (0.15)	0.97 (0.26)	-0.12 (0.05)	-0.04 (0.12)	0.02 (0.02)	1.00 (0.40)	-0.15 (0.07)			-0.08 (0.06)	0.014	0.915
66	0.18 (0.09)	-0.58 (0.22)	-0.34 (0.15)	0.95 (0.26)	-0.13 (0.05)	-0.09 (0.12)	0.03 (0.02)	1.11 (0.40)	-0.16 (0.07)	-0.13 (0.08)	-0.08 (0.07)	-0.03 (0.07)	0.014	0.929

Table S1.7. Low-ranked foragers' patch preference model 95% confidence set. See Table S1.3 note for notations.

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ invest	$\beta_9$ occ <sup>2</sup> invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
36	0.22 (0.09)	-0.72 (0.21)	-0.43 (0.15)	1.07 (0.22)	-0.10 (0.03)					-0.15 (0.10)	0.22 (0.08)		0.24	0.24
20	0.23 (0.09)	-0.72 (0.21)	-0.43 (0.15)	0.94 (0.20)	-0.09 (0.03)						0.20 (0.07)		0.22	0.46
60	0.22 (0.09)	-0.71 (0.21)	-0.43 (0.15)	1.05 (0.22)	-0.10 (0.03)					-0.16 (0.11)	0.21 (0.08)	-0.06 (0.10)	0.11	0.57
52	0.23 (0.09)	-0.72 (0.21)	-0.43 (0.15)	0.92 (0.20)	-0.09 (0.03)						0.19 (0.07)	-0.02 (0.09)	0.08	0.65
40	0.21 (0.09)	-0.71 (0.22)	-0.45 (0.15)	0.98 (0.23)	-0.09 (0.03)			0.35 (0.38)	0.00 (0.06)	-0.16 (0.10)	0.21 (0.08)		0.07	0.72
24	0.22 (0.09)	-0.71 (0.22)	-0.45 (0.15)	0.85 (0.21)	-0.08 (0.03)			0.31 (0.37)	0.00 (0.06)		0.19 (0.08)		0.05	0.77
38	0.22 (0.09)	-0.73 (0.21)	-0.44 (0.17)	0.99 (0.28)	-0.08 (0.05)	0.08 (0.15)	-0.02 (0.03)			-0.15 (0.10)	0.21 (0.08)		0.04	0.81
22	0.23 (0.09)	-0.73 (0.21)	-0.43 (0.17)	0.87 (0.26)	-0.07 (0.05)	0.07 (0.15)	-0.02 (0.03)				0.19 (0.08)		0.03	0.84
64	0.21 (0.09)	-0.70 (0.22)	-0.45 (0.15)	0.94 (0.24)	-0.09 (0.03)			0.40 (0.38)	-0.01 (0.06)	-0.18 (0.11)	0.20 (0.08)	-0.08 (0.10)	0.03	0.87
56	0.22 (0.09)	-0.71 (0.22)	-0.45 (0.15)	0.82 (0.22)	-0.08 (0.03)			0.33 (0.38)	0.00 (0.06)		0.18 (0.08)	-0.03 (0.09)	0.02	0.89
62	0.22 (0.09)	-0.72 (0.21)	-0.44 (0.17)	0.98 (0.28)	-0.07 (0.05)	0.08 (0.15)	-0.02 (0.03)			-0.17 (0.11)	0.20 (0.08)	-0.06 (0.10)	0.02	0.91
4	0.22	-0.68	-0.38	0.92	-0.09								0.02	0.93

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ x size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ x invest	$\beta_9$ occ <sup>2</sup> x invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
54	(0.09) 0.23 (0.09)	(0.21) -0.73 (0.21)	(0.14) -0.43 (0.17)	(0.19) 0.86 (0.27)	(0.03) -0.07 (0.05)									
						0.07 (0.15)	-0.02 (0.03)				0.19 (0.08)	-0.02 (0.09)	0.01	0.94
12	(0.09) 0.21 (0.09)	(0.21) -0.67 (0.21)	(0.14) -0.38 (0.14)	(0.21) 1.03 (0.21)	(0.03) -0.10 (0.03)									
										-0.11 (0.10)			0.01	0.95

Table S1.8. High-social-capital (high grooming bond symmetry score) foragers' patch preference model 95% confidence set. See Table S1.3 note for notations.

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ size	x	$\beta_7$ occ <sup>2</sup> size	x	$\beta_8$ occ invest	x	$\beta_9$ occ <sup>2</sup> invest	x	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
16	0.09 (0.08)	-0.51 (0.22)	-0.12 (0.13)	0.62 (0.20)	-0.04 (0.03)					0.90 (0.41)		-0.14 (0.11)		-0.18 (0.08)			0.22	0.22
40	0.09 (0.08)	-0.51 (0.22)	-0.11 (0.13)	0.62 (0.20)	-0.04 (0.03)					0.90 (0.42)		-0.14 (0.11)		-0.20 (0.09)	0.06 (0.07)		0.12	0.34
48	0.10 (0.08)	-0.50 (0.22)	-0.12 (0.13)	0.58 (0.21)	-0.03 (0.03)					0.93 (0.42)		-0.14 (0.12)		-0.18 (0.08)		-0.05 (0.07)	0.10	0.44
12	0.10 (0.08)	-0.58 (0.21)	-0.08 (0.12)	0.84 (0.18)	-0.07 (0.02)									-0.17 (0.08)			0.09	0.53
64	0.09 (0.08)	-0.50 (0.22)	-0.12 (0.13)	0.59 (0.21)	-0.04 (0.03)					0.92 (0.42)		-0.14 (0.12)		-0.20 (0.09)	0.06 (0.07)	-0.05 (0.07)	0.05	0.58
36	0.10 (0.08)	-0.58 (0.21)	-0.08 (0.13)	0.83 (0.18)	-0.07 (0.02)									-0.18 (0.09)	0.07 (0.07)		0.05	0.63
8	0.10 (0.08)	-0.50 (0.23)	-0.12 (0.13)	0.56 (0.20)	-0.04 (0.03)					0.87 (0.45)		-0.14 (0.14)					0.05	0.68
44	0.10 (0.08)	-0.57 (0.21)	-0.08 (0.12)	0.82 (0.18)	-0.07 (0.02)									-0.17 (0.08)		-0.03 (0.07)	0.03	0.71
18	0.09 (0.08)	-0.49 (0.23)	-0.14 (0.14)	0.61 (0.24)	-0.05 (0.05)	-0.01 (0.13)		0.01 (0.03)		0.97 (0.45)		-0.16 (0.13)		-0.18 (0.08)			0.03	0.74
4	0.11 (0.08)	-0.58 (0.21)	-0.08 (0.12)	0.77 (0.17)	-0.07 (0.02)												0.03	0.77
32	0.11	-0.49	-0.12	0.52	-0.03					0.90		-0.15				-0.06	0.02	0.79

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ x size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ x invest	$\beta_9$ occ <sup>2</sup> x invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
	(0.08)	(0.23)	(0.13)	(0.21)	(0.03)			(0.46)	(0.14)			(0.07)		
24	0.10 (0.08)	-0.50 (0.23)	-0.12 (0.13)	0.56 (0.20)	-0.04 (0.03)			0.86 (0.45)	-0.14 (0.14)		0.03 (0.06)		0.02	0.81
60	0.10 (0.08)	-0.58 (0.21)	-0.08 (0.13)	0.82 (0.18)	-0.07 (0.02)					-0.18 (0.09)	0.06 (0.07)	-0.03 (0.07)	0.02	0.83
42	0.09 (0.08)	-0.49 (0.23)	-0.14 (0.14)	0.62 (0.24)	-0.05 (0.05)	-0.01 (0.13)	0.01 (0.03)	0.97 (0.45)	-0.17 (0.13)	-0.20 (0.09)	0.06 (0.07)		0.02	0.85
14	0.10 (0.09)	-0.57 (0.21)	-0.09 (0.14)	0.73 (0.24)	-0.04 (0.04)	0.08 (0.12)	-0.02 (0.02)			-0.17 (0.08)			0.02	0.87
50	0.09 (0.08)	-0.48 (0.23)	-0.14 (0.14)	0.57 (0.25)	-0.05 (0.05)	-0.01 (0.13)	0.01 (0.03)	1.01 (0.45)	-0.17 (0.13)	-0.18 (0.08)		-0.05 (0.07)	0.01	0.88
20	0.11 (0.08)	-0.58 (0.21)	-0.08 (0.12)	0.77 (0.17)	-0.07 (0.02)						0.04 (0.06)		0.01	0.89
28	0.11 (0.08)	-0.57 (0.21)	-0.08 (0.12)	0.75 (0.17)	-0.07 (0.02)							-0.03 (0.07)	0.01	0.90
56	0.10 (0.08)	-0.49 (0.23)	-0.12 (0.13)	0.52 (0.21)	-0.03 (0.03)			0.90 (0.46)	-0.15 (0.14)		0.03 (0.06)	-0.05 (0.07)	0.01	0.91
38	0.09 (0.09)	-0.58 (0.21)	-0.09 (0.14)	0.73 (0.23)	-0.04 (0.04)	0.07 (0.12)	-0.02 (0.02)			-0.19 (0.09)	0.07 (0.07)		0.01	0.92
66	0.09 (0.08)	-0.48 (0.23)	-0.14 (0.14)	0.58 (0.25)	-0.05 (0.05)	-0.02 (0.13)	0.01 (0.03)	1.00 (0.45)	-0.17 (0.13)	-0.20 (0.09)	0.06 (0.07)	-0.05 (0.07)	0.01	0.93
10	0.10 (0.08)	-0.48 (0.23)	-0.14 (0.14)	0.57 (0.24)	-0.05 (0.05)	-0.02 (0.13)	0.01 (0.03)	0.94 (0.47)	-0.17 (0.14)				0.01	0.94
46	0.10 (0.09)	-0.57 (0.21)	-0.09 (0.14)	0.72 (0.24)	-0.04 (0.04)	0.07 (0.12)	-0.02 (0.02)			-0.17 (0.08)		-0.03 (0.07)	0.01	0.95

Table S1.9. Low-social-capital (low grooming bond symmetry score) patch preference model 95% confidence set. See Table S1.3 note for notations.

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ x size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ x invest	$\beta_9$ occ <sup>2</sup> x invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
16	0.28 (0.11)	-0.58 (0.21)	-0.57 (0.15)	1.07 (0.21)	-0.11 (0.03)			0.70 (0.38)	-0.04 (0.06)	-0.21 (0.08)			0.28	0.28
48	0.27 (0.11)	-0.58 (0.21)	-0.56 (0.15)	0.99 (0.22)	-0.10 (0.03)			0.69 (0.38)	-0.04 (0.06)	-0.19 (0.08)		-0.09 (0.08)	0.19	0.47
40	0.28 (0.11)	-0.58 (0.21)	-0.57 (0.15)	1.07 (0.22)	-0.11 (0.03)			0.70 (0.38)	-0.04 (0.06)	-0.21 (0.08)	0.01 (0.07)		0.10	0.57
18	0.28 (0.11)	-0.51 (0.22)	-0.58 (0.17)	1.20 (0.25)	-0.17 (0.05)	-0.13 (0.14)	0.04 (0.03)	0.99 (0.44)	-0.11 (0.08)	-0.22 (0.08)			0.09	0.66
64	0.27 (0.11)	-0.58 (0.21)	-0.56 (0.15)	1.00 (0.22)	-0.10 (0.03)			0.69 (0.38)	-0.04 (0.06)	-0.19 (0.08)	0.04 (0.08)	-0.11 (0.08)	0.08	0.74
50	0.27 (0.11)	-0.52 (0.22)	-0.59 (0.17)	1.11 (0.26)	-0.16 (0.05)	-0.11 (0.14)	0.03 (0.03)	0.96 (0.44)	-0.11 (0.08)	-0.21 (0.08)		-0.09 (0.08)	0.06	0.80
42	0.28 (0.11)	-0.51 (0.22)	-0.58 (0.17)	1.20 (0.25)	-0.17 (0.05)	-0.13 (0.14)	0.04 (0.03)	0.99 (0.44)	-0.11 (0.08)	-0.22 (0.08)	-0.01 (0.07)		0.03	0.83
12	0.30 (0.11)	-0.55 (0.20)	-0.51 (0.14)	1.24 (0.20)	-0.12 (0.03)					-0.15 (0.07)			0.02	0.85
66	0.27 (0.11)	-0.52 (0.22)	-0.58 (0.17)	1.12 (0.26)	-0.16 (0.05)	-0.11 (0.14)	0.03 (0.03)	0.96 (0.44)	-0.11 (0.08)	-0.21 (0.08)	0.03 (0.08)	-0.10 (0.09)	0.02	0.87
32	0.26 (0.10)	-0.58 (0.21)	-0.51 (0.14)	1.00 (0.22)	-0.11 (0.03)			0.56 (0.38)	-0.03 (0.06)			-0.12 (0.08)	0.02	0.89
44	0.29 (0.11)	-0.55 (0.20)	-0.50 (0.14)	1.15 (0.21)	-0.11 (0.03)					-0.14 (0.07)		-0.09 (0.08)	0.02	0.91
8	0.27	-0.58	-0.50	1.12	-0.12			0.57	-0.04				0.02	0.93



Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ x size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ x invest	$\beta_9$ occ <sup>2</sup> x invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
	(0.10)	(0.21)	(0.14)	(0.21)	(0.03)			(0.38)	(0.06)					
14	0.30 (0.11)	-0.55 (0.20)	-0.59 (0.17)	1.32 (0.24)	-0.17 (0.05)	-0.04 (0.12)	0.02 (0.02)			-0.17 (0.07)			0.01	0.94
36	0.30 (0.11)	-0.55 (0.20)	-0.51 (0.14)	1.26 (0.20)	-0.12 (0.03)					-0.15 (0.07)	0.03 (0.07)		0.01	0.95

Table S1.10. High numbers of close kin foragers' patch preference model 95% confidence set. See table S1.3 note for notations.

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ x size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ x invest	$\beta_9$ occ <sup>2</sup> x invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
12	0.83 (0.31)	-0.76 (0.24)	-0.33 (0.17)	1.44 (0.36)	-0.40 (0.12)					-0.21 (0.11)			0.20	0.20
44	0.84 (0.31)	-0.76 (0.24)	-0.34 (0.17)	1.50 (0.37)	-0.41 (0.12)					-0.22 (0.12)		0.07 (0.09)	0.10	0.30
4	0.81 (0.31)	-0.77 (0.24)	-0.29 (0.16)	1.32 (0.34)	-0.37 (0.11)								0.08	0.38
36	0.83 (0.31)	-0.76 (0.24)	-0.33 (0.17)	1.45 (0.37)	-0.40 (0.12)					-0.21 (0.11)	0.01 (0.09)		0.07	0.45
14	0.92 (0.29)	-0.77 (0.24)	-0.40 (0.19)	1.10 (0.45)	-0.31 (0.16)	0.35 (0.25)	-0.09 (0.08)			-0.20 (0.12)			0.07	0.52
16	0.85 (0.29)	-0.77 (0.29)	-0.38 (0.17)	1.39 (0.39)	-0.41 (0.13)			0.35 (0.76)	0.06 (0.28)	-0.22 (0.11)			0.06	0.58
6	0.90 (0.28)	-0.78 (0.24)	-0.38 (0.19)	0.95 (0.43)	-0.28 (0.16)	0.39 (0.24)	-0.09 (0.07)						0.04	0.62
28	0.82 (0.32)	-0.76 (0.24)	-0.29 (0.17)	1.36 (0.35)	-0.37 (0.11)							0.06 (0.08)	0.04	0.66
60	0.84 (0.32)	-0.76 (0.24)	-0.34 (0.17)	1.51 (0.38)	-0.41 (0.12)					-0.22 (0.12)	0.02 (0.09)	0.08 (0.09)	0.03	0.69
46	0.93 (0.29)	-0.77 (0.25)	-0.41 (0.19)	1.16 (0.45)	-0.32 (0.16)	0.35 (0.25)	-0.09 (0.08)			-0.21 (0.12)		0.07 (0.09)	0.03	0.72
20	0.80 (0.31)	-0.77 (0.24)	-0.29 (0.17)	1.33 (0.34)	-0.37 (0.11)						0.02 (0.08)		0.03	0.75
18	1.10	-0.88	-0.43	1.00	-0.24	0.37	-0.14	-0.05	0.27	-0.21			0.03	0.78

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ x size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ x invest	$\beta_9$ occ <sup>2</sup> x invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
48	(0.33) 0.86 (0.29)	(0.31) -0.77 (0.29)	(0.19) -0.38 (0.17)	(0.46) 1.45 (0.41)	(0.17) -0.42 (0.13)	(0.25)	(0.09)	(0.83) 0.28 (0.77)	(0.34) 0.07 (0.28)	(0.12) -0.23 (0.12)		0.06 (0.09)	0.03	0.81
38	0.93 (0.29)	-0.77 (0.24)	-0.41 (0.19)	1.08 (0.46)	-0.31 (0.16)	0.37 (0.26)	-0.09 (0.08)			-0.20 (0.12)	-0.03 (0.09)		0.02	0.83
8	0.82 (0.29)	-0.79 (0.28)	-0.33 (0.17)	1.29 (0.37)	-0.38 (0.12)			0.22 (0.72)	0.08 (0.26)				0.02	0.85
40	0.85 (0.29)	-0.77 (0.29)	-0.38 (0.17)	1.39 (0.40)	-0.41 (0.13)			0.35 (0.76)	0.06 (0.28)	-0.22 (0.11)	0.00 (0.09)		0.02	0.87
30	0.91 (0.29)	-0.78 (0.24)	-0.39 (0.187)	1.00 (0.43)	-0.28 (0.16)	0.39 (0.24)	-0.09 (0.07)					0.06 (0.08)	0.02	0.89
10	1.08 (0.33)	-0.90 (0.30)	-0.41 (0.19)	0.86 (0.44)	-0.22 (0.17)	0.43 (0.24)	-0.15 (0.09)	-0.17 (0.79)	0.29 (0.33)				0.02	0.91
22	0.91 (0.28)	-0.78 (0.24)	-0.39 (0.19)	0.92 (0.44)	-0.28 (0.16)	0.41 (0.25)	-0.10 (0.07)				-0.02 (0.09)		0.02	0.93
52	0.82 (0.32)	-0.76 (0.24)	-0.30 (0.17)	1.38 (0.35)	-0.37 (0.11)						0.03 (0.08)	0.06 (0.08)	0.01	0.94
50	1.11 (0.34)	-0.88 (0.31)	-0.43 (0.19)	1.06 (0.47)	-0.26 (0.17)	0.37 (0.25)	-0.14 (0.09)	-0.11 (0.84)	0.28 (0.35)	-0.22 (0.12)		0.06 (0.09)	0.01	0.95

Table S1.11. Low numbers of close kin foragers' patch preference model 95% confidence set. See Table S1.3 note for notations.

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ x size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ x invest	$\beta_9$ occ <sup>2</sup> x invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
44	0.10 (0.08)	-0.28 (0.22)	-0.21 (0.14)	0.84 (0.19)	-0.06 (0.02)					-0.18 (0.08)		-0.18 (0.08)	0.17	0.17
48	0.09 (0.08)	-0.21 (0.23)	-0.24 (0.15)	0.55 (0.28)	-0.01 (0.05)			0.70 (0.40)	-0.10 (0.07)	-0.19 (0.08)		-0.20 (0.08)	0.12	0.29
46	0.08 (0.08)	-0.29 (0.22)	-0.37 (0.18)	0.49 (0.29)	-0.02 (0.04)	0.22 (0.13)	-0.02 (0.02)			-0.19 (0.08)		-0.21 (0.08)	0.11	0.40
60	0.10 (0.08)	-0.27 (0.22)	-0.23 (0.14)	0.86 (0.19)	-0.06 (0.02)					-0.17 (0.08)	-0.08 (0.09)	-0.15 (0.09)	0.09	0.49
62	0.09 (0.08)	-0.29 (0.22)	-0.40 (0.18)	0.52 (0.29)	-0.03 (0.04)	0.21 (0.13)	-0.02 (0.02)			-0.18 (0.08)	-0.09 (0.09)	-0.18 (0.09)	0.06	0.55
36	0.10 (0.08)	-0.29 (0.22)	-0.26 (0.14)	0.96 (0.18)	-0.07 (0.02)					-0.18 (0.08)	-0.14 (0.08)		0.06	0.61
64	0.10 (0.08)	-0.21 (0.23)	-0.26 (0.15)	0.56 (0.28)	-0.01 (0.05)			0.67 (0.40)	-0.10 (0.07)	-0.18 (0.08)	-0.08 (0.09)	-0.17 (0.09)	0.06	0.67
50	0.08 (0.08)	-0.20 (0.24)	-0.38 (0.18)	0.40 (0.31)	-0.03 (0.05)	0.12 (0.15)	0.00 (0.03)	0.73 (0.45)	-0.12 (0.08)	-0.20 (0.08)		-0.22 (0.09)	0.05	0.72
12	0.10 (0.08)	-0.30 (0.22)	-0.23 (0.14)	0.97 (0.19)	-0.07 (0.02)					-0.21 (0.08)			0.04	0.76
66	0.09 (0.08)	-0.20 (0.24)	-0.40 (0.18)	0.42 (0.31)	-0.03 (0.05)	0.11 (0.15)	0.00 (0.03)	0.72 (0.45)	-0.12 (0.08)	-0.19 (0.08)	-0.10 (0.09)	-0.19 (0.09)	0.03	0.79
28	0.11 (0.08)	-0.28 (0.22)	-0.19 (0.14)	0.86 (0.19)	-0.07 (0.02)							-0.20 (0.08)	0.03	0.82
40	0.10	-0.25	-0.28	0.74	-0.03			0.57	-0.08	-0.20	-0.14		0.03	0.85

Model no.	$\beta_1$ food	$\beta_2$ investment	$\beta_3$ size	$\beta_4$ occ	$\beta_5$ occ <sup>2</sup>	$\beta_6$ occ x size	$\beta_7$ occ <sup>2</sup> x size	$\beta_8$ occ x invest	$\beta_9$ occ <sup>2</sup> x invest	$\beta_{10}$ rank	$\beta_{11}$ symmetry	$\beta_{12}$ kinship	$w_i$	cumulative $w_i$
38	(0.08) 0.10 (0.08)	(0.23) -0.30 (0.22)	(0.15) -0.40 (0.18)	(0.25) 0.72 (0.26)	(0.04) -0.05 (0.04)			(0.38) 0.16 (0.12)	(0.06) -0.01 (0.02)	(0.08) -0.19 (0.08)	(0.09) -0.16 (0.09)		0.02	0.87
52	(0.08) 0.11 (0.08)	(0.22) -0.28 (0.22)	(0.14) -0.21 (0.14)	(0.19) 0.88 (0.19)	(0.02) -0.07 (0.02)						(0.09) -0.11 (0.09)	(0.08) -0.16 (0.08)	0.02	0.89
16	(0.08) 0.09 (0.08)	(0.23) -0.26 (0.23)	(0.14) -0.25 (0.14)	(0.24) 0.78 (0.24)	(0.04) -0.04 (0.04)			(0.38) 0.59 (0.38)	(0.06) -0.08 (0.06)	(0.08) -0.22 (0.08)			0.02	0.91
30	(0.08) 0.09 (0.08)	(0.22) -0.30 (0.22)	(0.17) -0.32 (0.17)	(0.29) 0.53 (0.29)	(0.05) -0.03 (0.05)	0.22 (0.13)	-0.03 (0.02)					(0.08) -0.23 (0.08)	0.02	0.93
32	(0.08) 0.11 (0.08)	(0.23) -0.21 (0.23)	(0.14) -0.21 (0.14)	(0.28) 0.60 (0.28)	(0.05) -0.02 (0.05)			(0.41) 0.62 (0.41)	(0.07) -0.10 (0.07)			(0.08) -0.23 (0.08)	0.01	0.94
14	(0.08) 0.09 (0.08)	(0.22) -0.32 (0.22)	(0.17) -0.34 (0.17)	(0.26) 0.75 (0.26)	(0.04) -0.05 (0.04)	0.16 (0.12)	-0.02 (0.02)			(0.08) -0.22 (0.08)			0.01	0.95

## Appendix S2

### Supporting Information for Chapter 5

Table S2.1. Details of parameter estimates for all models in the natural foraging conditions candidate set. The grouping vectors and variables in first column correspond to the annotations used in Chapter 5. Empty cells correspond to model where a variable was not included. Models are listed in order of decreasing Akaike's weight ( $w_i$ ) from left to right.

	Variable	Model no.									
		6	7	8	9	2	5	4	3	1	
	Intercept	4.06	4.06	4.07	4.07	4.11	4.11	3.59	3.57	3.59	
<i>c</i>	Patch species	✓	✓	✓	✓	✓	✓				
	Surface area	0.39	0.39	0.39	0.39	0.41	0.41				
	Handling time	✓	✓	✓	✓	✓	✓				
	No. of occupants	0.43	0.43	0.43	0.43	0.44	0.44				
	No. of occupants <sup>2</sup>	-0.35	-0.35	-0.35	-0.35	-0.36	-0.36				
	Focal rank	0.02	0.02	0.02	0.02	0.02	0.02				
	Focal mean social bond	-0.03	-0.03	-0.03	-0.03	-0.02	-0.02				
	Focal mean relatedness	0.03	0.03	0.04	0.03	0.01	0.01				
	Mean rank difference with co-foragers	0.02	0.02	0.02	0.02	0.02	0.02				
	Mean social bond with co-foragers	0.02	0.02	0.02	0.02	0.01	0.01				
	Mean relatedness with co-foragers	0.03	0.03	0.03	0.03	0.03	0.03				
<i>t</i>	Time in previous patch		0.01	0.02	0.02		0.02		0.10		
<i>h</i>	Mean patch density	-0.16	-0.15		-0.26			-0.32			
	Mean patch food content	-0.11	-0.11		0.32			0.08			
<i>h<sub>sd</sub></i> ( <i>x t</i> )	SD patch density			-0.14	0.17						
	x Time in previous patch			0.02	0.02						
	SD patch food content			-0.10	-0.40						
	x Time in previous patch			-0.01	-0.01						
	$w_i$	0.69	0.27	0.03	0.02	0.00	0.00	0.00	0.00	0.00	

Table S2.2. Details of parameter estimates for all models in the experimental foraging conditions candidate set. The grouping vectors and variables in first column correspond to the annotations used in Chapter 5. Empty cells correspond to model where a variable was not included. Models are listed in order of decreasing Akaike's weight ( $w_i$ ) from left to right.

		Model no.						
		7	6	5	2	4	3	1
	Intercept	4.08	4.11	4.09	4.12	3.88	3.86	3.86
<b>c</b>	Patch food density	0.67	0.20	0.67	0.21			
	Patch depletion	0.03	0.02	0.03	0.02			
	No. of occupants	0.60	0.61	0.60	0.61			
	No. of occupants <sup>2</sup>	-0.21	-0.23	-0.21	-0.22			
	Focal satiation	-0.01	0.00	0.02	0.03			
	Focal rank	0.06	0.05	0.06	0.05			
	Focal mean social bond	-0.07	-0.08	-0.07	-0.09			
	Focal mean relatedness	0.14	0.16	0.15	0.16			
	Mean rank difference with co-foragers	0.32	0.32	0.32	0.32			
	Mean social bond with co-foragers	0.02	0.02	0.02	0.02			
	Mean relatedness with co-foragers	-0.23	-0.22	-0.23	-0.22			
<b>t</b>	Time in previous patch	0.08	0.08				0.09	
<b>h</b>	Inter-patch distance	0.10		0.11		0.11		
	Mean patch food content	-0.60		-0.59		0.32		
	$w_i$	0.98	0.02	0.00	0.00	0.00	0.00	0.00

## Appendix S3

### Supporting Information for Chapter 6

#### Full Details of the All-subset Averaged Models Presented in Chapter 6

In all tables (S3.1 to S3.4) each variable's importance ( $w$ ) is measured by Akaike's weight. Missing importance values correspond to variables that were included in all candidate models as controls and whose importance is, as a result, fixed at 1. Variables with no coefficient, confidence interval or importance values were not included in any of candidate models in the corresponding analysis.

Table S3.1. The probability of foraging in an occupied patch under experimental foraging conditions.

Fixed effects	Coefficient	Lower C.I.	Upper C.I.	$w$
(Intercept)	2.27	0.42	4.11	
Patch food density	1.47	0.64	2.29	
Patch depletion	0.19	0.06	0.31	
Rank	0.40	0.20	0.61	1.00
Relatedness	-0.07	-0.39	0.26	0.57
Social bonds	0.40	0.10	0.70	0.99
Rank x Relatedness	0.13	-0.06	0.31	0.28
Rank x Social bonds	0.25	0.03	0.47	0.79
Relatedness x Social bonds	0.06	-0.20	0.32	0.17
Inter-patch distance	0.13	0.01	0.25	0.78
Mean patch food content	-1.52	-2.41	-0.63	0.98
Satiation	0.02	-0.09	0.12	0.28



Table S3.2. The probability of foraging in an occupied patch under natural foraging conditions.

Fixed effects	Coefficient	Lower C.I.	Upper C.I.	<i>w</i>
(Intercept)	0.22	-0.23	0.67	
Patch species <sup>a</sup> :				
<i>Faidherbia albida</i>	-0.65	-1.17	-0.13	
Herb/shrub	-2.28	-2.92	-1.64	
<i>Prosopis glandulosa</i>	-1.85	-2.33	-1.37	
<i>Salvadora persica</i>	-0.41	-1.05	0.24	
<i>Tapinanthus oleifolius</i>	0.01	-0.65	0.66	
<i>Acacia tortilis</i>	-0.03	-1.10	1.03	
Surface Area	0.74	0.63	0.86	
Handling time <sup>b</sup> :				
low	-0.20	-0.71	0.31	
Rank	0.58	0.42	0.74	1.00
Relatedness	0.12	-0.05	0.29	0.57
Social bonds	0.02	-0.21	0.25	0.78
Rank x Relatedness	0.00	-0.17	0.18	0.16
Rank x Social bonds	0.13	-0.02	0.27	0.46
Relatedness x Social bonds	-0.12	-0.26	0.03	0.25
Mean patch food content	-0.04	-0.13	0.05	0.34
Patch density	-0.48	-0.59	-0.37	1.00

<sup>a</sup>reference category: *A. erioloba*

<sup>b</sup>reference category: high

Table S3.3. The determinants of intake rate and patch residency time under natural foraging conditions.

Fixed effects	Initial intake rate (bites/ten seconds)				Patch residency time (s)			
	Coefficient	Lower C.I.	Upper C.I.	w	Coefficient	Lower C.I.	Upper C.I.	w
(Intercept)	1.03	0.80	1.26		4.99	4.60	5.37	
Rank	-0.05	-0.09	-0.01	0.91	0.01	-0.06	0.07	0.51
Relatedness	0.04	0.00	0.09	0.94	0.09	0.02	0.15	0.74
Social bonds	-0.03	-0.08	0.02	0.80	-0.12	-0.20	-0.05	0.99
Rank x Relatedness	-0.01	-0.06	0.04	0.26	0.04	-0.04	0.11	0.15
Rank x Social bonds	0.02	-0.02	0.06	0.27	-0.01	-0.07	0.06	0.14
Relatedness x Social bonds	0.05	0.01	0.09	0.65	0.02	-0.05	0.08	0.22
No. of patch occupants	0.01	-0.03	0.05	0.42	0.47	0.35	0.60	1.00
No. of patch occupants <sup>2</sup>	0.02	-0.03	0.06	0.13	-0.28	-0.38	-0.18	1.00
Initial intake rate					0.31	0.26	0.36	1.00
x Rank					-0.01	-0.06	0.04	0.15
x Social bonds					0.02	-0.03	0.06	0.34
x Patch density					0.05	0.00	0.09	0.78
Patch species <sup>a</sup> :								
<i>Faidherbia albida</i>	0.20	-0.08	0.48		-0.78	-1.27	-0.28	
Herb/shrub	0.63	0.32	0.95		-1.07	-1.65	-0.48	
<i>Prosopis glandulosa</i>	0.37	0.07	0.68		-0.51	-1.08	0.07	
<i>Salvadora persica</i>	0.95	0.62	1.27		-0.35	-0.95	0.26	
<i>Tapinanthus oleifolius</i>	0.42	0.09	0.76		0.09	-0.52	0.69	
<i>Acacia tortilis</i>	0.28	-0.20	0.75		-0.49	-1.27	0.28	
Patch surface area	0.02	-0.02	0.06		0.24	0.15	0.33	
Handling time <sup>b</sup> :								
low	0.23	0.00	0.46		0.05	-0.40	0.51	
Mean patch density					-0.19	-0.25	-0.13	
Mean patch food content					-0.19	-0.26	-0.12	

<sup>a</sup>reference category: *A. erioloba*<sup>b</sup>reference category: high

Table S3.4. The determinants of intake rate and patch residency time under experimental foraging conditions.

Fixed effects	Initial intake rate (bites/ten seconds)				Patch residency time (s)			
	Coefficient	Lower C.I.	Upper C.I.	<i>w</i>	Coefficient	Lower C.I.	Upper C.I.	<i>w</i>
(Intercept)	1.33	0.86	1.81		4.61	4.41	4.80	
Rank	0.29	0.17	0.42	1.00	0.35	0.21	0.48	1.00
Relatedness	0.03	-0.15	0.21	0.89	0.09	-0.04	0.22	0.93
Social bonds	-0.06	-0.22	0.10	0.57	-0.09	-0.22	0.03	0.92
Rank x Relatedness	-0.11	-0.21	-0.01	0.65	-0.09	-0.19	0.01	0.59
Rank x Social bonds	0.02	-0.11	0.16	0.17	0.00	-0.11	0.12	0.26
Relatedness x Social bonds	0.11	-0.03	0.25	0.29	0.08	-0.03	0.18	0.45
No. of patch occupants	0.18	0.05	0.30	1.00	0.36	0.17	0.55	1.00
No. of patch occupants <sup>2</sup>	-0.03	-0.22	0.16	0.28	0.00	-0.32	0.31	0.27
Satiation	-0.27	-0.37	-0.18	1.00	0.08	-0.06	0.22	0.40
Initial intake rate					0.00	-0.13	0.13	0.97
x Rank					0.19	0.04	0.34	0.90
x Social bonds					0.12	-0.02	0.26	0.57
x Inter-patch distance					-0.06	-0.17	0.04	0.40
x Mean patch food content					-0.10	-0.22	0.02	0.56
Patch food density	0.26	0.18	0.34		0.89	0.55	1.23	
Patch depletion	-0.36	-0.46	-0.27		-0.03	-0.16	0.10	
Time in previous patch					0.05	-0.04	0.15	
Inter patch distance					0.05	-0.08	0.17	
Mean patch food content					-0.83	-1.19	-0.47	

## 95% Confidence Model Sets for Each Analysis in Chapter 6

See Appendix S1 for an explanation of how 95% confidence model sets are calculated and interpreted. In all tables (S3.5 to S3.12) models are listed in order of decreasing Akaike's model weight ( $w_i$ ). In each model (one row), parameter estimates ( $\beta \pm \text{s.e.}$ ) for each explanatory variable are provided with the model's AIC(c) value and difference ( $\Delta$ ) from the best model's AIC(c). Due to space limitations, categorical variables are simply noted as being included in a model (✓) or not (empty cell).

Table S3.5. 95% confidence model set for the analysis of the probability of a baboon initiating agonism in the natural foraging conditions.

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social Bonds		Relatedness x Social Bonds		Mean patch food content		Patch density		AICc	$\Delta$ AICc	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.			
-0.55	0.11	1.25	0.12			0.26	0.14			-0.71	0.15			0.11	0.07			425.06	0.00	0.19
-0.53	0.11	1.24	0.12			0.26	0.14			-0.70	0.15							425.53	0.47	0.15
-0.53	0.12	1.25	0.12			0.26	0.14			-0.71	0.15			0.14	0.07	0.07	0.09	426.43	1.37	0.10
-0.54	0.11	1.26	0.12	0.09	0.11	0.22	0.15			-0.68	0.15			0.11	0.07			426.43	1.38	0.10
-0.53	0.11	1.25	0.12	0.08	0.11	0.22	0.15			-0.67	0.15							427.00	1.94	0.07
-0.52	0.11	1.26	0.12	0.12	0.11	0.26	0.15			-0.71	0.16	-0.12	0.12	0.11	0.07			427.56	2.50	0.05
-0.53	0.12	1.24	0.12			0.26	0.14			-0.70	0.15					0.01	0.08	427.60	2.55	0.05
-0.52	0.12	1.26	0.12	0.10	0.11	0.22	0.15			-0.67	0.15			0.14	0.07	0.08	0.09	427.74	2.69	0.05
-0.51	0.11	1.25	0.12	0.12	0.11	0.26	0.15			-0.71	0.16	-0.12	0.12					428.18	3.12	0.04
-0.54	0.11	1.26	0.12	0.09	0.11	0.22	0.15	0.01	0.12	-0.68	0.16			0.11	0.07			428.52	3.47	0.03
-0.50	0.11	1.27	0.12	0.13	0.11	0.26	0.15			-0.71	0.16	-0.12	0.12	0.14	0.07	0.08	0.09	428.89	3.84	0.03
-0.52	0.11	1.25	0.12	0.09	0.11	0.22	0.15	0.02	0.12	-0.68	0.16							429.07	4.01	0.03
-0.52	0.12	1.25	0.12	0.08	0.11	0.22	0.15			-0.67	0.15					0.01	0.08	429.08	4.02	0.03
-0.52	0.11	1.26	0.12	0.12	0.11	0.26	0.15	-0.03	0.13	-0.71	0.16	-0.13	0.13	0.11	0.07			429.64	4.58	0.02
-0.52	0.12	1.26	0.12	0.10	0.11	0.22	0.15	0.01	0.12	-0.68	0.16			0.14	0.07	0.08	0.09	429.85	4.79	0.02
-0.51	0.11	1.25	0.12	0.11	0.11	0.26	0.15	-0.02	0.13	-0.71	0.16	-0.13	0.13					430.25	5.20	0.01

Table S3.6. 95% confidence model set for the analysis of the probability of a baboon initiating agonism in the experimental foraging conditions.

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social Bond		Relatedness x Social Bond		Mean patch food content		Inter patch distance		AICc	$\Delta$ AICc	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.			
0.07	0.13	1.27	0.13	0.21	0.12	-0.19	0.16	0.25	0.12	-0.49	0.14			0.19	0.02	0.04	0.01	1010.67	0.00	0.36
0.01	0.14	1.24	0.14			-0.18	0.16			-0.44	0.14			0.19	0.02	0.04	0.01	1011.69	1.02	0.22
0.07	0.13	1.27	0.13	0.21	0.12	-0.21	0.16	0.32	0.14	-0.44	0.14	0.14	0.14	0.19	0.02	0.04	0.01	1012.10	1.43	0.18
0.04	0.14	1.26	0.14	0.13	0.12	-0.22	0.16			-0.41	0.14			0.19	0.02	0.04	0.01	1012.94	2.27	0.12
0.04	0.14	1.26	0.14	0.13	0.13	-0.22	0.16			-0.43	0.15	-0.04	0.12	0.19	0.02	0.04	0.01	1015.19	4.52	0.04
0.06	0.13	1.26	0.13	0.21	0.12	-0.19	0.16	0.25	0.12	-0.49	0.14			0.19	0.02			1016.30	5.63	0.02
0.01	0.14	1.23	0.14			-0.18	0.16			-0.44	0.14			0.19	0.02			1017.32	6.65	0.01
0.06	0.13	1.26	0.13	0.21	0.12	-0.21	0.16	0.31	0.14	-0.44	0.14	0.14	0.14	0.19	0.02			1017.68	7.01	0.01

Table S3.7. 95% confidence model set for the analysis of the probability of a baboon using an occupied patch in the natural foraging conditions.

Intercept		Patch Species	Surface Area		Handling time	Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		Mean patch food content		Patch density		AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.		$\beta$	s.e.		$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.			
0.23	0.24	✓	0.74	0.06	✓	0.61	0.08			0.00	0.10			0.12	0.07					-0.47	0.05	7128.59	0.00	0.12
0.19	0.24	✓	0.74	0.06	✓	0.57	0.08			0.11	0.07									-0.47	0.05	7129.22	0.64	0.09
0.19	0.24	✓	0.74	0.06	✓	0.53	0.07													-0.47	0.05	7129.34	0.76	0.08
0.24	0.21	✓	0.75	0.06	✓	0.62	0.08	0.15	0.08	-0.08	0.10			0.15	0.07					-0.48	0.05	7129.65	1.06	0.07
0.26	0.21	✓	0.75	0.06	✓	0.61	0.08	0.15	0.08	-0.04	0.11			0.11	0.08	-0.10	0.07			-0.47	0.05	7129.90	1.32	0.06
0.22	0.24	✓	0.74	0.06	✓	0.60	0.08			0.00	0.10			0.12	0.07			-0.04	0.05	-0.49	0.06	7129.95	1.36	0.06
0.23	0.22	✓	0.75	0.06	✓	0.58	0.07	0.09	0.08	0.09	0.07					-0.13	0.07			-0.47	0.05	7130.07	1.48	0.06
0.19	0.22	✓	0.75	0.06	✓	0.54	0.07	0.11	0.08											-0.47	0.05	7130.53	1.95	0.04
0.19	0.24	✓	0.74	0.06	✓	0.57	0.08			0.11	0.07							-0.04	0.05	-0.49	0.06	7130.57	1.98	0.04
0.19	0.24	✓	0.74	0.06	✓	0.53	0.07											-0.04	0.05	-0.49	0.06	7130.68	2.10	0.04
0.24	0.21	✓	0.74	0.06	✓	0.62	0.08	0.14	0.08	-0.08	0.10			0.15	0.07			-0.04	0.05	-0.49	0.06	7130.92	2.34	0.04
0.19	0.24	✓	0.74	0.06	✓	0.57	0.08	0.03	0.09	0.10	0.08									-0.47	0.05	7131.13	2.54	0.03
0.25	0.21	✓	0.74	0.06	✓	0.61	0.08	0.15	0.08	-0.04	0.11			0.11	0.08	-0.10	0.07	-0.04	0.05	-0.49	0.06	7131.17	2.58	0.03
0.23	0.21	✓	0.75	0.06	✓	0.58	0.08	0.13	0.08	0.08	0.07					-0.13	0.07	-0.04	0.05	-0.49	0.06	7131.32	2.74	0.03

Intercept		Patch Species	Surface Area		Handling time	Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		Mean patch food content		Patch density		AIC	ΔAIC	w <sub>i</sub>		
β	s.e.		β	s.e.		β	s.e.	β	s.e.	β	s.e.	β	s.e.	β	s.e.	β	s.e.	β	s.e.	β	s.e.					
0.24	0.21	✓	0.75	0.06	✓	0.62	0.08	0.14	0.08	-0.08	0.10	0.01	0.08	0.15	0.07					-0.48	0.05	7131.62	3.04	0.03		
0.26	0.21	✓	0.75	0.06	✓	0.61	0.08	0.15	0.08	-0.03	0.11	-0.03	0.09	0.11	0.08	-0.11	0.08			-0.47	0.05	7131.76	3.17	0.02		
0.19	0.21	✓	0.74	0.06	✓	0.54	0.07	0.13	0.08									-0.04	0.05	-0.49	0.06	7131.79	3.21	0.02		
0.23	0.22	✓	0.75	0.06	✓	0.58	0.07	0.09	0.08	0.09	0.07	-0.03	0.09			-0.14	0.08			-0.47	0.05	7131.96	3.37	0.02		
0.20	0.21	✓	0.75	0.06	✓	0.55	0.07	0.13	0.08			0.05	0.08							-0.47	0.05	7132.21	3.62	0.02		
0.19	0.23	✓	0.74	0.06	✓	0.57	0.08	0.04	0.09	0.10	0.08							-0.04	0.05	-0.49	0.06	7132.45	3.87	0.02		
0.24	0.21	✓	0.74	0.06	✓	0.62	0.08	0.14	0.08	-0.07	0.10	0.01	0.08	0.15	0.07					-0.04	0.05	-0.49	0.06	7132.90	4.31	0.01
0.19	0.23	✓	0.74	0.06	✓	0.57	0.08	0.04	0.09	0.10	0.08	0.03	0.08							-0.47	0.05	7132.96	4.38	0.01		

Table S3.8. 95% confidence model set for the analysis of the probability of a baboon using an occupied patch in the experimental foraging conditions.

Intercept		Patch food density		Patch depletion		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		Inter-patch distance		Mean patch food content		Satiation		AIC	ΔAIC	w <sub>i</sub>
β	s.e.	β	s.e.	β	s.e.	β	s.e.	β	s.e.	β	s.e.	β	s.e.	β	s.e.	β	s.e.	β	s.e.	β	s.e.	β	s.e.			
2.30	0.92	1.49	0.38	0.19	0.06	0.41	0.10			0.36	0.14			0.26	0.11			0.13	0.06	-1.51	0.45			5614.89	0.00	0.20
2.28	0.96	1.50	0.38	0.19	0.06	0.41	0.10	-0.09	0.14	0.40	0.15			0.24	0.11			0.13	0.06	-1.52	0.45			5616.49	1.60	0.09
2.30	0.92	1.48	0.38	0.18	0.08	0.40	0.11			0.36	0.14			0.27	0.11			0.13	0.06	-1.50	0.45	0.02	0.05	5616.80	1.92	0.08
2.29	0.96	1.50	0.38	0.19	0.06	0.41	0.10	0.00	0.16	0.40	0.15	0.11	0.09	0.21	0.11			0.13	0.06	-1.53	0.45			5617.05	2.16	0.07
2.30	0.92	1.51	0.38	0.19	0.06	0.41	0.10			0.36	0.14			0.26	0.11					-1.53	0.46			5617.37	2.48	0.06
2.28	0.97	1.49	0.38	0.19	0.06	0.41	0.10	0.00	0.16	0.39	0.15	0.15	0.10	0.24	0.12	0.11	0.13	0.13	0.06	-1.52	0.46			5618.24	3.35	0.04
2.28	0.96	1.49	0.38	0.18	0.08	0.40	0.11	-0.09	0.14	0.40	0.15			0.24	0.11			0.13	0.06	-1.51	0.46	0.02	0.05	5618.40	3.52	0.03
2.28	0.96	1.49	0.38	0.19	0.06	0.41	0.10	-0.10	0.15	0.40	0.15			0.25	0.12	0.03	0.12	0.13	0.06	-1.52	0.45			5618.41	3.53	0.03
2.16	0.99	1.51	0.38	0.19	0.06	0.39	0.10	-0.05	0.16	0.48	0.15	0.14	0.09					0.13	0.06	-1.53	0.46			5618.50	3.61	0.03
2.14	0.92	1.48	0.38	0.19	0.06	0.39	0.11			0.42	0.15							0.13	0.06	-1.50	0.45			5618.73	3.84	0.03
2.29	0.96	1.50	0.38	0.18	0.07	0.40	0.10	0.00	0.16	0.40	0.15	0.11	0.09	0.21	0.11			0.13	0.06	-1.52	0.46	0.02	0.05	5618.96	4.07	0.03
2.28	0.96	1.51	0.39	0.19	0.06	0.41	0.10	-0.09	0.14	0.40	0.15			0.24	0.11					-1.54	0.46			5618.99	4.11	0.03
2.12	1.00	1.50	0.38	0.19	0.06	0.39	0.11	-0.19	0.14	0.49	0.15							0.13	0.06	-1.52	0.46			5619.01	4.12	0.03
2.31	0.92	1.50	0.39	0.18	0.08	0.40	0.11			0.36	0.14			0.26	0.11					-1.52	0.46	0.02	0.05	5619.27	4.39	0.02
2.29	0.96	1.52	0.39	0.19	0.06	0.40	0.10	0.00	0.16	0.40	0.15	0.11	0.09	0.21	0.11					-1.54	0.46			5619.56	4.68	0.02
2.28	0.97	1.49	0.38	0.18	0.07	0.40	0.10	0.00	0.16	0.39	0.15	0.15	0.10	0.24	0.12	0.11	0.13	0.13	0.06	-1.51	0.46	0.02	0.05	5620.16	5.27	0.01
2.28	0.96	1.49	0.38	0.18	0.08	0.40	0.10	-0.10	0.15	0.40	0.15			0.25	0.12	0.03	0.12	0.13	0.06	-1.51	0.46	0.02	0.05	5620.33	5.44	0.01

Intercept		Patch food density		Patch depletion		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		Inter-patch distance		Mean patch food content		Satiation		AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.			
2.15	1.00	1.50	0.38	0.19	0.06	0.39	0.10	-0.05	0.16	0.47	0.15	0.16	0.10			0.04	0.13	0.13	0.06	-1.53	0.46			5620.40	5.52	0.01
2.16	0.99	1.50	0.38	0.18	0.07	0.38	0.11	-0.05	0.16	0.48	0.15	0.14	0.09					0.13	0.06	-1.52	0.46	0.01	0.05	5620.44	5.55	0.01
2.14	0.92	1.48	0.38	0.18	0.08	0.39	0.11			0.42	0.15							0.13	0.06	-1.50	0.45	0.01	0.05	5620.68	5.79	0.01
2.28	0.97	1.51	0.39	0.19	0.06	0.40	0.10	0.00	0.16	0.39	0.15	0.14	0.10	0.24	0.12	0.11	0.13			-1.53	0.46			5620.77	5.89	0.01
2.14	0.99	1.50	0.38	0.19	0.06	0.39	0.11	-0.17	0.15	0.49	0.15					-0.05	0.11	0.13	0.06	-1.53	0.46			5620.79	5.91	0.01
2.28	0.96	1.51	0.39	0.18	0.07	0.40	0.10	-0.09	0.14	0.40	0.15			0.24	0.11					-1.53	0.46	0.02	0.05	5620.90	6.01	0.01
2.28	0.96	1.51	0.39	0.19	0.06	0.41	0.10	-0.10	0.15	0.40	0.15			0.25	0.12	0.03	0.12			-1.53	0.46			5620.92	6.03	0.01
2.12	1.00	1.49	0.38	0.18	0.08	0.39	0.11	-0.19	0.14	0.49	0.15							0.13	0.06	-1.51	0.46	0.01	0.05	5620.96	6.07	0.01
2.16	1.00	1.52	0.39	0.19	0.06	0.39	0.10	-0.05	0.16	0.47	0.15	0.14	0.09							-1.55	0.46			5621.00	6.11	0.01
2.14	0.93	1.50	0.38	0.19	0.06	0.39	0.11			0.42	0.15									-1.52	0.46			5621.16	6.27	0.01
2.29	0.96	1.51	0.39	0.18	0.07	0.39	0.10	0.00	0.16	0.40	0.15	0.11	0.09	0.21	0.11					-1.54	0.46	0.02	0.05	5621.46	6.58	0.01
2.13	1.00	1.51	0.39	0.19	0.06	0.39	0.11	-0.19	0.14	0.49	0.15									-1.54	0.46			5621.48	6.60	0.01
2.45	0.60	0.24	0.06	0.18	0.06	0.41	0.10			0.36	0.14			0.26	0.11			0.13	0.06					5622.29	7.41	0.00
2.15	1.00	1.50	0.38	0.18	0.07	0.38	0.11	-0.05	0.16	0.47	0.15	0.16	0.10			0.04	0.13	0.13	0.06	-1.52	0.46	0.01	0.05	5622.35	7.46	0.00
2.28	0.97	1.50	0.39	0.18	0.07	0.39	0.10	0.00	0.16	0.39	0.15	0.14	0.10	0.24	0.12	0.11	0.13			-1.52	0.46	0.02	0.05	5622.68	7.80	0.00
2.14	0.99	1.50	0.38	0.18	0.08	0.39	0.11	-0.17	0.15	0.49	0.15					-0.05	0.11	0.13	0.06	-1.52	0.46	0.01	0.05	5622.73	7.85	0.00
2.28	0.96	1.50	0.39	0.18	0.07	0.40	0.10	-0.10	0.15	0.40	0.15			0.25	0.12	0.03	0.12			-1.52	0.46	0.02	0.05	5622.83	7.94	0.00

Table S3.9. 95% confidence model set for the analysis of the determinants of baboon intake rates in the natural foraging conditions.

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		No. of patch occupants		No. of patch occupants <sup>2</sup>		Patch species	Patch surface area		Handling time		AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.		$\beta$	s.e.					
1.02	0.12	-0.05	0.02	0.04	0.02	-0.03	0.02					0.05	0.02					✓	0.02	0.02	✓		3872.05	0.00	0.16
1.03	0.12	-0.05	0.02	0.05	0.02	-0.05	0.03			0.02	0.02	0.05	0.02					✓	0.02	0.02	✓		3873.04	0.99	0.10
1.02	0.12	-0.05	0.02	0.04	0.02	-0.03	0.02					0.05	0.02	0.01	0.02			✓	0.01	0.02	✓		3873.41	1.35	0.08
1.02	0.12	-0.05	0.02	0.04	0.02	-0.03	0.02	0.00	0.02			0.04	0.02					✓	0.02	0.02	✓		3874.05	1.99	0.06
1.03	0.12	-0.05	0.02	0.05	0.02	-0.05	0.03			0.02	0.02	0.05	0.02	0.01	0.02			✓	0.02	0.02	✓		3874.39	2.34	0.05
1.04	0.12	-0.04	0.02	0.04	0.02													✓	0.02	0.02	✓		3874.76	2.70	0.04
1.02	0.12	-0.05	0.02	0.04	0.02	-0.03	0.02					0.05	0.02	0.00	0.03	0.02	0.02	✓	0.02	0.02	✓		3874.99	2.93	0.04
1.03	0.12	-0.05	0.02	0.05	0.02	-0.05	0.03	0.00	0.02	0.02	0.02	0.05	0.02					✓	0.02	0.02	✓		3875.01	2.96	0.04

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		No. of patch occupants		No. of patch occupants <sup>2</sup>		Patch species	Patch surface area		Handling time	AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.		$\beta$	s.e.				
1.04	0.12	-0.05	0.02	0.05	0.02	-0.03	0.02											✓	0.02	0.02	✓	3875.39	3.34	0.03
1.02	0.12	-0.05	0.02	0.04	0.02	-0.03	0.02	0.00	0.02			0.04	0.02	0.01	0.02			✓	0.01	0.02	✓	3875.40	3.35	0.03
1.04	0.12	-0.04	0.02	0.04	0.02			-0.03	0.02									✓	0.02	0.02	✓	3875.47	3.41	0.03
1.03	0.12	-0.05	0.02	0.05	0.02	-0.05	0.03			0.02	0.02	0.05	0.02	0.00	0.03	0.02	0.02	✓	0.02	0.02	✓	3875.97	3.92	0.02
1.04	0.12	-0.04	0.02	0.04	0.02									0.01	0.02			✓	0.02	0.02	✓	3876.20	4.15	0.02
1.02	0.12			0.04	0.02	-0.01	0.02					0.04	0.02					✓	0.02	0.02	✓	3876.22	4.17	0.02
1.04	0.12			0.05	0.02													✓	0.02	0.02	✓	3876.29	4.23	0.02
1.03	0.12	-0.05	0.02	0.04	0.02	-0.05	0.03	0.00	0.02	0.02	0.02	0.05	0.02	0.01	0.02			✓	0.02	0.02	✓	3876.36	4.31	0.02
1.04	0.12	-0.05	0.02	0.05	0.02	-0.02	0.02	-0.02	0.02									✓	0.02	0.02	✓	3876.37	4.32	0.02
1.05	0.12	-0.04	0.02															✓	0.02	0.02	✓	3876.42	4.37	0.02
1.04	0.12	-0.05	0.02	0.05	0.02	-0.03	0.02							0.01	0.02			✓	0.02	0.02	✓	3876.81	4.76	0.01
1.04	0.12	-0.04	0.02	0.04	0.02			-0.03	0.02					0.01	0.02			✓	0.02	0.02	✓	3876.86	4.81	0.01
1.02	0.12	-0.05	0.02	0.04	0.02	-0.03	0.02	0.00	0.02			0.05	0.02	0.00	0.03	0.02	0.02	✓	0.02	0.02	✓	3876.98	4.93	0.01
1.04	0.12	-0.05	0.02	0.05	0.02	-0.03	0.03			0.00	0.02							✓	0.02	0.02	✓	3877.38	5.33	0.01
1.04	0.12	-0.05	0.02	0.05	0.02	-0.02	0.02	-0.02	0.02					0.01	0.02			✓	0.02	0.02	✓	3877.74	5.69	0.01
1.04	0.12	-0.05	0.02											0.01	0.02			✓	0.02	0.02	✓	3877.78	5.72	0.01
1.04	0.12	-0.04	0.02	0.04	0.02									0.00	0.03	0.02	0.02	✓	0.02	0.02	✓	3877.80	5.75	0.01
1.02	0.12			0.04	0.02	-0.01	0.02					0.04	0.02	0.01	0.02			✓	0.02	0.02	✓	3877.82	5.77	0.01
1.04	0.12			0.05	0.02									0.01	0.02			✓	0.02	0.02	✓	3877.89	5.84	0.01
1.03	0.12	-0.05	0.02	0.04	0.02	-0.05	0.03	0.00	0.02	0.02	0.02	0.05	0.02	0.00	0.03	0.02	0.02	✓	0.02	0.02	✓	3877.94	5.89	0.01
1.05	0.12	-0.05	0.02			-0.01	0.02											✓	0.02	0.02	✓	3878.05	5.99	0.01
1.04	0.12			0.05	0.02	-0.01	0.02											✓	0.02	0.02	✓	3878.16	6.11	0.01
1.04	0.12	-0.05	0.02	0.05	0.02	-0.03	0.03	-0.02	0.02	0.01	0.02							✓	0.02	0.02	✓	3878.27	6.22	0.01
1.04	0.12	-0.05	0.02	0.05	0.02	-0.03	0.02							0.00	0.03	0.01	0.02	✓	0.02	0.02	✓	3878.42	6.37	0.01
1.04	0.12	-0.04	0.02	0.04	0.02			-0.03	0.02					0.00	0.03	0.02	0.02	✓	0.02	0.02	✓	3878.46	6.41	0.01
1.04	0.12																	✓	0.02	0.02	✓	3878.72	6.67	0.01
1.04	0.12	-0.05	0.02	0.05	0.02	-0.03	0.03			0.00	0.02			0.01	0.02			✓	0.02	0.02	✓	3878.80	6.75	0.01



Table S3.10. 95% confidence model set for the analysis of the determinants of baboon patch residency times in the natural foraging conditions. Right-hand half of table continued below.

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		No. of patch occupants		No. of patch occupants <sup>2</sup>	
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.
4.97	0.19			0.09	0.03	-0.13	0.03							0.47	0.06	-0.28	0.05
4.99	0.20					-0.10	0.03							0.48	0.06	-0.28	0.05
4.98	0.19			0.09	0.03	-0.13	0.03							0.47	0.06	-0.28	0.05
4.96	0.19			0.09	0.03	-0.13	0.03					0.01	0.03	0.47	0.06	-0.28	0.05
4.97	0.19	0.00	0.03	0.09	0.03	-0.13	0.03							0.47	0.06	-0.28	0.05
5.00	0.20					-0.11	0.03							0.47	0.06	-0.28	0.05
5.02	0.19			0.08	0.03	-0.13	0.03							0.48	0.06	-0.29	0.05
4.99	0.20	0.01	0.03			-0.10	0.03							0.48	0.06	-0.28	0.05
4.97	0.19			0.08	0.03	-0.13	0.03					0.01	0.03	0.47	0.06	-0.28	0.05
4.97	0.19	0.01	0.03	0.09	0.03	-0.13	0.03	0.03	0.04					0.47	0.06	-0.28	0.05
4.98	0.19	0.00	0.03	0.09	0.03	-0.13	0.03							0.47	0.06	-0.28	0.05
4.98	0.19	0.01	0.03	0.09	0.03	-0.13	0.03							0.47	0.06	-0.28	0.05
5.03	0.19			0.08	0.03	-0.13	0.03							0.47	0.06	-0.28	0.05
5.04	0.20					-0.11	0.03							0.48	0.06	-0.29	0.05
4.96	0.19	0.00	0.03	0.09	0.03	-0.13	0.03					0.01	0.03	0.47	0.06	-0.28	0.05
4.97	0.19	0.00	0.04	0.09	0.03	-0.13	0.04			0.00	0.03			0.47	0.06	-0.28	0.05
5.00	0.20	0.01	0.03			-0.10	0.03							0.47	0.06	-0.28	0.05
5.01	0.19			0.08	0.03	-0.13	0.03					0.01	0.03	0.47	0.06	-0.28	0.05
4.95	0.19	0.00	0.03	0.09	0.03	-0.14	0.03	0.05	0.04			0.03	0.03	0.47	0.06	-0.28	0.05
5.02	0.19	0.01	0.03	0.08	0.03	-0.13	0.03							0.47	0.06	-0.28	0.05
4.98	0.19	0.01	0.03	0.09	0.03	-0.13	0.03	0.03	0.04					0.47	0.06	-0.28	0.05
4.98	0.20	0.00	0.04			-0.08	0.04			-0.02	0.03			0.48	0.06	-0.28	0.05
5.00	0.20	0.01	0.03			-0.10	0.03							0.47	0.06	-0.28	0.05
4.98	0.19	0.01	0.03	0.09	0.03	-0.13	0.03	0.03	0.04					0.47	0.06	-0.28	0.05
5.05	0.20					-0.11	0.03							0.47	0.06	-0.28	0.05
4.97	0.19	0.00	0.04	0.09	0.03	-0.12	0.04	0.04	0.04	-0.01	0.03			0.47	0.06	-0.28	0.05
4.97	0.19	0.00	0.03	0.08	0.03	-0.13	0.03					0.01	0.03	0.47	0.06	-0.28	0.05
4.98	0.19	0.00	0.03	0.08	0.03	-0.13	0.03							0.47	0.06	-0.28	0.05

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		No. of patch occupants		No. of patch occupants <sup>2</sup>	
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.
4.98	0.19	0.00	0.04	0.08	0.03	-0.13	0.04			0.00	0.03			0.47	0.06	-0.28	0.05
4.97	0.19	0.00	0.03	0.08	0.03	-0.13	0.03					0.01	0.03	0.47	0.06	-0.28	0.05
5.02	0.19			0.08	0.03	-0.13	0.03					0.01	0.03	0.47	0.06	-0.28	0.05
4.97	0.19	0.00	0.04	0.09	0.03	-0.13	0.04			-0.01	0.03			0.47	0.06	-0.28	0.05
5.03	0.19	0.01	0.03	0.08	0.03	-0.13	0.03							0.47	0.06	-0.28	0.05
5.04	0.20	0.01	0.03			-0.10	0.03							0.48	0.06	-0.28	0.05
5.02	0.19	0.01	0.03	0.09	0.03	-0.13	0.03	0.03	0.04					0.47	0.06	-0.29	0.05
4.96	0.19	0.00	0.03	0.09	0.03	-0.14	0.03	0.05	0.04			0.03	0.03	0.47	0.06	-0.28	0.05
4.99	0.20	0.00	0.04			-0.08	0.04			-0.02	0.03			0.47	0.06	-0.28	0.05
4.96	0.19	0.00	0.04	0.09	0.03	-0.13	0.05			0.00	0.03	0.01	0.03	0.47	0.06	-0.28	0.05
4.96	0.19	0.01	0.03	0.09	0.03	-0.14	0.03	0.05	0.04			0.03	0.03	0.47	0.06	-0.28	0.05
5.00	0.20	0.01	0.03			-0.10	0.03							0.47	0.06	-0.28	0.05
5.02	0.19	0.01	0.03	0.08	0.03	-0.13	0.03							0.47	0.06	-0.28	0.05
4.99	0.20	0.00	0.04			-0.08	0.04			-0.02	0.03			0.47	0.06	-0.28	0.05
5.01	0.19	0.00	0.03	0.08	0.03	-0.13	0.03					0.01	0.03	0.47	0.06	-0.28	0.05
4.95	0.19	0.00	0.03	0.09	0.03	-0.13	0.04	0.05	0.04	0.00	0.03	0.03	0.04	0.47	0.06	-0.28	0.05
5.01	0.19	0.00	0.04	0.08	0.03	-0.12	0.04			-0.01	0.03			0.47	0.06	-0.28	0.05
4.98	0.19	0.00	0.03	0.09	0.03	-0.13	0.04	0.03	0.04	-0.01	0.03			0.47	0.06	-0.28	0.05
4.98	0.19	0.01	0.03	0.09	0.03	-0.13	0.03	0.03	0.04					0.47	0.06	-0.28	0.05
4.97	0.19	0.00	0.04	0.09	0.03	-0.12	0.04	0.04	0.04	-0.01	0.03			0.47	0.06	-0.28	0.05
5.05	0.20	0.01	0.03			-0.10	0.03							0.47	0.06	-0.28	0.05
4.98	0.19	0.00	0.03	0.08	0.03	-0.13	0.03					0.01	0.03	0.47	0.06	-0.28	0.05
5.03	0.19	0.01	0.03	0.09	0.03	-0.13	0.03	0.03	0.04					0.47	0.06	-0.28	0.05
5.01	0.19	0.01	0.03	0.09	0.03	-0.14	0.03	0.04	0.04			0.03	0.03	0.47	0.06	-0.28	0.05
4.97	0.19	0.00	0.04	0.08	0.03	-0.13	0.05			0.00	0.03	0.01	0.03	0.47	0.06	-0.28	0.05
5.03	0.20	0.00	0.04			-0.08	0.04			-0.02	0.03			0.48	0.06	-0.29	0.05
4.98	0.19	0.00	0.04	0.08	0.03	-0.13	0.04			-0.01	0.03			0.47	0.06	-0.28	0.05
4.97	0.19	0.00	0.04	0.08	0.03	-0.13	0.05			0.00	0.03	0.01	0.03	0.47	0.06	-0.28	0.05
5.05	0.20	0.01	0.03			-0.10	0.03							0.48	0.06	-0.28	0.05
5.02	0.19	0.00	0.03	0.08	0.03	-0.13	0.03					0.01	0.03	0.47	0.06	-0.28	0.05
5.02	0.19	0.01	0.03	0.09	0.03	-0.13	0.03	0.03	0.04					0.47	0.06	-0.28	0.05
5.01	0.19	0.00	0.04	0.09	0.03	-0.12	0.04	0.03	0.04	-0.01	0.03			0.47	0.06	-0.29	0.05
5.03	0.19	0.00	0.04	0.08	0.03	-0.12	0.04			-0.01	0.03			0.47	0.06	-0.28	0.05

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		No. of patch occupants		No. of patch occupants <sup>2</sup>	
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.
4.97	0.19	0.00	0.03	0.09	0.03	-0.14	0.03	0.05	0.04			0.03	0.03	0.47	0.06	-0.28	0.05

Table S3.10. continued.

Initial intake rate		Intake rate x Rank		Intake rate x Social bonds		Intake rate x Patch density		Patch species	Patch surface area		Handling time	Mean patch density		Mean patch food content		AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.		B	s.e.		$\beta$	s.e.	$\beta$	s.e.			
0.31	0.02					0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11201.52	0.00	0.12
0.31	0.02					0.05	0.02	✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11202.60	1.07	0.07
0.31	0.02			0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11202.80	1.28	0.07
0.31	0.02					0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11203.34	1.82	0.05
0.31	0.02					0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11203.51	1.98	0.05
0.31	0.02			0.02	0.02	0.05	0.02	✓	0.23	0.05	✓	-0.19	0.03	-0.18	0.04	11203.77	2.24	0.04
0.32	0.02							✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11203.96	2.43	0.04
0.31	0.02					0.05	0.02	✓	0.23	0.05	✓	-0.19	0.03	-0.18	0.04	11204.54	3.02	0.03
0.31	0.02			0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11204.64	3.11	0.03
0.31	0.02					0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11204.65	3.12	0.03
0.31	0.02			0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11204.79	3.27	0.02
0.31	0.02	-0.01	0.02			0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11205.13	3.61	0.02
0.32	0.02			0.02	0.02			✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11205.18	3.66	0.02
0.32	0.02							✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11205.24	3.71	0.02
0.31	0.02					0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11205.34	3.81	0.02
0.31	0.02					0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11205.49	3.97	0.02
0.31	0.02			0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.18	0.04	11205.72	4.20	0.02
0.32	0.02							✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11205.79	4.27	0.01
0.31	0.02					0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11205.85	4.33	0.01
0.32	0.02							✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11205.92	4.40	0.01
0.31	0.02			0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11206.02	4.49	0.01
0.31	0.02					0.05	0.02	✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11206.13	4.60	0.01
0.31	0.02	-0.01	0.02			0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.18	0.04	11206.21	4.68	0.01
0.31	0.02	-0.01	0.02			0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11206.29	4.77	0.01

Initial intake rate		Intake rate x Rank		Intake rate x Social bonds		Intake rate x Patch density		Patch surface area	Handling time	Mean patch density		Mean patch food content		AIC	$\Delta$ AIC	$w_i$		
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	B	s.e.	$\beta$	s.e.	$\beta$	s.e.					
0.32	0.02			0.02	0.02			✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11206.34	4.82	0.01
0.31	0.02					0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11206.54	5.01	0.01
0.31	0.02			0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11206.64	5.11	0.01
0.31	0.02	-0.01	0.02	0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11206.68	5.16	0.01
0.31	0.02			0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11206.77	5.25	0.01
0.31	0.02	-0.02	0.02			0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11206.92	5.39	0.01
0.32	0.02			0.02	0.02			✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11207.03	5.51	0.01
0.31	0.02	-0.01	0.02			0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11207.11	5.58	0.01
0.32	0.02			0.02	0.02			✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11207.15	5.63	0.01
0.32	0.02							✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11207.16	5.64	0.01
0.32	0.02							✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11207.25	5.73	0.01
0.31	0.02			0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11207.29	5.77	0.01
0.31	0.02			0.02	0.02	0.05	0.02	✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11207.31	5.78	0.01
0.31	0.02					0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11207.34	5.81	0.01
0.30	0.02	-0.02	0.02			0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11207.40	5.88	0.01
0.31	0.02	-0.01	0.02	0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.18	0.04	11207.65	6.13	0.01
0.32	0.02	-0.01	0.02					✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11207.70	6.18	0.01
0.31	0.02	-0.01	0.02			0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11207.77	6.24	0.01
0.32	0.02							✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11207.77	6.25	0.01
0.31	0.02					0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11207.84	6.32	0.01
0.32	0.02							✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11207.86	6.34	0.01
0.31	0.02			0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11207.91	6.38	0.01
0.31	0.02	-0.01	0.02	0.01	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11207.91	6.38	0.01
0.31	0.02	-0.01	0.02			0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11208.16	6.64	0.00
0.32	0.02			0.02	0.02			✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11208.28	6.76	0.00
0.31	0.02	-0.01	0.02	0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11208.50	6.98	0.00
0.32	0.02			0.02	0.02			✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11208.56	7.04	0.00
0.32	0.02							✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11208.60	7.07	0.00
0.31	0.02			0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11208.63	7.11	0.00
0.32	0.02							✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11208.65	7.13	0.00
0.31	0.02	-0.01	0.02	0.02	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11208.66	7.13	0.00
0.31	0.02	-0.02	0.02			0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11208.92	7.39	0.00
0.32	0.02	-0.01	0.02					✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11208.96	7.44	0.00

Initial intake rate		Intake rate x Rank		Intake rate x Social bonds		Intake rate x Patch density		Patch species	Patch surface area		Handling time	Mean patch density		Mean patch food content		AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.		B	s.e.		$\beta$	s.e.	$\beta$	s.e.			
0.32	0.02			0.02	0.02			✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11209.02	7.50	0.00
0.32	0.02	-0.01	0.02					✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11209.05	7.52	0.00
0.32	0.02							✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11209.06	7.54	0.00
0.32	0.02			0.02	0.02			✓	0.23	0.05	✓	-0.19	0.03	-0.19	0.04	11209.09	7.56	0.00
0.31	0.02	-0.01	0.02	0.01	0.02	0.05	0.02	✓	0.24	0.05	✓	-0.19	0.03	-0.19	0.04	11209.11	7.59	0.00

Table S3.11. 95% confidence model set for the analysis of the determinants of baboon intake rates in the experimental foraging conditions.

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		No. of patch occupants		No. of patch occupants <sup>2</sup>		Satiation		Patch food density		Patch depletion		AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.			
1.33	0.24	0.30	0.06	0.00	0.08			-0.12	0.05					0.17	0.04			-0.27	0.05	0.26	0.04	-0.36	0.05	2146.92	0.00	0.22
1.33	0.23	0.28	0.06	0.02	0.08	-0.06	0.08	-0.12	0.05					0.17	0.04			-0.27	0.05	0.26	0.04	-0.36	0.05	2148.36	1.44	0.11
1.33	0.24	0.30	0.06	0.00	0.08			-0.12	0.05					0.19	0.10	-0.03	0.10	-0.27	0.05	0.26	0.04	-0.36	0.05	2148.85	1.93	0.08
1.31	0.24	0.28	0.06	0.01	0.08	-0.06	0.08	-0.08	0.06			0.08	0.07	0.17	0.04			-0.27	0.05	0.26	0.04	-0.36	0.05	2149.03	2.11	0.08
1.31	0.25	0.29	0.06	0.06	0.08	-0.06	0.08					0.13	0.06	0.17	0.04			-0.27	0.05	0.26	0.04	-0.36	0.05	2149.15	2.24	0.07
1.35	0.27	0.30	0.06											0.17	0.04			-0.27	0.05	0.26	0.04	-0.37	0.05	2149.77	2.86	0.05
1.36	0.23	0.31	0.06	0.10	0.08									0.17	0.04			-0.27	0.05	0.26	0.04	-0.36	0.05	2150.15	3.24	0.04
1.34	0.23	0.28	0.06	0.03	0.09	-0.07	0.08	-0.12	0.05	0.02	0.06			0.17	0.04			-0.27	0.05	0.26	0.04	-0.36	0.05	2150.26	3.34	0.04
1.33	0.23	0.28	0.06	0.02	0.08	-0.06	0.08	-0.12	0.05					0.20	0.10	-0.03	0.10	-0.27	0.05	0.26	0.04	-0.36	0.05	2150.28	3.36	0.04
1.33	0.24	0.29	0.06	0.03	0.09	-0.07	0.08	-0.09	0.06	0.04	0.07	0.09	0.07	0.17	0.04			-0.27	0.05	0.26	0.04	-0.36	0.05	2150.64	3.72	0.03
1.33	0.25	0.30	0.06	0.07	0.08	-0.07	0.08			0.04	0.07	0.14	0.06	0.17	0.04			-0.27	0.05	0.26	0.04	-0.37	0.05	2150.88	3.96	0.03
1.31	0.24	0.28	0.06	0.01	0.08	-0.06	0.08	-0.08	0.06			0.08	0.07	0.20	0.10	-0.03	0.10	-0.27	0.05	0.26	0.04	-0.36	0.05	2150.96	4.04	0.03
1.31	0.25	0.29	0.06	0.06	0.08	-0.06	0.08					0.13	0.06	0.19	0.10	-0.02	0.10	-0.27	0.05	0.26	0.04	-0.37	0.05	2151.09	4.17	0.03
1.36	0.22	0.30	0.07	0.12	0.08	-0.06	0.08							0.17	0.04			-0.27	0.05	0.26	0.04	-0.36	0.05	2151.63	4.72	0.02
1.35	0.27	0.30	0.06											0.19	0.10	-0.03	0.10	-0.27	0.05	0.26	0.04	-0.37	0.05	2151.70	4.78	0.02
1.34	0.27	0.29	0.07			-0.02	0.08							0.17	0.04			-0.27	0.05	0.26	0.04	-0.37	0.05	2151.72	4.81	0.02
1.36	0.23	0.31	0.06	0.10	0.08									0.19	0.10	-0.03	0.10	-0.27	0.05	0.26	0.04	-0.36	0.05	2152.08	5.17	0.02
1.34	0.23	0.28	0.06	0.03	0.09	-0.07	0.08	-0.12	0.05	0.02	0.06			0.20	0.10	-0.03	0.10	-0.27	0.05	0.26	0.04	-0.36	0.05	2152.19	5.27	0.02
1.33	0.24	0.29	0.06	0.03	0.09	-0.07	0.08	-0.09	0.06	0.04	0.07	0.09	0.07	0.19	0.10	-0.02	0.10	-0.27	0.05	0.26	0.04	-0.37	0.05	2152.58	5.67	0.01
1.33	0.24	0.30	0.06	0.07	0.08	-0.07	0.08			0.04	0.07	0.14	0.06	0.19	0.10	-0.02	0.10	-0.27	0.05	0.26	0.04	-0.37	0.05	2152.82	5.91	0.01

Table S3.12. 80% confidence model set for the analysis of the determinants of baboon patch residency times in the natural foraging conditions (95% confidence set to large to present). Right-hand half of table continued below.

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		No. of patch occupants		No. of patch occupants <sup>2</sup>		Satiation	
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.
4.62	0.10	0.37	0.06	0.09	0.06	-0.09	0.06	-0.11	0.04					0.37	0.06				
4.60	0.09	0.38	0.06	0.09	0.06	-0.09	0.06	-0.11	0.04					0.36	0.06				
4.61	0.10	0.33	0.07	0.09	0.06	-0.09	0.06	-0.10	0.04					0.36	0.06			0.08	0.07
4.62	0.10	0.36	0.06	0.10	0.06	-0.09	0.06	-0.11	0.04					0.37	0.06				
4.60	0.09	0.34	0.07	0.09	0.06	-0.09	0.06	-0.11	0.04					0.36	0.06			0.08	0.07
4.61	0.10	0.39	0.06	0.10	0.06	-0.08	0.06			0.09	0.04			0.36	0.06				
4.60	0.09	0.37	0.06	0.10	0.06	-0.09	0.06	-0.11	0.04					0.37	0.06				
4.61	0.10	0.33	0.07	0.09	0.06	-0.09	0.06	-0.10	0.04					0.37	0.06			0.09	0.07
4.61	0.10	0.37	0.06	0.09	0.06	-0.08	0.06	-0.08	0.05			0.05	0.05	0.37	0.06				
4.59	0.09	0.38	0.06	0.08	0.06	-0.08	0.06	-0.08	0.05			0.06	0.05	0.36	0.06				
4.60	0.09	0.40	0.06	0.09	0.06	-0.08	0.06					0.10	0.04	0.36	0.06				
4.60	0.09	0.34	0.07	0.09	0.06	-0.09	0.06	-0.11	0.04					0.36	0.06			0.09	0.07
4.61	0.10	0.33	0.06	0.09	0.07	-0.11	0.06	-0.10	0.05					0.37	0.06				
4.61	0.10	0.39	0.06	0.10	0.06	-0.07	0.06			0.09	0.04			0.37	0.06				
4.61	0.10	0.37	0.06	0.09	0.06	-0.08	0.06	-0.08	0.05			0.05	0.05	0.37	0.06				
4.60	0.10	0.35	0.06	0.09	0.07	-0.10	0.06					0.09	0.05	0.36	0.06				
4.60	0.10	0.34	0.07	0.08	0.06	-0.08	0.06	-0.08	0.05			0.04	0.05	0.36	0.06			0.08	0.07
4.59	0.09	0.38	0.06	0.09	0.06	-0.08	0.06	-0.08	0.05			0.06	0.05	0.37	0.06				
4.61	0.10	0.36	0.07	0.09	0.06	-0.08	0.06					0.09	0.04	0.36	0.06			0.08	0.07
4.59	0.09	0.35	0.07	0.08	0.06	-0.08	0.06	-0.08	0.05			0.05	0.05	0.36	0.06			0.08	0.07
4.59	0.09	0.40	0.06	0.10	0.06	-0.07	0.06					0.10	0.04	0.36	0.06				
4.62	0.10	0.37	0.06	0.09	0.06	-0.10	0.06	-0.11	0.05	0.00	0.05			0.37	0.06				
4.62	0.10	0.37	0.06	0.09	0.06	-0.09	0.06	-0.11	0.04					0.37	0.16	0.00	0.16		
4.59	0.10	0.33	0.06	0.09	0.07	-0.11	0.06	-0.10	0.05					0.36	0.06				
4.59	0.09	0.37	0.07	0.09	0.06	-0.07	0.06					0.09	0.04	0.35	0.06			0.08	0.07
4.60	0.10	0.29	0.07	0.09	0.06	-0.11	0.06	-0.09	0.05					0.36	0.06			0.08	0.07
4.60	0.10	0.34	0.07	0.09	0.06	-0.08	0.06	-0.08	0.05			0.05	0.05	0.37	0.06			0.08	0.07
4.58	0.10	0.36	0.06	0.09	0.07	-0.09	0.06					0.10	0.05	0.36	0.06				
4.61	0.10	0.32	0.06	0.09	0.07	-0.11	0.06	-0.10	0.05					0.37	0.06				
4.61	0.10	0.37	0.06	0.09	0.06	-0.09	0.06	-0.11	0.05	0.00	0.05			0.36	0.06				

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		No. of patch occupants		No. of patch occupants <sup>2</sup>		Satiation	
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.
4.60	0.09	0.38	0.06	0.09	0.06	-0.09	0.06	-0.11	0.04					0.37	0.16	-0.01	0.16		
4.61	0.10	0.35	0.07	0.10	0.06	-0.07	0.06					0.09	0.04	0.36	0.06			0.08	0.07
4.60	0.10	0.35	0.06	0.09	0.07	-0.09	0.06					0.10	0.05	0.37	0.06				
4.60	0.10	0.34	0.06	0.08	0.07	-0.10	0.06	-0.06	0.06			0.06	0.06	0.37	0.06				
4.59	0.09	0.35	0.07	0.08	0.06	-0.08	0.06	-0.08	0.05			0.05	0.05	0.36	0.06			0.08	0.07
4.62	0.10	0.33	0.07	0.09	0.06	-0.10	0.06	-0.11	0.05	0.01	0.05			0.36	0.06			0.09	0.07
4.61	0.10	0.33	0.07	0.09	0.06	-0.09	0.06	-0.10	0.04					0.39	0.16	-0.03	0.16	0.09	0.07
4.62	0.10	0.36	0.06	0.10	0.06	-0.09	0.06	-0.11	0.04					0.38	0.16	-0.01	0.16		
4.62	0.10	0.36	0.06	0.10	0.06	-0.09	0.06	-0.11	0.05	0.00	0.05			0.37	0.06				
4.61	0.10	0.37	0.06	0.04	0.07			-0.10	0.05					0.36	0.06				
4.60	0.10	0.32	0.07	0.09	0.07	-0.09	0.06					0.09	0.05	0.36	0.06			0.07	0.07
4.58	0.10	0.30	0.07	0.09	0.06	-0.11	0.06	-0.10	0.05					0.36	0.06			0.08	0.07
4.60	0.10	0.34	0.07	0.09	0.06	-0.09	0.06	-0.11	0.05	0.01	0.05			0.36	0.06			0.09	0.07
4.60	0.09	0.34	0.07	0.09	0.06	-0.09	0.06	-0.11	0.04					0.38	0.16	-0.03	0.16	0.09	0.07
4.58	0.10	0.34	0.06	0.08	0.07	-0.10	0.06	-0.07	0.06			0.06	0.06	0.36	0.06				
4.59	0.09	0.37	0.07	0.10	0.06	-0.07	0.06					0.10	0.04	0.36	0.06			0.08	0.07
4.60	0.10	0.29	0.07	0.09	0.06	-0.11	0.06	-0.10	0.04					0.37	0.06			0.09	0.07
4.59	0.10	0.33	0.06	0.09	0.07	-0.11	0.06	-0.11	0.05					0.37	0.06				
4.61	0.10	0.39	0.06	0.10	0.07	-0.08	0.07			0.00	0.05	0.09	0.05	0.36	0.06				
4.62	0.10	0.37	0.06	0.09	0.06	-0.09	0.06	-0.08	0.05	0.02	0.05	0.06	0.05	0.36	0.06				
4.61	0.10	0.39	0.06	0.10	0.06	-0.08	0.06					0.09	0.04	0.36	0.16	0.00	0.16		
4.60	0.09	0.38	0.06	0.09	0.06	-0.09	0.06	-0.08	0.05	0.02	0.05	0.06	0.05	0.36	0.06				
4.60	0.10	0.37	0.06	0.10	0.06	-0.09	0.06	-0.11	0.05	0.00	0.05			0.37	0.06				
4.60	0.09	0.37	0.06	0.10	0.06	-0.09	0.06	-0.11	0.04					0.38	0.16	-0.01	0.16		
4.61	0.10	0.33	0.07	0.09	0.06	-0.09	0.06	-0.10	0.04					0.39	0.16	-0.03	0.16	0.09	0.07
4.62	0.10	0.32	0.07	0.10	0.06	-0.09	0.06	-0.11	0.05	0.01	0.05			0.37	0.06			0.09	0.07
4.61	0.10	0.37	0.06	0.09	0.06	-0.08	0.06	-0.08	0.05			0.05	0.05	0.37	0.16	0.00	0.16		
4.60	0.10	0.33	0.06	0.08	0.07	-0.10	0.06	-0.06	0.06			0.06	0.05	0.37	0.06				
4.58	0.10	0.36	0.06	0.09	0.07	-0.09	0.06					0.10	0.05	0.36	0.06				
4.59	0.09	0.38	0.06	0.08	0.06	-0.08	0.06	-0.08	0.05			0.06	0.05	0.36	0.16	0.00	0.16		
4.59	0.10	0.37	0.06	0.04	0.07			-0.11	0.05					0.36	0.06				
4.64	0.10	0.38	0.06	0.13	0.07	-0.10	0.06							0.36	0.06				
4.60	0.10	0.40	0.06	0.10	0.07	-0.08	0.07			0.01	0.05	0.10	0.05	0.36	0.06				
4.60	0.09	0.40	0.06	0.09	0.06	-0.08	0.06					0.10	0.04	0.36	0.16	0.00	0.16		
4.58	0.10	0.33	0.07	0.09	0.07	-0.09	0.06					0.10	0.05	0.36	0.06			0.07	0.07

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		No. of patch occupants		No. of patch occupants <sup>2</sup>		Satiation	
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.
4.59	0.10	0.30	0.07	0.08	0.07	-0.10	0.06	-0.07	0.06			0.05	0.05	0.36	0.06			0.08	0.07
4.59	0.10	0.32	0.07	0.09	0.07	-0.09	0.06					0.09	0.05	0.36	0.06			0.08	0.07
4.61	0.10	0.36	0.06	0.05	0.06			-0.10	0.05					0.37	0.06				
4.60	0.09	0.34	0.07	0.09	0.06	-0.09	0.06	-0.11	0.04					0.39	0.16	-0.03	0.16	0.09	0.07
4.60	0.10	0.33	0.07	0.09	0.06	-0.09	0.06	-0.11	0.05	0.01	0.05			0.36	0.06			0.09	0.07
4.60	0.10	0.33	0.06	0.04	0.06			-0.10	0.05					0.36	0.06			0.08	0.07
4.61	0.11	0.33	0.06	0.09	0.07	-0.12	0.07	-0.10	0.05	0.01	0.05			0.37	0.06				
4.62	0.10	0.37	0.06	0.09	0.06	-0.09	0.06	-0.08	0.05	0.02	0.05	0.06	0.05	0.37	0.06				
4.58	0.10	0.30	0.07	0.09	0.06	-0.11	0.06	-0.10	0.04					0.36	0.06			0.09	0.07
4.61	0.10	0.33	0.06	0.09	0.07	-0.11	0.06	-0.10	0.05					0.36	0.16	0.01	0.16		
4.61	0.10	0.39	0.06	0.10	0.06	-0.08	0.07			0.00	0.05	0.10	0.05	0.37	0.06				
4.61	0.10	0.39	0.06	0.10	0.06	-0.07	0.06					0.09	0.04	0.37	0.16	0.00	0.16		
4.61	0.10	0.37	0.06	0.09	0.06	-0.08	0.06	-0.08	0.05			0.05	0.05	0.38	0.16	-0.01	0.16		
4.63	0.10	0.35	0.06	0.12	0.07	-0.12	0.07							0.36	0.06				
4.58	0.10	0.34	0.06	0.08	0.07	-0.10	0.06	-0.07	0.06			0.06	0.05	0.37	0.06				
4.61	0.10	0.34	0.07	0.09	0.06	-0.09	0.06	-0.08	0.05	0.02	0.05	0.05	0.05	0.36	0.06			0.08	0.07
4.61	0.11	0.35	0.06	0.10	0.07	-0.10	0.07			0.02	0.05	0.10	0.05	0.36	0.06				
4.60	0.10	0.38	0.06	0.09	0.06	-0.09	0.06	-0.08	0.05	0.02	0.05	0.06	0.05	0.36	0.06				
4.60	0.10	0.35	0.07	0.09	0.06	-0.09	0.06	-0.08	0.05	0.02	0.05	0.06	0.05	0.36	0.06			0.08	0.07
4.57	0.10	0.31	0.07	0.08	0.07	-0.10	0.06	-0.07	0.05			0.06	0.05	0.36	0.06			0.08	0.07
4.60	0.10	0.35	0.06	0.09	0.07	-0.10	0.06					0.09	0.05	0.35	0.16	0.01	0.16		
4.63	0.10	0.34	0.07	0.13	0.06	-0.10	0.06							0.36	0.06			0.09	0.07
4.60	0.10	0.34	0.07	0.08	0.06	-0.08	0.06	-0.08	0.05			0.04	0.05	0.38	0.16	-0.02	0.16	0.08	0.07
4.59	0.09	0.38	0.06	0.09	0.06	-0.08	0.06	-0.08	0.05			0.06	0.05	0.37	0.16	-0.01	0.16		
4.61	0.10	0.36	0.07	0.10	0.06	-0.08	0.06			0.01	0.05	0.09	0.05	0.36	0.06			0.08	0.07
4.61	0.10	0.36	0.07	0.09	0.06	-0.08	0.06					0.09	0.04	0.38	0.16	-0.02	0.16	0.08	0.07
4.59	0.09	0.35	0.07	0.08	0.06	-0.08	0.06	-0.08	0.05			0.05	0.05	0.38	0.16	-0.02	0.16	0.08	0.07
4.59	0.10	0.30	0.07	0.08	0.06	-0.10	0.06	-0.07	0.05			0.05	0.05	0.37	0.06			0.08	0.07
4.63	0.11	0.37	0.06											0.36	0.06				
4.58	0.10	0.34	0.06	0.04	0.06			-0.10	0.05					0.36	0.06			0.08	0.07
4.60	0.10	0.33	0.06	0.09	0.07	-0.12	0.07	-0.11	0.05	0.02	0.05			0.36	0.06				
4.64	0.10	0.38	0.06	0.13	0.07	-0.10	0.06							0.37	0.06				
4.60	0.10	0.33	0.06	0.05	0.06			-0.10	0.05					0.36	0.06			0.08	0.07
4.60	0.10	0.40	0.06	0.10	0.06	-0.07	0.07			0.01	0.05	0.10	0.05	0.36	0.06				
4.59	0.09	0.40	0.06	0.10	0.06	-0.07	0.06					0.10	0.04	0.37	0.16	0.00	0.16		



Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		No. of patch occupants		No. of patch occupants <sup>2</sup>		Satiation	
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.
4.59	0.10	0.37	0.06	0.05	0.06			-0.11	0.05					0.37	0.06				
4.62	0.10	0.37	0.06	0.09	0.06	-0.10	0.06	-0.11	0.05	0.00	0.05			0.37	0.16	0.00	0.16		
4.61	0.11	0.29	0.07	0.09	0.07	-0.12	0.06	-0.10	0.05	0.02	0.05			0.36	0.06			0.09	0.07
4.58	0.10	0.33	0.07	0.09	0.07	-0.09	0.06					0.10	0.05	0.36	0.06			0.07	0.07
4.59	0.10	0.33	0.06	0.09	0.07	-0.11	0.06	-0.10	0.05					0.36	0.16	0.00	0.16		
4.61	0.10	0.33	0.07	0.09	0.06	-0.09	0.06	-0.08	0.05	0.02	0.05	0.05	0.05	0.36	0.06			0.08	0.07
4.59	0.10	0.37	0.07	0.10	0.06	-0.08	0.06			0.01	0.05	0.10	0.05	0.35	0.06			0.08	0.07
4.59	0.10	0.36	0.06	0.09	0.07	-0.10	0.07			0.02	0.05	0.11	0.05	0.36	0.06				
4.59	0.09	0.37	0.07	0.09	0.06	-0.07	0.06					0.09	0.04	0.37	0.16	-0.02	0.16	0.08	0.07
4.60	0.10	0.32	0.06	0.09	0.07	-0.12	0.06					0.09	0.05	0.34	0.06				
4.61	0.10	0.34	0.06	0.09	0.07	-0.11	0.07	-0.07	0.06	0.03	0.05	0.06	0.06	0.36	0.06				
4.62	0.10	0.39	0.06	0.13	0.07	-0.10	0.06							0.36	0.06				
4.61	0.11	0.32	0.06	0.10	0.07	-0.12	0.07	-0.10	0.05	0.01	0.05			0.37	0.06				
4.60	0.10	0.29	0.07	0.09	0.06	-0.11	0.06	-0.09	0.05					0.38	0.16	-0.02	0.16	0.08	0.07
4.60	0.10	0.34	0.07	0.09	0.06	-0.08	0.06	-0.08	0.05			0.05	0.05	0.39	0.16	-0.03	0.16	0.08	0.07
4.58	0.10	0.36	0.06	0.09	0.07	-0.09	0.06					0.10	0.05	0.35	0.16	0.01	0.16		
4.61	0.10	0.32	0.06	0.09	0.07	-0.11	0.06	-0.10	0.05					0.37	0.16	0.00	0.16		
4.61	0.10	0.38	0.06	0.09	0.06	-0.09	0.06	-0.11	0.05	0.00	0.05			0.37	0.16	-0.01	0.16		
4.61	0.10	0.35	0.07	0.10	0.06	-0.08	0.06			0.01	0.05	0.09	0.05	0.36	0.06			0.08	0.07
4.61	0.10	0.35	0.07	0.10	0.06	-0.07	0.06					0.09	0.04	0.39	0.16	-0.03	0.16	0.08	0.07
4.59	0.10	0.34	0.07	0.09	0.06	-0.09	0.06	-0.08	0.05	0.02	0.05	0.06	0.05	0.36	0.06			0.08	0.07
4.62	0.11	0.31	0.07	0.12	0.07	-0.11	0.06							0.36	0.06			0.08	0.07
4.61	0.11	0.35	0.06	0.10	0.07	-0.10	0.07			0.02	0.05	0.10	0.05	0.37	0.06				
4.62	0.11	0.31	0.06	0.09	0.07	-0.13	0.06					0.08	0.05	0.35	0.06				
4.57	0.10	0.31	0.07	0.08	0.06	-0.09	0.06	-0.07	0.05			0.06	0.05	0.36	0.06			0.08	0.07
4.59	0.10	0.34	0.06	0.09	0.07	-0.11	0.07	-0.08	0.06	0.03	0.05	0.07	0.06	0.36	0.06				
4.63	0.10	0.34	0.07	0.13	0.06	-0.10	0.06							0.36	0.06			0.09	0.07
4.60	0.10	0.35	0.06	0.09	0.07	-0.09	0.06					0.10	0.05	0.36	0.16	0.00	0.16		
4.60	0.10	0.34	0.06	0.08	0.07	-0.10	0.06	-0.06	0.06			0.06	0.06	0.36	0.16	0.01	0.16		
4.59	0.09	0.35	0.07	0.08	0.06	-0.08	0.06	-0.08	0.05			0.05	0.05	0.39	0.16	-0.03	0.16	0.08	0.07
4.63	0.11	0.38	0.06	0.08	0.07									0.36	0.06				
4.62	0.10	0.33	0.07	0.09	0.06	-0.10	0.06	-0.11	0.05	0.01	0.05			0.38	0.16	-0.02	0.16	0.09	0.07
4.63	0.10	0.34	0.06	0.13	0.07	-0.11	0.06							0.37	0.06				
4.59	0.10	0.30	0.07	0.09	0.07	-0.12	0.06	-0.11	0.05	0.02	0.05			0.36	0.06			0.09	0.07
4.60	0.11	0.32	0.07	0.10	0.07	-0.10	0.07			0.02	0.05	0.10	0.05	0.36	0.06			0.07	0.07

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		No. of patch occupants		No. of patch occupants <sup>2</sup>		Satiation	
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.
4.62	0.10	0.36	0.06	0.10	0.06	-0.09	0.06	-0.11	0.05	0.00	0.05			0.38	0.16	-0.01	0.16		
4.62	0.10	0.38	0.06	0.11	0.07	-0.08	0.07			-0.04	0.05			0.37	0.06				
4.61	0.11	0.29	0.06	0.10	0.06	-0.12	0.06	-0.10	0.05	0.02	0.05			0.36	0.06			0.09	0.07
4.58	0.10	0.34	0.06	0.05	0.06			-0.10	0.05					0.36	0.06			0.08	0.07
4.61	0.10	0.37	0.06	0.04	0.07			-0.10	0.05					0.34	0.16	0.03	0.16		
4.64	0.10	0.37	0.06			-0.06	0.06							0.36	0.06				
4.63	0.11	0.34	0.06			-0.07	0.06							0.36	0.06				
4.60	0.10	0.32	0.07	0.09	0.07	-0.09	0.06					0.09	0.05	0.37	0.16	-0.01	0.16	0.07	0.07
4.58	0.10	0.30	0.07	0.09	0.06	-0.11	0.06	-0.10	0.05					0.37	0.16	-0.02	0.16	0.08	0.07
4.60	0.10	0.34	0.07	0.09	0.06	-0.09	0.06	-0.11	0.05	0.01	0.05			0.38	0.16	-0.03	0.16	0.09	0.07
4.62	0.11	0.34	0.07											0.36	0.06			0.08	0.07
4.62	0.10	0.36	0.07	0.13	0.06	-0.10	0.06							0.36	0.06			0.09	0.07
4.59	0.10	0.36	0.07	0.10	0.06	-0.07	0.06			0.01	0.05	0.10	0.05	0.36	0.06			0.08	0.07
4.61	0.10	0.36	0.06	0.13	0.07	-0.11	0.07							0.36	0.06				
4.59	0.09	0.37	0.07	0.10	0.06	-0.07	0.06					0.09	0.04	0.38	0.16	-0.03	0.16	0.08	0.07
4.58	0.10	0.34	0.06	0.08	0.07	-0.10	0.06	-0.07	0.06			0.06	0.06	0.36	0.16	0.01	0.16		
4.61	0.10	0.33	0.06	0.09	0.07	-0.11	0.07	-0.07	0.06	0.03	0.05	0.07	0.05	0.37	0.06				
4.60	0.10	0.29	0.07	0.09	0.06	-0.11	0.06	-0.10	0.04					0.39	0.16	-0.02	0.16	0.09	0.07
4.60	0.10	0.33	0.06	0.09	0.07	-0.12	0.07	-0.11	0.05	0.02	0.05			0.37	0.06				
4.60	0.11	0.30	0.07	0.09	0.06	-0.12	0.06	-0.07	0.05	0.04	0.05	0.06	0.05	0.36	0.06			0.08	0.07
4.63	0.11	0.37	0.06											0.36	0.06				
4.59	0.10	0.33	0.06	0.09	0.07	-0.11	0.06	-0.11	0.05					0.37	0.16	0.00	0.16		
4.61	0.10	0.39	0.06	0.10	0.07	-0.08	0.07			0.00	0.05	0.09	0.05	0.36	0.16	0.00	0.16		
4.62	0.10	0.37	0.06	0.09	0.06	-0.09	0.06	-0.08	0.05	0.02	0.05	0.06	0.05	0.36	0.16	0.00	0.16		
4.60	0.09	0.38	0.06	0.09	0.06	-0.09	0.06	-0.08	0.05	0.02	0.05	0.06	0.05	0.36	0.16	0.00	0.16		
4.59	0.10	0.36	0.06	0.10	0.07	-0.10	0.07			0.02	0.05	0.11	0.05	0.36	0.06				
4.62	0.10	0.32	0.07	0.10	0.06	-0.09	0.06	-0.11	0.05	0.01	0.05			0.39	0.16	-0.03	0.16	0.09	0.07
4.60	0.10	0.37	0.06	0.10	0.06	-0.09	0.06	-0.11	0.05	0.00	0.05			0.38	0.16	-0.01	0.16		
4.59	0.10	0.33	0.07	0.10	0.07	-0.10	0.07			0.02	0.05	0.10	0.05	0.35	0.06			0.07	0.07
4.61	0.10	0.38	0.06											0.36	0.06				
4.62	0.11	0.31	0.07	0.12	0.07	-0.11	0.06							0.36	0.06			0.09	0.07
4.60	0.10	0.33	0.06	0.08	0.07	-0.10	0.06	-0.06	0.06			0.06	0.05	0.37	0.16	0.00	0.16		
4.58	0.10	0.36	0.06	0.09	0.07	-0.09	0.06					0.10	0.05	0.36	0.16	0.00	0.16		
4.64	0.11	0.31	0.06	0.12	0.07	-0.14	0.07							0.35	0.06				
4.59	0.10	0.37	0.06	0.04	0.07			-0.11	0.05					0.33	0.16	0.03	0.16		

Intercept		Rank		Relatedness		Social bonds		Rank x Relatedness		Rank x Social bonds		Relatedness x Social bonds		No. of patch occupants		No. of patch occupants <sup>2</sup>		Satiation	
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.
4.59	0.10	0.31	0.07	0.09	0.06	-0.12	0.06	-0.08	0.05	0.04	0.05	0.06	0.05	0.35	0.06			0.08	0.07
4.62	0.10	0.39	0.06	0.13	0.07	-0.10	0.06							0.36	0.06				
4.60	0.11	0.32	0.07	0.10	0.07	-0.10	0.06			0.02	0.05	0.10	0.05	0.36	0.06			0.08	0.07
4.64	0.10	0.38	0.06	0.13	0.07	-0.10	0.06							0.37	0.16	0.00	0.16		
4.61	0.10	0.30	0.06	0.09	0.07	-0.14	0.06	-0.07	0.05					0.34	0.06				
4.63	0.11	0.29	0.06	0.09	0.07	-0.14	0.06	-0.07	0.05					0.35	0.06				
4.59	0.10	0.34	0.06	0.09	0.07	-0.11	0.06	-0.08	0.06	0.03	0.05	0.07	0.05	0.36	0.06				
4.61	0.10	0.38	0.06			-0.03	0.07			-0.06	0.05			0.37	0.06				
4.60	0.10	0.40	0.06	0.10	0.07	-0.08	0.07			0.01	0.05	0.10	0.05	0.36	0.16	0.00	0.16		
4.58	0.10	0.33	0.07	0.09	0.07	-0.09	0.06					0.10	0.05	0.37	0.16	-0.01	0.16	0.07	0.07
4.62	0.11	0.35	0.06	0.08	0.07									0.36	0.06			0.08	0.07
4.59	0.10	0.29	0.06	0.10	0.06	-0.12	0.06	-0.11	0.05	0.02	0.05			0.36	0.06			0.09	0.07
4.62	0.11	0.31	0.06	0.09	0.07	-0.12	0.06					0.08	0.05	0.35	0.06				
4.59	0.10	0.30	0.07	0.08	0.07	-0.10	0.06	-0.07	0.06			0.05	0.05	0.37	0.16	-0.01	0.16	0.08	0.07
4.63	0.11	0.38	0.06	0.08	0.07									0.37	0.06				
4.62	0.10	0.32	0.06	0.12	0.07	-0.14	0.07							0.34	0.06				
4.59	0.10	0.32	0.07	0.09	0.07	-0.09	0.06					0.09	0.05	0.38	0.16	-0.02	0.16	0.08	0.07
4.61	0.10	0.36	0.06	0.05	0.06			-0.10	0.05					0.35	0.16	0.02	0.16		
4.62	0.10	0.35	0.07	0.11	0.07	-0.08	0.07			-0.03	0.05			0.36	0.06			0.08	0.07
4.63	0.10	0.34	0.07			-0.06	0.06							0.36	0.06			0.08	0.07
4.62	0.11	0.34	0.06	0.11	0.07	-0.10	0.07			-0.03	0.05			0.37	0.06				
4.62	0.10	0.38	0.06	0.12	0.07	-0.08	0.07			-0.04	0.05			0.37	0.06				
4.60	0.10	0.33	0.07	0.09	0.06	-0.09	0.06	-0.11	0.05	0.01	0.05			0.39	0.16	-0.03	0.16	0.09	0.07
4.60	0.11	0.30	0.07	0.09	0.06	-0.11	0.06	-0.07	0.05	0.04	0.05	0.06	0.05	0.36	0.06			0.08	0.07
4.60	0.10	0.33	0.06	0.04	0.06			-0.10	0.05					0.35	0.16	0.01	0.16	0.08	0.07
4.61	0.11	0.33	0.06	0.09	0.07	-0.12	0.07	-0.10	0.05	0.01	0.05			0.36	0.16	0.01	0.16		
4.62	0.10	0.37	0.06	0.09	0.06	-0.09	0.06	-0.08	0.05	0.02	0.05	0.06	0.05	0.37	0.16	0.00	0.16		
4.62	0.11	0.31	0.07			-0.07	0.06							0.36	0.06			0.08	0.07
4.58	0.10	0.30	0.07	0.09	0.06	-0.11	0.06	-0.10	0.04					0.38	0.16	-0.02	0.16	0.09	0.07
4.60	0.10	0.32	0.07	0.12	0.07	-0.11	0.06							0.36	0.06			0.08	0.07
4.61	0.10	0.39	0.06	0.08	0.07									0.36	0.06				
4.61	0.10	0.39	0.06	0.10	0.06	-0.08	0.07			0.00	0.05	0.10	0.05	0.37	0.16	0.00	0.16		
4.60	0.10	0.39	0.06	0.12	0.07	-0.08	0.07			-0.04	0.05			0.36	0.06				

Table 3.12. continued.

Initial intake rate		Intake rate x Rank		Intake rate x Social bonds		Intake rate x Inter-patch distance		Intake rate x Mean patch food content		Patch food density		Patch depletion		Time in previous patch		Inter patch distance		Mean patch food content		AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.			
0.00	0.06	0.22	0.07	0.13	0.07			-0.09	0.06	0.94	0.17	-0.01	0.06	0.05	0.05	0.05	0.07	-0.88	0.18	4479.04	0.00	0.02
0.01	0.06	0.24	0.07	0.13	0.07					0.94	0.16	0.00	0.06	0.06	0.05	0.05	0.06	-0.88	0.17	4479.28	0.24	0.02
0.01	0.06	0.23	0.07	0.13	0.07			-0.09	0.06	0.91	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.85	0.17	4479.57	0.53	0.02
0.01	0.06	0.22	0.07	0.13	0.07	-0.06	0.05	-0.10	0.06	0.93	0.16	-0.01	0.06	0.06	0.05	0.04	0.07	-0.88	0.17	4479.63	0.59	0.02
0.02	0.06	0.25	0.07	0.14	0.07					0.90	0.16	-0.05	0.07	0.04	0.05	0.05	0.06	-0.84	0.17	4479.81	0.76	0.01
-0.01	0.06	0.19	0.07	0.11	0.07			-0.09	0.06	0.88	0.17	-0.01	0.06	0.06	0.05	0.05	0.07	-0.81	0.18	4479.97	0.93	0.01
0.02	0.06	0.24	0.07	0.14	0.07	-0.06	0.05			0.93	0.16	0.00	0.06	0.06	0.05	0.04	0.06	-0.88	0.17	4480.03	0.99	0.01
0.02	0.06	0.24	0.07	0.13	0.07	-0.07	0.05	-0.10	0.06	0.90	0.16	-0.05	0.07	0.04	0.05	0.04	0.06	-0.85	0.17	4480.07	1.03	0.01
0.00	0.06	0.22	0.07	0.13	0.07			-0.09	0.06	0.90	0.17	-0.01	0.06	0.06	0.05	0.05	0.07	-0.84	0.18	4480.08	1.03	0.01
0.01	0.06	0.23	0.07	0.13	0.07					0.90	0.17	0.00	0.06	0.06	0.05	0.05	0.06	-0.83	0.18	4480.14	1.09	0.01
0.01	0.06	0.20	0.07	0.12	0.07					0.87	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.80	0.18	4480.27	1.23	0.01
0.03	0.06	0.25	0.07	0.14	0.07	-0.06	0.05			0.90	0.16	-0.05	0.07	0.04	0.05	0.04	0.06	-0.84	0.17	4480.48	1.44	0.01
-0.03	0.06	0.13	0.05					-0.10	0.06	0.94	0.17	-0.02	0.06	0.06	0.05	0.05	0.07	-0.88	0.18	4480.55	1.50	0.01
0.00	0.06	0.19	0.07	0.12	0.07	-0.06	0.05	-0.10	0.06	0.87	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.81	0.18	4480.56	1.52	0.01
0.01	0.06	0.22	0.07	0.13	0.07	-0.07	0.05	-0.09	0.06	0.90	0.17	-0.01	0.06	0.06	0.05	0.04	0.06	-0.84	0.18	4480.60	1.56	0.01
-0.03	0.06	0.12	0.05					-0.10	0.06	0.88	0.18	-0.02	0.06	0.06	0.05	0.05	0.07	-0.81	0.19	4480.75	1.70	0.01
0.01	0.06	0.23	0.07	0.13	0.07			-0.09	0.06	0.88	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.81	0.18	4480.81	1.76	0.01
0.02	0.06	0.24	0.07	0.13	0.07	-0.06	0.05			0.89	0.16	-0.01	0.06	0.07	0.05	0.05	0.06	-0.83	0.17	4480.81	1.77	0.01
0.00	0.06	0.20	0.07	0.12	0.07			-0.09	0.06	0.85	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.79	0.18	4480.85	1.80	0.01
0.02	0.06	0.25	0.07	0.13	0.07					0.87	0.16	-0.05	0.07	0.05	0.05	0.05	0.06	-0.81	0.17	4480.88	1.84	0.01
0.02	0.06	0.21	0.07	0.12	0.07	-0.06	0.05			0.87	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.80	0.18	4481.02	1.97	0.01
0.00	0.06	0.22	0.07	0.13	0.07			-0.09	0.06	0.94	0.17	-0.01	0.06	0.06	0.05	0.05	0.07	-0.88	0.18	4481.04	2.00	0.01
0.00	0.06	0.22	0.07	0.13	0.07			-0.09	0.06	0.94	0.17	-0.01	0.06	0.05	0.05	0.05	0.07	-0.88	0.18	4481.04	2.00	0.01
-0.01	0.06	0.14	0.05							0.94	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.87	0.18	4481.07	2.03	0.01
0.02	0.06	0.22	0.07	0.12	0.07					0.85	0.17	-0.04	0.07	0.05	0.05	0.05	0.06	-0.78	0.17	4481.16	2.11	0.01
-0.02	0.06	0.15	0.06					-0.10	0.06	0.91	0.17	-0.06	0.07	0.04	0.05	0.05	0.07	-0.85	0.18	4481.22	2.18	0.01
0.02	0.06	0.23	0.07	0.13	0.07	-0.07	0.05	-0.09	0.06	0.87	0.17	-0.05	0.07	0.04	0.05	0.04	0.06	-0.81	0.17	4481.26	2.22	0.01
-0.01	0.06	0.13	0.05							0.87	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.80	0.18	4481.26	2.22	0.01
-0.02	0.06	0.14	0.05			-0.06	0.05	-0.10	0.06	0.94	0.17	-0.02	0.06	0.06	0.05	0.05	0.07	-0.88	0.18	4481.27	2.23	0.01
0.01	0.06	0.24	0.07	0.13	0.07					0.94	0.17	0.00	0.06	0.06	0.05	0.05	0.06	-0.88	0.18	4481.28	2.24	0.01
0.01	0.06	0.24	0.07	0.13	0.07					0.94	0.16	0.00	0.06	0.06	0.05	0.05	0.06	-0.88	0.17	4481.28	2.24	0.01
0.01	0.06	0.21	0.07	0.12	0.07	-0.07	0.05	-0.10	0.06	0.85	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.79	0.18	4481.34	2.29	0.01

Initial intake rate		Intake rate x Rank		Intake rate x Social bonds		Intake rate x Inter-patch distance		Intake rate x Mean patch food content		Patch food density		Patch depletion		Time in previous patch		Inter patch distance		Mean patch food content		AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.			
-0.02	0.06	0.12	0.05			-0.06	0.05	-0.10	0.06	0.88	0.17	-0.02	0.06	0.06	0.05	0.05	0.06	-0.81	0.18	4481.46	2.42	0.01
-0.03	0.06	0.13	0.05					-0.10	0.06	0.90	0.17	-0.02	0.06	0.06	0.05	0.05	0.07	-0.83	0.19	4481.47	2.42	0.01
0.03	0.06	0.25	0.07	0.13	0.07	-0.06	0.05			0.86	0.16	-0.05	0.07	0.05	0.05	0.05	0.06	-0.80	0.17	4481.50	2.46	0.01
0.01	0.06	0.23	0.07	0.13	0.07			-0.09	0.06	0.91	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.85	0.18	4481.54	2.49	0.01
0.01	0.06	0.24	0.07	0.13	0.07			-0.09	0.06	0.91	0.17	-0.06	0.07	0.04	0.05	0.05	0.06	-0.85	0.17	4481.54	2.50	0.01
0.01	0.06	0.22	0.07	0.13	0.07	-0.06	0.05	-0.10	0.06	0.93	0.16	-0.01	0.06	0.06	0.05	0.04	0.07	-0.88	0.17	4481.63	2.58	0.01
0.01	0.06	0.22	0.07	0.13	0.07	-0.06	0.05	-0.10	0.06	0.94	0.17	-0.01	0.06	0.06	0.05	0.04	0.07	-0.88	0.18	4481.63	2.58	0.01
-0.02	0.06	0.15	0.05					-0.10	0.06	0.88	0.17	-0.01	0.06	0.07	0.05	0.05	0.07	-0.81	0.18	4481.72	2.67	0.01
-0.02	0.06	0.13	0.05					-0.10	0.06	0.86	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.79	0.18	4481.73	2.69	0.01
0.00	0.06	0.16	0.05							0.91	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.84	0.18	4481.75	2.71	0.01
0.02	0.06	0.25	0.07	0.13	0.07					0.91	0.16	-0.05	0.07	0.04	0.05	0.05	0.06	-0.85	0.17	4481.77	2.72	0.01
0.02	0.06	0.25	0.07	0.14	0.07					0.90	0.16	-0.05	0.07	0.04	0.05	0.05	0.06	-0.84	0.17	4481.78	2.73	0.01
-0.01	0.06	0.14	0.05							0.90	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.82	0.18	4481.80	2.76	0.01
0.03	0.06	0.22	0.07	0.12	0.07	-0.06	0.05			0.84	0.16	-0.05	0.07	0.05	0.05	0.05	0.06	-0.78	0.17	4481.81	2.77	0.01
-0.01	0.06	0.15	0.06			-0.06	0.05	-0.10	0.06	0.90	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.85	0.18	4481.84	2.79	0.01
0.00	0.06	0.15	0.05			-0.06	0.05			0.93	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.87	0.18	4481.96	2.92	0.00
-0.01	0.06	0.19	0.07	0.11	0.07			-0.09	0.06	0.88	0.17	-0.01	0.06	0.06	0.05	0.05	0.07	-0.81	0.18	4481.97	2.92	0.00
0.00	0.06	0.22	0.07	0.12	0.07			-0.09	0.06	0.91	0.17	-0.01	0.06	0.06	0.05	0.05	0.07	-0.85	0.18	4481.97	2.93	0.00
-0.01	0.06	0.19	0.07	0.11	0.07			-0.09	0.06	0.88	0.17	-0.01	0.06	0.06	0.05	0.05	0.07	-0.81	0.18	4481.97	2.93	0.00
0.01	0.06	0.23	0.07	0.13	0.07					0.91	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.84	0.18	4482.00	2.96	0.00
0.02	0.06	0.24	0.07	0.14	0.07	-0.06	0.05			0.93	0.16	0.00	0.06	0.06	0.05	0.04	0.06	-0.88	0.17	4482.03	2.98	0.00
0.02	0.06	0.24	0.07	0.14	0.07	-0.06	0.05			0.93	0.16	0.00	0.06	0.06	0.05	0.04	0.06	-0.88	0.17	4482.03	2.98	0.00
0.02	0.06	0.24	0.07	0.13	0.07	-0.07	0.05	-0.10	0.06	0.90	0.16	-0.06	0.07	0.04	0.05	0.04	0.06	-0.85	0.17	4482.03	2.99	0.00
0.02	0.06	0.24	0.07	0.13	0.07	-0.07	0.05	-0.10	0.06	0.90	0.17	-0.06	0.07	0.04	0.05	0.04	0.06	-0.85	0.17	4482.04	3.00	0.00
0.00	0.06	0.22	0.07	0.13	0.07			-0.09	0.06	0.90	0.17	-0.01	0.06	0.06	0.05	0.05	0.07	-0.84	0.18	4482.08	3.03	0.00
-0.02	0.06	0.13	0.05			-0.06	0.05	-0.10	0.06	0.90	0.17	-0.02	0.06	0.07	0.05	0.05	0.06	-0.83	0.18	4482.13	3.09	0.00
0.00	0.06	0.13	0.05			-0.06	0.05			0.87	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.80	0.18	4482.14	3.09	0.00
0.01	0.06	0.23	0.07	0.13	0.07					0.90	0.17	0.00	0.06	0.06	0.05	0.05	0.06	-0.83	0.18	4482.14	3.09	0.00
0.00	0.06	0.16	0.05							0.87	0.17	0.00	0.06	0.07	0.05	0.05	0.06	-0.80	0.18	4482.18	3.13	0.00
-0.01	0.06	0.17	0.07	0.11	0.07			-0.11	0.06	0.94	0.17	-0.01	0.06	0.05	0.05	0.05	0.07	-0.89	0.18	4482.19	3.14	0.00
0.01	0.06	0.20	0.07	0.12	0.07					0.87	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.80	0.18	4482.26	3.22	0.00
0.01	0.06	0.20	0.07	0.12	0.07					0.87	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.80	0.18	4482.27	3.23	0.00
0.00	0.06	0.14	0.05							0.85	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.78	0.18	4482.27	3.23	0.00
-0.02	0.06	0.14	0.06					-0.10	0.06	0.88	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.81	0.18	4482.34	3.30	0.00

Initial intake rate		Intake rate x Rank		Intake rate x Social bonds		Intake rate x Inter-patch distance		Intake rate x Mean patch food content		Patch food density		Patch depletion		Time in previous patch		Inter patch distance		Mean patch food content		AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.			
-0.01	0.06	0.13	0.05			-0.06	0.05	-0.10	0.06	0.85	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.78	0.18	4482.35	3.31	0.00
-0.01	0.06	0.15	0.05			-0.06	0.05	-0.10	0.06	0.88	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.81	0.18	4482.39	3.35	0.00
0.03	0.06	0.25	0.07	0.14	0.07	-0.06	0.05			0.90	0.16	-0.05	0.07	0.04	0.05	0.04	0.06	-0.84	0.17	4482.45	3.40	0.00
0.03	0.06	0.25	0.07	0.13	0.07	-0.06	0.05			0.90	0.16	-0.05	0.07	0.05	0.05	0.04	0.06	-0.85	0.17	4482.45	3.41	0.00
0.00	0.06	0.16	0.05					-0.10	0.06	0.85	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.78	0.18	4482.46	3.41	0.00
-0.03	0.06	0.13	0.05					-0.10	0.06	0.95	0.17	-0.02	0.06	0.06	0.05	0.05	0.07	-0.89	0.18	4482.48	3.43	0.00
0.01	0.06	0.22	0.07	0.13	0.07	-0.07	0.05	-0.09	0.06	0.91	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.85	0.18	4482.49	3.45	0.00
0.01	0.06	0.16	0.05			-0.06	0.05			0.90	0.16	-0.05	0.07	0.05	0.05	0.05	0.06	-0.84	0.17	4482.54	3.49	0.00
-0.03	0.06	0.13	0.05					-0.10	0.06	0.94	0.17	-0.01	0.06	0.06	0.05	0.05	0.07	-0.88	0.18	4482.54	3.50	0.00
0.00	0.06	0.19	0.07	0.12	0.07	-0.06	0.05	-0.10	0.06	0.88	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.81	0.18	4482.56	3.52	0.00
0.00	0.06	0.19	0.07	0.12	0.07	-0.06	0.05	-0.10	0.06	0.87	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.81	0.18	4482.56	3.52	0.00
0.01	0.06	0.22	0.07	0.13	0.07	-0.07	0.05	-0.09	0.06	0.90	0.17	-0.01	0.06	0.06	0.05	0.04	0.06	-0.84	0.18	4482.60	3.55	0.00
-0.03	0.06	0.10	0.05					-0.11	0.06	0.95	0.18	-0.02	0.06	0.05	0.05	0.05	0.07	-0.89	0.19	4482.61	3.57	0.00
0.00	0.06	0.15	0.05			-0.06	0.05			0.89	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.82	0.18	4482.62	3.58	0.00
0.01	0.06	0.23	0.07	0.12	0.07			-0.09	0.06	0.88	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.82	0.18	4482.63	3.59	0.00
-0.03	0.06	0.12	0.05					-0.10	0.06	0.89	0.18	-0.02	0.06	0.06	0.05	0.05	0.07	-0.82	0.19	4482.65	3.61	0.00
0.02	0.06	0.24	0.07	0.13	0.07	-0.06	0.05			0.90	0.16	-0.01	0.06	0.07	0.05	0.05	0.06	-0.84	0.17	4482.67	3.63	0.00
0.02	0.06	0.24	0.07	0.13	0.07					0.88	0.16	-0.05	0.07	0.05	0.05	0.05	0.06	-0.81	0.17	4482.67	3.63	0.00
0.00	0.06	0.16	0.05							0.87	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.80	0.18	4482.69	3.64	0.00
-0.03	0.06	0.12	0.05					-0.10	0.06	0.88	0.18	-0.02	0.06	0.06	0.05	0.05	0.07	-0.81	0.19	4482.74	3.70	0.00
0.01	0.06	0.19	0.07	0.11	0.07			-0.11	0.06	0.91	0.17	-0.06	0.07	0.03	0.05	0.05	0.07	-0.86	0.18	4482.76	3.72	0.00
0.01	0.06	0.23	0.07	0.13	0.07			-0.09	0.06	0.88	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.81	0.18	4482.79	3.74	0.00
0.02	0.06	0.24	0.07	0.13	0.07	-0.06	0.05			0.89	0.16	-0.01	0.06	0.07	0.05	0.05	0.06	-0.83	0.17	4482.81	3.76	0.00
0.00	0.06	0.20	0.07	0.12	0.07			-0.09	0.06	0.86	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.79	0.18	4482.82	3.78	0.00
0.00	0.06	0.20	0.07	0.12	0.07			-0.09	0.06	0.85	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.79	0.18	4482.83	3.79	0.00
0.02	0.06	0.25	0.07	0.13	0.07					0.87	0.16	-0.05	0.07	0.05	0.05	0.05	0.06	-0.81	0.17	4482.86	3.82	0.00
-0.01	0.06	0.15	0.06			-0.07	0.05	-0.10	0.06	0.87	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.81	0.18	4482.91	3.87	0.00
-0.02	0.06	0.11	0.05					-0.11	0.06	0.79	0.17	-0.02	0.06	0.06	0.05	0.05	0.06	-0.71	0.17	4482.92	3.88	0.00
0.01	0.06	0.17	0.05							0.85	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.77	0.18	4482.92	3.88	0.00
-0.01	0.06	0.15	0.05							0.95	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.89	0.18	4482.98	3.94	0.00
0.00	0.06	0.17	0.07	0.11	0.07	-0.06	0.05	-0.11	0.06	0.94	0.17	-0.01	0.06	0.05	0.05	0.04	0.07	-0.89	0.18	4483.00	3.95	0.00
0.01	0.06	0.17	0.05			-0.07	0.05	-0.10	0.06	0.85	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.78	0.18	4483.01	3.96	0.00
0.02	0.06	0.21	0.07	0.12	0.07	-0.06	0.05			0.87	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.80	0.18	4483.01	3.96	0.00
0.02	0.06	0.21	0.07	0.12	0.07	-0.06	0.05			0.87	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.80	0.18	4483.02	3.97	0.00

Initial intake rate		Intake rate x Rank		Intake rate x Social bonds		Intake rate x Inter-patch distance		Intake rate x Mean patch food content		Patch food density		Patch depletion		Time in previous patch		Inter patch distance		Mean patch food content		AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.			
0.01	0.06	0.16	0.05			-0.06	0.05			0.87	0.17	0.00	0.06	0.07	0.05	0.05	0.06	-0.80	0.18	4483.02	3.98	0.00
0.00	0.06	0.22	0.07	0.13	0.07			-0.09	0.06	0.94	0.17	-0.01	0.06	0.06	0.05	0.05	0.07	-0.88	0.18	4483.04	4.00	0.00
-0.02	0.06	0.15	0.06					-0.10	0.06	0.92	0.17	-0.06	0.07	0.05	0.05	0.05	0.07	-0.86	0.18	4483.05	4.01	0.00
0.01	0.06	0.14	0.05			-0.06	0.05			0.84	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.77	0.18	4483.06	4.02	0.00
-0.01	0.06	0.14	0.05							0.94	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.87	0.18	4483.07	4.03	0.00
0.02	0.06	0.23	0.07	0.12	0.07	-0.07	0.05	-0.09	0.06	0.88	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.82	0.18	4483.10	4.06	0.00
0.02	0.06	0.22	0.07	0.12	0.07					0.85	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.78	0.18	4483.12	4.08	0.00
-0.01	0.06	0.13	0.05							0.88	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.81	0.18	4483.14	4.10	0.00
0.02	0.06	0.22	0.07	0.12	0.07					0.85	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.78	0.17	4483.14	4.10	0.00
										0.90	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.84	0.18	4483.16	4.11	0.00
-0.03	0.06	0.14	0.05					-0.09	0.06	0.91	0.17	-0.02	0.06	0.07	0.05	0.05	0.07	-0.85	0.19	4483.17	4.12	0.00
0.01	0.06	0.18	0.07	0.11	0.07					0.94	0.17	0.00	0.06	0.05	0.05	0.05	0.06	-0.88	0.18	4483.18	4.13	0.00
-0.02	0.06	0.14	0.05			-0.06	0.05	-0.10	0.06	0.94	0.17	-0.02	0.06	0.06	0.05	0.05	0.07	-0.89	0.18	4483.20	4.16	0.00
-0.02	0.06	0.15	0.06					-0.10	0.06	0.91	0.17	-0.06	0.07	0.04	0.05	0.05	0.07	-0.85	0.18	4483.21	4.17	0.00
0.02	0.06	0.23	0.07	0.13	0.07	-0.07	0.05	-0.09	0.06	0.87	0.17	-0.05	0.07	0.04	0.05	0.04	0.06	-0.81	0.17	4483.24	4.19	0.00
-0.01	0.06	0.13	0.05							0.87	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.80	0.18	4483.26	4.22	0.00
-0.02	0.06	0.14	0.05			-0.06	0.05	-0.10	0.06	0.94	0.17	-0.02	0.06	0.06	0.05	0.05	0.07	-0.88	0.18	4483.27	4.23	0.00
0.01	0.06	0.24	0.07	0.13	0.07					0.94	0.17	0.00	0.06	0.06	0.05	0.05	0.06	-0.88	0.17	4483.28	4.24	0.00
0.02	0.06	0.21	0.07	0.12	0.07	-0.07	0.05	-0.10	0.06	0.85	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.79	0.18	4483.31	4.27	0.00
0.02	0.06	0.21	0.07	0.12	0.07	-0.07	0.05	-0.10	0.06	0.85	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.79	0.18	4483.31	4.27	0.00
0.03	0.06	0.25	0.07	0.13	0.07	-0.06	0.05			0.87	0.16	-0.05	0.07	0.05	0.05	0.05	0.06	-0.81	0.17	4483.32	4.27	0.00
-0.02	0.06	0.11	0.05					-0.11	0.06	0.92	0.18	-0.06	0.07	0.04	0.05	0.05	0.07	-0.86	0.19	4483.33	4.28	0.00
-0.02	0.06	0.12	0.05			-0.06	0.05	-0.10	0.06	0.88	0.17	-0.02	0.06	0.07	0.05	0.05	0.06	-0.82	0.19	4483.36	4.32	0.00
-0.05	0.06							-0.12	0.06	0.90	0.18	-0.02	0.06	0.06	0.05	0.05	0.07	-0.83	0.19	4483.39	4.35	0.00
0.01	0.06	0.16	0.05			-0.06	0.05			0.87	0.17	-0.05	0.07	0.06	0.05	0.05	0.06	-0.80	0.18	4483.42	4.37	0.00
-0.01	0.06	0.15	0.05							0.91	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.84	0.18	4483.43	4.39	0.00
0.02	0.06	0.19	0.07	0.11	0.07	-0.06	0.05	-0.11	0.06	0.91	0.17	-0.06	0.07	0.03	0.05	0.04	0.07	-0.86	0.18	4483.44	4.40	0.00
-0.02	0.06	0.12	0.05			-0.06	0.05	-0.10	0.06	0.88	0.17	-0.02	0.06	0.06	0.05	0.05	0.06	-0.81	0.18	4483.46	4.42	0.00
-0.03	0.06	0.13	0.05					-0.10	0.06	0.90	0.17	-0.02	0.06	0.06	0.05	0.05	0.07	-0.83	0.19	4483.46	4.42	0.00
0.03	0.06	0.25	0.07	0.13	0.07	-0.06	0.05			0.86	0.16	-0.05	0.07	0.05	0.05	0.05	0.06	-0.80	0.17	4483.48	4.43	0.00
-0.02	0.06	0.12	0.05					-0.11	0.06	0.88	0.18	-0.01	0.06	0.06	0.05	0.05	0.07	-0.81	0.19	4483.48	4.44	0.00
0.01	0.06	0.24	0.07	0.13	0.07			-0.09	0.06	0.91	0.17	-0.06	0.07	0.04	0.05	0.05	0.06	-0.85	0.18	4483.51	4.47	0.00
-0.02	0.06	0.10	0.05			-0.06	0.05	-0.11	0.06	0.94	0.18	-0.02	0.06	0.06	0.05	0.05	0.07	-0.89	0.19	4483.51	4.47	0.00
0.00	0.06	0.16	0.05							0.92	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.86	0.18	4483.55	4.50	0.00

Initial intake rate		Intake rate x Rank		Intake rate x Social bonds		Intake rate x Inter-patch distance		Intake rate x Mean patch food content		Patch food density		Patch depletion		Time in previous patch		Inter patch distance		Mean patch food content		AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.			
-0.02	0.06	0.13	0.05					-0.10	0.06	0.86	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.80	0.18	4483.57	4.53	0.00
0.01	0.06	0.22	0.07	0.13	0.07	-0.06	0.05	-0.10	0.06	0.94	0.17	-0.01	0.06	0.06	0.05	0.04	0.07	-0.88	0.18	4483.62	4.58	0.00
-0.01	0.06	0.18	0.07	0.12	0.07			-0.11	0.06	0.92	0.18	-0.01	0.06	0.05	0.05	0.04	0.07	-0.86	0.19	4483.65	4.60	0.00
-0.01	0.06	0.15	0.06			-0.06	0.05	-0.10	0.06	0.92	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.86	0.18	4483.65	4.61	0.00
0.02	0.06	0.18	0.05			-0.06	0.05			0.84	0.16	-0.05	0.07	0.06	0.05	0.05	0.06	-0.77	0.17	4483.65	4.61	0.00
-0.02	0.06	0.15	0.05					-0.10	0.06	0.88	0.17	-0.01	0.06	0.07	0.05	0.05	0.07	-0.81	0.18	4483.68	4.64	0.00
-0.01	0.06	0.16	0.07	0.10	0.07			-0.11	0.06	0.80	0.16	-0.02	0.06	0.05	0.05	0.05	0.06	-0.72	0.17	4483.72	4.68	0.00
-0.03	0.06	0.10	0.05					-0.11	0.06	0.81	0.16	-0.02	0.06	0.06	0.05	0.05	0.07	-0.72	0.17	4483.72	4.68	0.00
-0.02	0.06	0.13	0.05					-0.10	0.06	0.86	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.79	0.18	4483.73	4.69	0.00
0.00	0.06	0.16	0.06							0.91	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.84	0.18	4483.74	4.70	0.00
0.02	0.06	0.25	0.07	0.13	0.07					0.91	0.16	-0.05	0.07	0.04	0.05	0.05	0.06	-0.85	0.17	4483.74	4.70	0.00
-0.01	0.06	0.12	0.05					-0.11	0.06	0.77	0.16	-0.06	0.07	0.04	0.05	0.05	0.06	-0.69	0.17	4483.74	4.70	0.00
0.02	0.06	0.20	0.07	0.11	0.07					0.91	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.85	0.18	4483.77	4.73	0.00
0.03	0.06	0.22	0.07	0.12	0.07	-0.06	0.05			0.84	0.16	-0.05	0.07	0.05	0.05	0.05	0.06	-0.78	0.17	4483.77	4.73	0.00
-0.01	0.06	0.11	0.05							0.94	0.18	-0.01	0.06	0.06	0.05	0.05	0.06	-0.88	0.19	4483.78	4.74	0.00
0.03	0.06	0.22	0.07	0.12	0.07	-0.06	0.05			0.84	0.16	-0.05	0.07	0.05	0.05	0.05	0.06	-0.78	0.17	4483.78	4.74	0.00
-0.01	0.06	0.14	0.05							0.90	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.82	0.18	4483.80	4.75	0.00
-0.02	0.06	0.14	0.05			-0.06	0.05	-0.10	0.06	0.91	0.17	-0.02	0.06	0.07	0.05	0.05	0.06	-0.85	0.18	4483.82	4.77	0.00
-0.01	0.06	0.15	0.06			-0.06	0.05	-0.10	0.06	0.90	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.85	0.18	4483.82	4.77	0.00
0.00	0.06	0.15	0.05			-0.06	0.05			0.94	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.88	0.18	4483.87	4.82	0.00
-0.02	0.06	0.15	0.06					-0.09	0.06	0.89	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.83	0.18	4483.89	4.85	0.00
-0.01	0.06	0.11	0.05			-0.05	0.05	-0.11	0.06	0.79	0.16	-0.02	0.06	0.06	0.05	0.05	0.06	-0.71	0.17	4483.91	4.87	0.00
0.00	0.06	0.15	0.05			-0.06	0.05			0.93	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.87	0.18	4483.96	4.92	0.00
-0.01	0.06	0.19	0.07	0.11	0.07			-0.09	0.06	0.88	0.17	-0.01	0.06	0.06	0.05	0.05	0.07	-0.81	0.18	4483.97	4.92	0.00
0.00	0.06	0.22	0.07	0.12	0.07			-0.09	0.06	0.91	0.17	-0.01	0.06	0.06	0.05	0.05	0.07	-0.85	0.18	4483.97	4.93	0.00
0.01	0.06	0.23	0.07	0.13	0.07					0.91	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.84	0.18	4484.00	4.96	0.00
0.00	0.06	0.13	0.05			-0.06	0.05			0.88	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.81	0.18	4484.00	4.96	0.00
0.02	0.06	0.24	0.07	0.13	0.07	-0.07	0.05	-0.10	0.06	0.90	0.17	-0.06	0.07	0.04	0.05	0.04	0.06	-0.85	0.17	4484.01	4.97	0.00
0.02	0.06	0.24	0.07	0.14	0.07	-0.06	0.05			0.93	0.16	0.00	0.06	0.06	0.05	0.04	0.06	-0.88	0.17	4484.02	4.98	0.00
0.00	0.06	0.14	0.05							0.86	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.79	0.18	4484.07	5.03	0.00
0.00	0.06	0.12	0.05							0.79	0.16	-0.01	0.06	0.06	0.05	0.05	0.06	-0.70	0.17	4484.07	5.03	0.00
-0.01	0.06	0.12	0.05			-0.06	0.05	-0.11	0.06	0.91	0.17	-0.06	0.07	0.04	0.05	0.05	0.07	-0.86	0.18	4484.11	5.07	0.00
-0.02	0.06	0.13	0.05			-0.06	0.05	-0.10	0.06	0.90	0.17	-0.02	0.06	0.07	0.05	0.05	0.06	-0.83	0.18	4484.13	5.09	0.00
0.00	0.06	0.13	0.05			-0.06	0.05			0.87	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.80	0.18	4484.13	5.09	0.00



Initial intake rate		Intake rate x Rank		Intake rate x Social bonds		Intake rate x Inter-patch distance		Intake rate x Mean patch food content		Patch food density		Patch depletion		Time in previous patch		Inter patch distance		Mean patch food content		AIC	$\Delta$ AIC	$w_i$
$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.	$\beta$	s.e.			
-0.04	0.06							-0.12	0.06	0.96	0.18	-0.02	0.06	0.05	0.05	0.04	0.07	-0.90	0.19	4484.14	5.10	0.00
0.00	0.06	0.16	0.05							0.87	0.17	0.00	0.06	0.07	0.05	0.05	0.06	-0.80	0.18	4484.15	5.10	0.00
0.00	0.06	0.16	0.05							0.89	0.17	-0.05	0.07	0.06	0.05	0.05	0.06	-0.82	0.18	4484.16	5.11	0.00
0.02	0.06	0.19	0.07	0.11	0.07	-0.05	0.05			0.94	0.17	0.00	0.06	0.05	0.05	0.04	0.06	-0.88	0.18	4484.17	5.13	0.00
-0.01	0.06	0.13	0.05			-0.06	0.05	-0.10	0.06	0.86	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.79	0.18	4484.18	5.14	0.00
-0.01	0.06	0.17	0.07	0.11	0.07			-0.11	0.06	0.94	0.17	-0.01	0.06	0.05	0.05	0.05	0.07	-0.89	0.18	4484.19	5.14	0.00
										0.96	0.17	-0.01	0.06	0.06	0.05	0.04	0.06	-0.90	0.18	4484.20	5.15	0.00
-0.05	0.06							-0.12	0.06	0.95	0.18	-0.02	0.06	0.06	0.05	0.04	0.07	-0.89	0.19	4484.22	5.18	0.00
0.00	0.06	0.15	0.05			-0.06	0.05			0.91	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.84	0.18	4484.23	5.19	0.00
-0.01	0.06	0.17	0.07	0.11	0.07			-0.11	0.06	0.79	0.16	-0.01	0.06	0.05	0.05	0.05	0.07	-0.70	0.17	4484.26	5.22	0.00
0.01	0.06	0.20	0.07	0.12	0.07					0.87	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.80	0.18	4484.26	5.22	0.00
0.00	0.06	0.14	0.05							0.85	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.78	0.18	4484.27	5.23	0.00
0.00	0.06	0.13	0.05					-0.11	0.06	0.85	0.18	-0.05	0.07	0.04	0.05	0.05	0.06	-0.79	0.19	4484.30	5.26	0.00
0.01	0.06	0.17	0.05			-0.06	0.05			0.91	0.16	-0.06	0.07	0.05	0.05	0.05	0.06	-0.86	0.17	4484.32	5.27	0.00
-0.04	0.06					-0.06	0.05	-0.12	0.06	0.90	0.18	-0.02	0.06	0.06	0.05	0.04	0.06	-0.83	0.19	4484.33	5.28	0.00
-0.02	0.06	0.15	0.06					-0.10	0.06	0.88	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.81	0.18	4484.34	5.29	0.00
-0.01	0.06	0.12	0.05			-0.06	0.05	-0.11	0.06	0.88	0.18	-0.01	0.06	0.06	0.05	0.05	0.07	-0.81	0.19	4484.34	5.29	0.00
										0.96	0.18	-0.01	0.06	0.06	0.05	0.04	0.06	-0.91	0.19	4484.34	5.30	0.00
-0.01	0.06	0.13	0.05			-0.06	0.05	-0.10	0.06	0.85	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.78	0.18	4484.34	5.30	0.00
-0.01	0.06	0.15	0.05			-0.06	0.05	-0.10	0.06	0.88	0.17	-0.01	0.06	0.07	0.05	0.05	0.06	-0.81	0.18	4484.37	5.32	0.00
0.00	0.06	0.19	0.07	0.12	0.07			-0.11	0.06	0.90	0.17	-0.05	0.07	0.03	0.05	0.05	0.07	-0.84	0.18	4484.37	5.33	0.00
0.00	0.06	0.17	0.07	0.10	0.07			-0.11	0.06	0.77	0.16	-0.06	0.07	0.04	0.05	0.05	0.06	-0.70	0.17	4484.38	5.34	0.00
-0.03	0.06	0.10	0.05					-0.11	0.06	0.93	0.18	-0.01	0.06	0.05	0.05	0.05	0.07	-0.87	0.19	4484.38	5.34	0.00
0.00	0.06	0.18	0.07	0.12	0.07	-0.06	0.05	-0.11	0.06	0.92	0.17	-0.01	0.06	0.05	0.05	0.04	0.07	-0.86	0.19	4484.42	5.37	0.00
0.03	0.06	0.25	0.07	0.13	0.07	-0.06	0.05			0.90	0.16	-0.05	0.07	0.04	0.05	0.04	0.06	-0.85	0.17	4484.42	5.38	0.00
-0.01	0.06	0.15	0.06			-0.07	0.05	-0.10	0.06	0.88	0.17	-0.06	0.07	0.05	0.05	0.05	0.06	-0.83	0.18	4484.43	5.39	0.00
0.00	0.06	0.16	0.05					-0.10	0.06	0.85	0.17	-0.05	0.07	0.05	0.05	0.05	0.06	-0.78	0.18	4484.45	5.41	0.00
-0.03	0.06	0.13	0.05					-0.10	0.06	0.95	0.17	-0.02	0.06	0.06	0.05	0.05	0.07	-0.89	0.18	4484.47	5.43	0.00
0.01	0.06	0.22	0.07	0.13	0.07	-0.07	0.05	-0.09	0.06	0.91	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.85	0.18	4484.49	5.44	0.00
-0.02	0.06	0.11	0.05					-0.11	0.06	0.78	0.16	-0.06	0.07	0.04	0.05	0.05	0.06	-0.70	0.17	4484.49	5.45	0.00
0.01	0.06	0.16	0.05			-0.06	0.05			0.90	0.16	-0.06	0.07	0.05	0.05	0.05	0.06	-0.84	0.17	4484.51	5.47	0.00
0.00	0.06	0.13	0.05							0.91	0.17	-0.05	0.07	0.04	0.05	0.05	0.06	-0.85	0.18	4484.52	5.48	0.00
0.00	0.06	0.13	0.05							0.88	0.18	-0.01	0.06	0.06	0.05	0.05	0.06	-0.81	0.19	4484.54	5.49	0.00
0.00	0.06	0.19	0.07	0.12	0.07	-0.06	0.05	-0.10	0.06	0.88	0.17	-0.01	0.06	0.06	0.05	0.05	0.06	-0.81	0.18	4484.56	5.52	0.00

## Appendix S4

### Supporting Information for Chapter 7

#### Analysis of Baboon Intake Rates

Intake rates recorded during foraging behaviour focals ( $n = 301$ , mean  $\pm$  s.d. of  $12 \pm 4$  per adult female) were analysed using a generalised linear mixed model with patch species and food density (items/m<sup>2</sup>) as fixed effects. Intake rates were overdispersed and so the model was fitted with an observation level random intercept and lognormal-Poisson error structure with a logit link function. Focal ID, nested within troop ID, were also included as random intercepts. This showed (Table S4.1), as in Chapter 6, that intake rates were independent of patch quality.

Table S4.1. The effect ( $\beta \pm$  s.e.) of patch food density (items/m<sup>2</sup>) and species on intake rate (bites per ten seconds).

	$\beta$	s.e.	z	p
Intercept	1.46	0.39	3.71	<0.001
Food density	$-9.43 \times 10^{-6}$	$3.30 \times 10^{-4}$	0.03	0.98
Patch species <sup>a</sup> :				
<i>Faidherbia albida</i>	0.52	0.41	1.26	0.21
Herb/shrub	0.61	0.39	1.54	0.12
<i>Prosopis glandulosa</i>	0.39	0.40	0.96	0.34
<i>Salvadora persica</i>	0.21	0.41	0.53	0.60
<i>Acacia tortilis</i>	-0.74	0.87	0.85	0.39

<sup>a</sup>reference category: *A. erioloba*