

**The evolutionary ecology of animal
information use and social dominance**

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Abstract

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Organisms are frequently faced with uncertainty regarding how best to exploit vital resources, and may benefit from collecting information about their distribution through space and time. However, the ways in which competition over resources might systematically facilitate or constrain an individual's ability to use information has been largely overlooked. In this thesis, I develop a conceptual framework for considering how the distribution of limited resources might underpin interdependencies between competition and information use. I focus on the evolutionary ecology of relationships between social dominance and social information use. I begin with an observational study of wild chacma baboons (*Papio ursinus*) suggesting that, when resources can be monopolised, individuals with low competitive ability are limited in their ability to use social information. Building on these findings, I then develop a general model exploring selection on social information use in a competitive context across three axes of 'resource ecology' (scarcity, depletion rate, monopolisability). This study makes predictions regarding the resource conditions under which competitive ability might constrain social information use, and the potential importance of social information use in the evolution of social dominance. I go on to test these predictions in chacma baboons using a field experiment. This experiment also explores whether the predictability of resource distribution might facilitate the decoupling of social information use from the competitive context in which it was collected. Taken together, these findings provide general insights into the combinations of ecological conditions and behavioural mechanisms that should underpin the benefits of social dominance. I end by building a simple population matrix model to study social dominance using an eco-evolutionary approach, in which feedback loops between ecological and evolutionary processes are considered. By modelling relationships between dominance rank and survival, reproduction, inheritance, and development, I am able to derive estimates of long-term fitness associated with dominance. Using these estimates, I generate predictions regarding how dominance hierarchies should impact the dynamics of group stability, viability, and fission.

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Chapter 1

Introduction

There is a growing interest in how the predictability of environments through space and time can shape organismal evolution, in particular the degree to which individuals are adapted to respond plastically to their environment (Jablonka *et al.* 1995; Wolf *et al.* 2008; Chevin *et al.* 2010; Dingemanse *et al.* 2010; Botero *et al.* 2015). In the short term, individuals may be able to collect information to reduce their uncertainty about the distribution of resources – such as mates, food, territories, and safety from predation – that are essential for survival and reproduction (Dall & Johnstone 2002; McNamara *et al.* 2006; Valone 2006). Such flexibility at the level of behaviour has been termed animal information use (Danchin *et al.* 2004; Dall *et al.* 2005), and is expected to evolve only when the improved decision-making resulting from uncertainty reduction outweighs the costs of information collection (DeWitt *et al.* 1998; McNamara & Dall 2010).

The fact that information use has been shown to be both taxonomically widespread and a common feature of the acquisition of many different types of resource (Danchin *et al.* 2004; Dall *et al.* 2005; Valone 2006, 2007; Grüter & Leadbeater 2014) indicates that resources are, in general, heterogeneously distributed through space and time. However, spatiotemporal heterogeneity in distribution is also a characteristic of resource limitation, which drives the competition between individuals that is fundamental to the evolutionary process (MacArthur 1962; Roughgarden 1971; Metcalf & Pavard 2007; Smallegange & Coulson 2013). We may thus expect individual information use to be tied up with competitive processes, and that resource distribution may modulate interdependencies between the two.

Despite a general realisation that contexts in which collecting information is useful will usually open up the opportunity for social exploitation (Barnard & Sibly 1981; Barnard 1984; Giraldeau & Dubois 2008; Rendell *et al.* 2010), a more fundamental relationship between competition over resources and information use has been largely overlooked. How might competitive processes result in between-individual differences in the benefits that can be gained from using information? How will such differences affect population-level processes and evolutionary dynamics? The aim of this thesis is to develop a conceptual framework – using a combination of empirical and theoretical approaches – in which resource distribution, and the competitive pressures that result, are considered as playing a key role in the evolutionary ecology of animal information use. Within this framework, the particular focus is on the ways in which contest competition might facilitate or constrain individuals in their ability to use information based on their social dominance, and the consequences that such between-individual differences in information use might have for the evolution of social systems. Such an approach may improve our understanding of the evolutionary and ecological causes and consequences of variation in information use across taxa.

In this introductory section, I begin with an outline of the study of animal information use, in particular the distinction made between personally and socially acquired information. I go on to consider the important role that competition over resources might play in the evolutionary ecology of animal information use. I then explore how such competition may lead to between-individual differences in

information use that are relevant to the evolutionary ecology of social dominance.

To conclude, I outline the thesis structure.

Personal versus social information

There are two distinct channels through which an individual can gather novel information. First, information can be collected personally, by interacting directly with the environment through sensory assessments such as the detection of visual cues or trial-and-error sampling. Second, an individual can collect information socially, by observing the behaviours of others (Valone & Templeton 2002; Danchin *et al.* 2004). Collecting and using social information has generally been viewed as a cheaper alternative to collecting and using personal information (Barnard 1984; Clark & Mangel 1984). Personally sampling a heterogeneous environment may involve long, energetically demanding search times, or require risk-taking that can directly impact the probability of survival or recruitment. For instance, consuming novel food items may have toxic consequences, or trial-and-error sampling of different breeding sites might lower lifetime reproductive success. An individual may be able to reduce or bypass these costs by exploiting the search efforts of others (Boyd & Richerson 1985; Danchin *et al.* 2004; Laland 2004; King & Cowlshaw 2007). For example, northern wheatears (*Oenanthe oenanthe*) have been shown to assess the quality of a territory by collecting social information about the previous breeding success of conspecifics, in addition to other environmental variables (Pärt *et al.* 2011).

There is some empirical evidence that individuals perceive the personal sampling of unknown environments as more costly or risky than relying on social information. Kendal et al. (2004) showed experimentally that when individual guppies (*Poecilia reticulata*) had no prior information during foraging, they would forgo the collection of personal information, favouring social cues instead. This result was in contrast to control conditions in which the guppies were provided with prior personal information, and would ignore conflicting social information. Additionally, Carter et al. (2013) found that when reliable visual cues were absent from food patches, bold and shy chacma baboons (*Papio ursinus*) would favour personal and social information, respectively. These findings support theoretical work suggesting that social information use could act as a risk-averse behavioural strategy (Giraldeau & Caraco 2000).

While collecting social information may be less costly or risky than collecting personal information, relying on it indiscriminately is unlikely to be adaptive. This is because socially acquired information may be of lower quality than personal information, or may rapidly become out-dated (Boyd & Richerson 1985; Kameda & Nakanishi 2002). Whether individuals should preferentially rely on either personal or social information has thus been suggested to be determined by trade-offs regarding the costs associated with collecting each source, and the benefits associated with how the uncertainty reduction resulting from such collection improves decision-making (Kendal *et al.* 2004, 2009b; Rieucou & Giraldeau 2011). Nonetheless, it is clear that social information use is a common and widespread phenomenon. Individuals have been shown to use social information when making decisions

involving foraging (e.g., Rosa *et al.* 2012), mating (e.g., Mery *et al.* 2009), breeding site selection (e.g., Doligez *et al.* 2002), territory selection (e.g., Pärt *et al.* 2011), navigation (e.g., Pettit *et al.* 2013), predator avoidance (e.g., Cresswell *et al.* 2000), and tool-use development (e.g., Biro *et al.* 2003). Such studies have been taxonomically diverse, involving fish (Coolen *et al.* 2003; Kendal *et al.* 2004, 2009a), birds (Doligez *et al.* 2002; Betts *et al.* 2008; Rosa *et al.* 2012), humans and other mammals (Thornton & Clutton-Brock 2011; Derex *et al.* 2013b; van de Waal *et al.* 2013), and insects (Mery *et al.* 2009; Grüter & Leadbeater 2014) at the very least.

Social information use and competition over resources

Intense research into social information use over the past decade has increasingly focussed on the concept of social learning (Hoppitt & Laland 2013), characterised by the social transmission of behavioural innovations between individuals. This has led to major advances in a suite of areas, including our understanding of the development of behavioural repertoires in young individuals (Thornton & Clutton-Brock 2011), the emergence and spread of novel behavioural traits through social networks in groups and populations (Franz & Nunn 2009; Allen *et al.* 2013), the mechanisms and cognitive underpinnings of behaviours involving copying or conformity (Hoppitt & Laland 2013; van de Waal *et al.* 2013), and the role of cultural inheritance in the evolutionary process (Enquist *et al.* 2010; Danchin *et al.* 2011; Whiten *et al.* 2011). However, much of the study of social learning has become abstracted from the competitive environment in which it, and its phenotypic underpinnings, must have evolved and will continue to be maintained. For instance, the concept of social learning strategies has provided insight into how individuals

might use rules to adaptively balance their use of personal versus social information when learning about their environment (Laland 2004; Kendal *et al.* 2005, 2009b; Valone 2007), yet the majority of experimental studies in this field have done so outside of a competitive, social context (see Kendal *et al.* 2009b). Such an approach overlooks the fundamental role that competition has in the evolutionary process, and in shaping animal behaviour as a consequence. The ability to respond to socially generated information will only evolve if individuals with this trait outcompete those without it. Since the utility of information is in its reduction of environmental uncertainty, its prevalence should reflect an improved efficiency of resource exploitation (e.g., rate of acquisition or quality of decision-making) that enhances individual fitness relative to competitors.

Competition over resources was a central theme of the earliest studies in animal information use. The idea that animals might collect information to reduce environmental uncertainty first emerged in the foraging literature, as a response to the traditional assumption that animals behave as if they have perfect knowledge of their environment (Charnov 1976; Pyke *et al.* 1977; Pyke 1984; Stephens & Krebs 1986). In a more social context, ideal free distribution theory was developed to describe how individuals should optimally spread across heterogeneously distributed resources (Fretwell & Lucas 1970; Fretwell 1972). However, researchers realised that if individuals instead face uncertainty regarding resource distributions, social environments should provide opportunities for individuals to exploit the information generated by competitors. The study of social information use that followed quickly split into two types, based on two distinct game-theoretic frameworks. In the first,

social information represents a sharing of information between individuals that doesn't impair an individual's ability to collect personal information (Clark & Mangel 1984). This 'information-sharing' model has mutualistic effects such that individuals able to use social information outcompete competitors unable to do so (Clark & Mangel 1984). In the second, collecting personal and social information represents mutually exclusive tactics, termed 'producer' and 'scrounger', respectively (Barnard & Sibly 1981). In this 'producer-scrounger' model, producers 'work' to discover resources while scroungers exploit this work, such that social information use represents a parasitic, or 'cheater', tactic. As such, scrounging behaviour can invade a population of producers by avoiding the costs of personal information collection while reaping the resource-based benefits. However, since its competitive advantages over producers rely on the presence of producers, scrounging shows negative frequency-dependent payoffs, its relative benefits decreasing as it spreads through a group until both tactics receive equal payoffs (Barnard & Sibly 1981). At this equilibrium, a group is expected to exhibit a stable mixture of producing and scrounging behaviours.

In the context of social foraging, there has been a protracted debate regarding the relative merits of the information-sharing versus the producer-scrounger framework, fuelled by the fundamental differences in their predicted outcomes at the population level (Beauchamp & Giraldeau 1996; Giraldeau & Beauchamp 1999; Giraldeau & Caraco 2000). A long-held view is that the per capita rate of food consumption in a population will be directly proportional to its per capita growth rate, and the mutualistic basis of the information-sharing framework and parasitic

basis of the producer-scrounger framework is predicted to increase or decrease per capita consumption rates, respectively (Clark & Mangel 1984; Beauchamp & Giraldeau 1996; Giraldeau & Caraco 2000; Coolen *et al.* 2007). However, there is no empirical evidence supporting an effect of either type of process on average individual survival or reproduction. Furthermore, it is not clear whether differences in the two models' assumptions will translate to comparable population-level consequences when considering the acquisition of resources other than food. What is clear, yet overlooked, is the presence of important commonalities between information-sharing and producer-scrounger frameworks. First, that the utility of information will be closely tied to its effect on the acquisition of resources that affect individual survival and reproduction. Second, that social information is cheaper to collect than personal information. Third, that any improvement in resource acquisition achieved through social information use will also involve some competition between individuals. These commonalities highlight the importance of studying social information use in a competitive, social context.

Despite such early links between competition over resources and social information use, there has been little development of a conceptual or theoretical framework that considers competitive processes more systematically in the evolutionary ecology of animal information use. This likely reflects the widespread idea that information is shareable and replicable in a way that resources are not (Lachmann *et al.* 2000). Such a distinction may lead to an intuition that information should not be subject to competitive pressures, because the number or identity of individuals possessing information should have no impact on its content or ability to be transmitted.

However, this intuition may not hold if the advantages associated with information relate to the acquisition of resources over which individuals are in competition. For example, while information may be very easily transmitted without depletion, the benefits associated with its use may still be dependent on the distribution and limitation of the resource about which it is informative, and so the strength and nature of competition between individuals that arises as a consequence. This process could be seen as analogous to the importance of context in the evolutionary dynamics of genetic information: transmission from parent to offspring may occur with fidelity, but the conferred fitness benefits will depend on the genotype of the offspring (i.e., epistasis) as well as the distribution of competing genotypes (or phenotypes) in the population.

The producer-scrounger model provides a useful starting point for considering the interplay between information about resources and competition over resources – although this interplay has rarely been mentioned or explored. In fact, the links between scrounging behaviour and social information use have become increasingly unclear (Giraldeau & Dubois 2008), and some studies use the two terms interchangeably while others will use only one or the other depending on whether the research focus is resource competition or information use. However, the producer-scrounger model is an explicitly information-driven game in which individuals scramble for limited resources under uncertainty (Vickery *et al.* 1991; Giraldeau & Caraco 2000). Uncertainty is modelled such that collecting social information is more efficient than collecting personal information in terms of rate of resource discovery: scroungers access all resource discoveries. While producers have

to share their resource discovery with scroungers, they gain some advantage before the arrival of scroungers. In the producer-scrounger model, scrounging thus simultaneously represents social information use and a competitive social interaction at a resource discovery, and all predictions that follow from the theory will apply to conditions where this is true. Consistent with this, experimental studies of producer-scrounger dynamics often involve resource environments that have been designed to maintain the link between scrounging interactions and social information use (Beauchamp & Giraldeau 1997; Mottley & Giraldeau 2000; David *et al.* 2011; Morand-Ferron *et al.* 2011a). For example, David *et al.* (2011) recorded individual scrounging behaviour in a foraging grid as a proxy for social information use when investigating the relationship between exploratory behaviour and social information use in zebra finches (*Taeniopygia guttata*). The accuracy of this proxy was maintained because the birds were faced with randomly distributed, concealed food patches that were depleted in the short-term (i.e., ephemeral), such that individuals' uncertainty levels remained high through time, and collecting and using social information was more efficient than trial-and-error sampling. Future conceptual and theoretical developments should consider in more detail how resource distribution might strengthen or weaken linkages between social information use and competitive interaction. The better characterisation of the fundamental relationship between information and resource that will follow should help to advance our understanding of the evolutionary and ecological causes and consequences of animal information use.

Social information use and dominance

If competition plays an important role in animal information use, it follows that there may be important and general links between social information use and social dominance. Dominance interactions occur when asymmetries in competitive ability between individuals result in asymmetries in access to resources through monopolisation (also termed ‘contest’ competition). Such directed suppression of competitors’ access to resources is distinct from ‘scramble’ competition, in which the competitive pressures of resource depletion are experienced by all individuals (Nicholson 1954; Sutherland & Parker 1992; Łomnicki 2009). Within the context of scramble competition, ‘interference’ competition may occur when individuals differ in the efficiency with which they can exploit resources (Parker 2000). While the distinction between interference and contest competition has not been clearly defined in the literature, here I use the term contest to refer to competitive processes in which inequity in access to resources is driven by some form of behavioural or physiological suppression of subordinate competitors by dominant ones, regardless of any differences in exploitation efficiency *per se*.

Contest competition is biologically significant as it gives rise to hierarchical dominance structures in groups or populations, which can range from despotic to near-egalitarian, can be relatively steep or shallow, can be stable or unstable, and can be transitive or non-transitive (Farentinos 1972; Bernstein 1981; Kaufmann 1983; Vehrencamp 1983; Hemelrijk 1999; de Vries *et al.* 2005; Stevens *et al.* 2007; Broom *et al.* 2009; Norscia & Palagi 2015). Dominance asymmetries or hierarchies are taxonomically widespread and ecologically common, observed across all types of

social organisation from solitary living (Kaufmann 1983; Moore 1990; Piper *et al.* 2000), through fission-fusion and stable social groups (Kappeler & van Schaik 2002; Aureli *et al.* 2008; Smith *et al.* 2008), to cooperative breeding and eusociality (Creel *et al.* 1992; Abbott 1993; Keller & Reeve 1994; Clarke & Faulkes 1997; Clutton-Brock *et al.* 2001; Clutton-Brock 2002). A fundamental prerequisite for the maintenance of dominance asymmetries is that dominant competitors gain fitness benefits in a way that negatively impacts the fitness of subordinate competitors (Nicholson 1954; Łomnicki 2009). Empirical studies have generally supported this logic (Ellis 1995). For instance, dominant female meerkats (*Suricata suricatta*) monopolise access to mates within groups (Clutton-Brock *et al.* 2001), developing a suite of morphological, physiological, and behavioural traits to suppress competitors (Clutton-Brock *et al.* 2006). The rare cases in which dominance seems not to confer fitness benefits might represent contexts where life-history trade-offs have emerged due to costs associated with dominance (e.g., Packer *et al.* 1995; Frank *et al.* 2002; Muehlenbein & Watts 2010), or traits associated with subordinate phenotypes have evolved to reduce the strength of contest competition (e.g., Smith *et al.* 2007).

Ideal free distribution and resource defence studies have long realised the basic importance of unequal competitors and resource distribution in dominance interactions. In addition to a range of other theoretical and empirical work (Parker & Sutherland 1986; Theimer 1987; Grant 1993; Grant & Guha 1993), Vahl *et al.* (2005) showed experimentally that dominant ruddy turnstones (*Arenaria interpres*) had a higher foraging success than subordinates only when food resources were spatially clumped. In contrast, research into social information use has generally only

considered social dominance as a potential correlate of social information use (Beauchamp 2006; McCormack *et al.* 2007; King *et al.* 2009; Morand-Ferron *et al.* 2011b). The consequence has been a lack of clarity regarding the role of social dominance in animal information use and its evolutionary and ecological consequences, with a range of empirical producer-scrounger studies reporting either a positive relationship or no relationship between dominance and scrounging, but no systematic attempt to determine why (Giraldeau & Dubois 2008). However, a small body of theoretical research has explored how social dominance might systematically influence social information use when individuals must search for resources (Ranta *et al.* 1993; Barta & Giraldeau 1998; Dubois & Giraldeau 2005). In particular, Barta and Giraldeau (1998) predicted a positive relationship between dominance rank, scrounging behaviour, and resource monopolisation. Differences in competitive ability may thus lead to between-individual differences in the benefits of using social information, regardless of how easy this information is to collect.

Individual variation in the ability to reap benefits from social information as a result of competitive asymmetries may have important evolutionary implications both at the individual and population level. For example, social constraints on social information use due to low dominance rank may impede the flow of information through a group or population, and could influence the spread of fitness-enhancing behavioural innovations (Whiten *et al.* 2011; Hoppitt & Laland 2013) as a consequence. Similarly, social information use may be important in the evolution of dominance if uncertainty associated with a given resource's distribution means that contest competition over that resource can only occur through the use of social

information. Thus, in some cases, the individual benefits of dominance may be dependent on social information use in conjunction with the ability to monopolise resources. A full understanding of both the evolutionary ecology of animal information use and social dominance will require more formal characterisation of how resource distribution can drive interdependencies between the benefits of using social information and the competitive regimes between individuals.

Thesis structure

Following from the background provided above, and the ideas and challenges outlined therein, the aim of this thesis is to develop a conceptual and theoretical framework for studying animal information use. This framework will explicitly provide a fundamental role for resource distribution in simultaneously driving competitive pressures between individuals and the costs and benefits associated with using different types of information. Within this framework, the main focus will be on the interdependencies that may be required between social information use and social dominance interactions in order for contest competition to occur, and the evolutionary and population dynamic consequences that might follow.

The main thesis is structured into four analytical chapters, each presented in the style of a journal article and intended for independent publication. This begins with *Chapter 2*, which is an observational study of the natural social foraging behaviour of a wild population of chacma baboons. The purpose of this study is to explore whether resource monopolisability influences the relationship between social dominance and scrounging behaviour, as predicted theoretically by Barta and

Giraldeau (1998). In doing so, however, the study highlights some of the key issues associated with the producer-scrouter framework with regards to the relationships between resource distribution, the benefits of personal versus social information use, and competition between individuals. These issues are discussed at the end of this study, before being addressed in the two chapters that follow.

In *Chapter 3*, I present a game-theoretic model which expands the producer-scrouter framework to make it applicable to a broad diversity of ecological conditions. In doing so, I highlight the general relationship between information about resources and competition over resources that is at the heart of the producer-scrouter framework. This provides insight into the resource distributions that should promote contest competition and the important interdependencies between dominance and social information use that might ensue.

Chapter 4 is a field experiment conducted to test some of the predictions generated by the model presented in the preceding chapter. Wild chacma baboons were provided with novel feeding environments in order to test whether dominant individuals used social information to maximise their foraging success at the expense of subordinates, leading to intense contest competition, when faced with environmental uncertainty. This experiment also allowed exploration of the ways in which the predictability of resource distribution through time and space might alter the relationships between information and resource in a way that relaxes or strengthens the competitive constraints on an individual's ability to use information.

In *Chapter 5*, the final analytical chapter, I present a demographic model designed to explore the complexities of the evolutionary dynamics of social dominance. While the preceding chapters investigated the behavioural processes and ecological conditions that might underpin the phenomenon of social dominance, this model provides insight into their population-level consequences. Specifically, the model employs an eco-evolutionary approach to the study of contest competition, which suggests important implications for the ecological and evolutionary consequences of social dominance.

I conclude with *Chapter 6*, in which I highlight the key insights generated in the four analytical chapters, identify how these insights combine to begin to address the challenges outlined in this Introduction, and propose possible avenues for the continued development of a systematic framework for understanding animal information use, social dominance, and the interactions between the two.

Chapter 2

Switching spatial scale reveals dominance-dependent social foraging tactics in a wild primate

A version of this chapter is in review as follows:

Lee, A. E. G. & Cowlshaw, G. In review. Switching spatial scale reveals dominance-dependent social foraging tactics in a wild primate. *Animal Behaviour*.

Abstract

When foraging in a social group, individuals are faced with the choice of either sampling their environment directly or exploiting the discoveries of others. The evolutionary dynamics of this trade-off have been explored mathematically through the producer-scrounger game, which has highlighted socially exploitative behaviours as a major potential cost of group living. However, relatively little attention has been given to the tight interplay that may exist between social dominance and scrounging behaviour. To date, only one theoretical study has explored this relationship, demonstrating that scrounging should become exclusive to high-ranking individuals only when resources are monopolisable. In this study, we explore the predictions of this model through observations of the natural social foraging behaviour of a wild population of chacma baboons (*Papio ursinus*). We collected data through over 800 hours of focal follows of 101 adults and juveniles across two troops over two 3-month periods. By recording over 7,900 producer-scrounger decisions at two spatial scales – the ‘patch’ and the ‘sub-patch’ – we show that, when resources are large and economically indefensible, scrounging behaviour is common across all social ranks. When, in contrast, dominant individuals can aggressively appropriate a resource, the scrounger tactic becomes increasingly rare with decreasing social rank. Specifically, we demonstrate that, under these conditions, adult baboons can only exploit individuals lower ranking than themselves. Our study highlights potentially important individual constraints on the ability to use social information associated with low social rank, driven by competition with dominant conspecifics over monopolisable resources.

Introduction

The study of socially exploitative behaviour, in which individuals make use of the resources of competitors, has been the focus of much theoretical and empirical research over recent decades (Giraldeau & Dubois 2008), and represents one of the major potential costs of group living. Because resources such as food, mates, breeding territories, or safety from predation generally show variation in their distribution through space or time, individuals should benefit from gathering information about their local environment to improve decision-making (Valone 1989, 2006; McNamara *et al.* 2006). However, since doing so requires search effort, selection should favour the avoidance of these costs by exploiting the efforts of others in a social group (for review see Valone & Templeton 2002; Danchin *et al.* 2004; Rieucou & Giraldeau 2011).

The dynamics of these interactions have been formalised as the producer-scrounger game (Barnard & Sibly 1981; Barnard 1984; Vickery *et al.* 1991), which has, with some empirical support (e.g., Koops & Giraldeau 1996; Mottley & Giraldeau 2000; Morand-Ferron *et al.* 2007), emerged as the prevailing theoretical framework in which to study social foraging decisions (Vickery *et al.* 1991; Giraldeau & Caraco 2000). In this game, producers actively search for resources, while scroungers exploit the discoveries of producers. The two tactics are considered mutually exclusive. Scrounging – analogous with ‘cheater’ tactics seen in studies of cooperation (Rankin *et al.* 2007) – is thus under negatively frequency-dependent selection, since its success is dependent on the efforts of producers. This dynamic is expected to lead populations to an evolutionarily or behaviourally stable mix of producing and

scrounging (Giraldeau & Dubois 2008; Fawcett *et al.* 2013). As such, scrounging behaviour has the potential to reduce the per capita rate of resource discovery (Vickery *et al.* 1991), which may act to reduce average individual fitness in a population (Coolen *et al.* 2007).

However, the basic producer-scrounger model assumes that an individual's phenotype has no influence on its decision or ability to play either tactic. As such, all individuals are expected to receive equal payoffs. Yet many empirical studies have shown that an individual's tactic choice may be strongly influenced or constrained by its phenotype (e.g., Beauchamp 2001; di Bitetti & Janson 2001; Stahl *et al.* 2001; Kurvers *et al.* 2010). This has potentially important fitness implications, since theory predicts that phenotype-limited games may not reach an evolutionarily stable mix of strategies, resulting in differential payoffs across individuals (Parker 1982).

Since scrounging behaviour represents the exploitation of another's resource, one might expect social dominance to play an important role in scrounging behaviour, as the competitive advantage of high-ranking individuals should allow them to scrounge from others more easily. Despite this expectation, empirical studies have not been unanimous: while some experiments have demonstrated a relationship between social dominance and scrounging behaviour (Stahl *et al.* 2001; Liker & Barta 2002; Lendvai *et al.* 2006; McCormack *et al.* 2007), other studies have found no link between the two (Robinette Ha & Ha 2003; Beauchamp 2006). This conflict might be reconciled by considering more systematically the spatiotemporal distribution of resources in an individual's environment. The competitive benefits of social

dominance are expected to be associated with priority of access to resources, manifest as contest competition (Kaufmann 1983; Łomnicki 2009). Consistent with this, resource defence theory predicts that individuals should be more aggressive when defending a resource in accordance with both its value and its economic defensibility (Grant 1993; Grant & Guha 1993; Robb & Grant 1998). Empirical studies into dominance and resource defence have demonstrated higher foraging success for socially dominant individuals only when limited food patches are monopolisable (Theimer 1987; Vahl *et al.* 2005).

The integration of producer-scrounger and resource defence theory might elucidate an interesting relationship between socially exploitative behaviour and contest competition (Barta & Giraldeau 1998; Giraldeau & Dubois 2008). Specifically, dominant individuals should benefit disproportionately if they can use their competitive advantage to ensure that only they can use the scrounger tactic effectively. Barta & Giraldeau (1998) explored this hypothesis by modelling the effects of between-individual asymmetries in competitive ability on producer-scrounger dynamics in a group. They found that when social rank conferred no competitive advantage to an individual – that is, resources were not monopolisable – groups converged on basic producer-scrounger equilibria in which all individuals behave equivalently and receive equal payoffs. In contrast, when individuals could use their social rank to gain a competitive advantage in monopolising a resource, scrounging behaviour was strongly associated with dominance, and dominant individuals achieved the highest payoffs (Barta & Giraldeau 1998). However, to date

there has been no attempt to test these predictions empirically, either in the laboratory or under natural conditions.

In this study, we present the first attempt to explore a key prediction generated by the unification of producer-scrounger and resource defence theories, namely that there should be a strong link between social dominance and the scrounger tactic – defined here as joining a resource being utilised by a competitor – only when resources are monopolisable. We do this by studying the natural social foraging decisions made by wild chacma baboons (*Papio ursinus*) across two spatial scales that are expected to differ in the degree to which dominant individuals can monopolise food: the patch and the sub-patch. Specifically, we asked three questions: 1) How does the relationship between scrounging and social dominance rank change across spatial scales? 2) What is the difference in dominance rank between scroungers and the individuals they exploit at each spatial scale? 3) How does the frequency of competitive exclusion associated with scrounging change between spatial scales?

Materials and Methods

Study Site and Species

Fieldwork was conducted at Tsaobis Nature Park, Namibia (22°23'S, 15°45'E), during two three-month periods between August and October in 2012 and 2013. Two groups of chacma baboons, hereafter referred to as troop 'J' (group size: $N_{2012} = 54$; $N_{2013} = 58$) and troop 'L' ($N_{2012} = 51$; $N_{2013} = 62$), were the focus of study. All individuals were individually recognisable and habituated to the presence of

observers at close proximity, and each group was followed daily from dawn until dusk (see Huchard *et al.* 2009 for further information). For each year, data were collected for all individual baboons >6 months of age (the age at which young baboons begin to forage independently of their mother) at the start of the study period, resulting in a total sample of 101 individuals (2012: 54 adults, 43 juveniles; 2013: 50 adults, 41 juveniles). Differences in the sample of individuals across years were due to death, emigration, or passing the minimum age threshold.

Chacma baboons are an ideal model system for our study, since they live in large, stable social groups in which linear dominance hierarchies are clear (Altmann & Altmann 1973) and socially exploitative foraging interactions are common (King *et al.* 2009; Marshall *et al.* 2012a). Furthermore, our study troops spent approximately 80% of their foraging time during the study period in a riparian woodland environment, characterised by large trees such as *Faidherbia albida* (see Marshall *et al.* 2012a for further details). Within this feeding environment, we defined two spatial scales between which the ability of dominant individuals to monopolise food were predicted to differ: the patch and the sub-patch.

The patch represents the scale traditionally used in foraging theory and ecology, defined as a spatially discrete unit of a food resource (Wiens 1976). Here, we refined this definition slightly such that the operational definition of a patch was a single tree or shrub, or a collection of conspecifics growing together with a continuous canopy separated by no more than 1 m. In contrast, the sub-patch was defined as the area in a patch within which an individual could feed without travelling (i.e.,

within arm's reach of a stationary baboon). This was equivalent to the 'feeding station' scale that has received some attention in the foraging literature (Kotliar & Wiens 1990; see Searle *et al.* 2005 for a review). Where a patch extended in space beyond the reach of a stationary forager, the sub-patch represented a spatial scale nested within the patch. As such, study at the sub-patch scale captured social foraging dynamics at a resolution higher than at the patch scale. Dominant individuals should be able to competitively exclude competitors more easily at the sub-patch scale compared with the patch scale.

Data Collection and Processing

Information regarding individual social foraging decisions and interactions at each spatial scale was recorded through focal sampling (Altmann 1974) on Motorola ES400 Personal Digital Assistants and Google Nexus 4 Smartphones using a customised data capture application in the database-driven software Cybertracker v.3.317 (<http://cybertracker.org>). Focal follows lasted between 15 and 30 minutes, and the same individual was not studied more than once within a 6-hour period. Individuals were selected for focal observation using a pseudorandom sampling process, which ensured even coverage across different times of day (based on four consecutive 3-hour time blocks from 06:00 to 18:00) and different months.

A patch entry event was recorded whenever the focal individual actively searched for or consumed food in a new patch for 5 seconds or more. Once in a patch, the focal individual could move between sub-patches. A sub-patch entry was recorded when an individual relocated into a new area of a patch to forage, and either

remained stationary for ≥ 5 seconds while standing, or sat for ≥ 1 second, in this location. At each spatial scale, a foraging decision was assigned to every entry event. The decision was defined as 'produce' if the patch or sub-patch being entered was unoccupied, and 'scrounge' if occupied by a conspecific. For each scrounge event, the number and identity of individuals occupying the resource was recorded. In cases where visibility was poor, a minimum number of occupants was estimated and, where known, their identity recorded.

Since the size of a patch is variable, while sub-patch size is fixed, the relationship between them is such that at the smallest, or 'critical', patch size they reach equivalence. With this in mind, social foraging decisions were included only for those where a sub-patch structure could be defined (i.e., where more than one sub-patch was present). This allowed us to avoid conflating processes working at the two different spatial scales. The data were then filtered further to exclude all ambiguous foraging decisions that could not clearly be classified as either produce or scrounge (<10%). A total of 801 focal hours were carried out across the two study periods on 101 individual baboons (mean \pm s.e. = 7.9 ± 0.1 hours per individual), resulting in a dataset of 1861 patch entry and 5050 sub-patch entry decisions for analysis.

A dominance hierarchy was generated for each troop-year combination using pairwise agonistic interactions occurring within each study period. These interactions were collected both during focal follows and through ad libitum sampling, and were used to make actor-receiver matrices indicating the number of agonistic interactions occurring between each dyad in each direction. No dominance interactions occurring

during foraging decisions were included in the matrices. In addition, all interactions involving individuals not yet weaned from their mother were excluded, because dominance asymmetry at this age is strongly influenced by the mother's presence and behaviour (Cheney 1977). Each actor-receiver matrix ($N_{2012,J} = 1010$; $N_{2012,L} = 1025$; $N_{2013,J} = 833$; $N_{2013,L} = 1073$) was reordered using Matman 1.1.4 (Noldus Information Technology 2003), optimised by selecting the hierarchy with the lowest level of conflict (i.e., minimising the number of interactions inconsistent with the predicted hierarchy) using a heuristic search algorithm with ten thousand randomisations. Linearity was supported for all four hierarchies (Landau's corrected linearity index: $h'_{2012,J} = 0.19$; $h'_{2012,L} = 0.32$; $h'_{2013,J} = 0.18$; $h'_{2013,L} = 0.15$, $p < 0.001$ in all cases). Individuals not yet weaned were then re-entered into the appropriate dominance hierarchy based on their maternal rank (i.e., one position below their mother), producing complete hierarchies that included all members of the group for each year. To control for differences in the size of groups within and across years, all absolute ranks (ranging from 1 to n) were standardised to between 0 (lowest rank) and 1 (highest rank) following $1 - ((1-r)/(1-n))$, where r is the absolute rank of an individual.

Statistical analyses

Our analysis was divided into three sections consistent with the three study questions outlined above. First, we used generalised linear mixed-effects modelling (GLMM) to explore how the relationship between social dominance and scrounging behaviour changed across spatial scales due to differences in resource monopolisability. Our prediction was that all individuals would exhibit scrounging

behaviour at the patch scale. In contrast, we predicted that there would be a strong positive relationship between rank and scrounging at the sub-patch scale. However, since juvenile individuals are often tolerated at feeding sites (e.g., Huchard *et al.* 2013), we predicted that this positive relationship would only hold for adults. In order to characterise robustly any interactions between social rank and age at each spatial scale, we analysed patch level and sub-patch level decisions in separate models. In each model, the response variable was given as a binary indicator of the decision at each entry to either ‘produce’ or ‘scrounge’, scored as 0 or 1, respectively. We fit a binomial error structure to the GLMMs. Both models were constructed with an interaction between dominance rank and age class (‘juvenile’ or ‘adult’). A likelihood ratio test was then used to judge whether those models with or without the interaction term provided the better fit to the data, and if the latter, whether those models with or without the main effects of dominance rank and age class provided the better fit. Troop and year were included as control fixed effects, and were thus retained in all models. Focal identity and focal follow number were included as random effects in all models.

Second, we asked whether scrounge ‘events’ were consistently associated with asymmetries in social rank at each spatial scale. We predicted that individuals would consistently scrounge individuals lower ranked than themselves at the sub-patch level, but would scrounge individuals regardless of rank differences at the patch level (i.e., no relationship). Again, we predicted that the relationship at the sub-patch level would not hold for juvenile individuals. We built linear mixed-effects models at each spatial scale with rank difference at each scrounge event as the response variable.

For those events where multiple individuals were scrounged in a patch or sub-patch, their mean rank difference with the focal individual was used. Rank difference was calculated as $\text{Rank}_{\text{Scrounger}} - \text{Rank}_{\text{Scrounged}}$, bounded between -1 and +1, with positive values representing a focal individual scrounging lower ranking individuals, and negative values indicating that the focal individual scrounged higher ranked individuals. Control fixed effects and random effects were included as above.

Third, we built a generalised linear model to establish whether scrounge events at different spatial scales were associated with differences in the competitive exclusion experienced by the scrounged individual. Competitive exclusion was modelled as a binary response variable: individuals were either supplanted from the resource or were not. Spatial scale ('patch' or 'sub-patch') and age class (as above) were included as fixed effects, assessed using likelihood ratio tests. Since these data were not available for patch level decisions in 2012, only decisions from 2013 were used in this analysis. We predicted that scrounging behaviour in adults would cause competitive exclusion of the scrounged individual at the sub-patch but not the patch scale, and that scrounging behaviour in juveniles would result broadly in lower levels of competitive exclusion.

All analyses were conducted in R version 3.0.2. using the lme4 package (Bates *et al.* 2013; R Core Team 2013).

Results

Dominance and producer-scrounger decisions at different spatial scales

At the patch scale, scrounging behaviour was common regardless of social rank (Fig. 1a; Table 1, P_{ps}), consistent with our predictions. Although there was a weak increase in scrounging with social dominance, even the lowest ranked individuals entered occupied patches more than 50% of the time. In addition, there was a general age class effect: regardless of rank, juveniles were approximately 15% more likely than adults to scrounge at the patch scale (Fig. 1a; Table 1, P_{ps}).

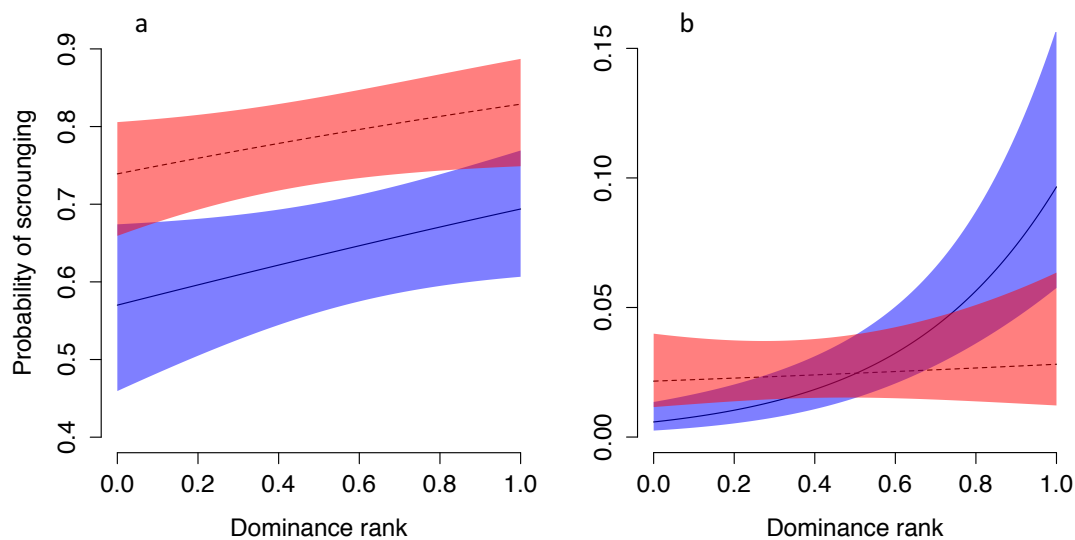


Figure 1. Predicted relationship between the probability of scrounging behaviour and dominance rank at the (a) patch and (b) sub-patch level. For both panels, solid blue and dashed red lines represent predictions for adults and juveniles, respectively. Colour-matched shaded regions are bounded by upper and lower 95% confidence intervals.

Table 1. Factors predicting the probability of scrounging behaviour (p_{ps}) and the dominance asymmetry (r_d) associated with scrounging at different spatial scales: the patch and the sub-patch.

Spatial Scale	Response	N	Fixed Effect	β	s.e.	χ^2	p
Patch (P_{ps})	Probability of scrounging	1861	Intercept	0.40	0.21		
			Rank	0.54	0.28	3.47	0.06
			Age class (Juvenile)	0.76	0.17	18.86	<0.001
			Troop (L)	-0.13	0.15		
			Year (2013)	-0.11	0.14		
			Intercept	0.03	0.05		
			Age class (Juvenile)	-0.16	0.05	10.88	<0.001
			Troop (L)	0.02	0.05		
			Year (2013)	0.03	0.05		
			Intercept	-5.75	0.44		
Sub-patch (SP_{ps})	Probability of scrounging	5050	Intercept	2.90	0.53		
			Rank	1.33	0.45		
			Age class (Juvenile)	0.49	0.19		
			Troop (L)	0.72	0.20		
			Year (2013)	-2.63	0.78	11.74	<0.001
			Intercept	0.26	0.04		
			Age class (Juvenile)	-0.25	0.04	28.16	<0.001
			Troop (L)	-0.01	0.04		
			Year (2013)	0.02	0.04		
			Intercept	-2.26	0.29		
Both (CE)	Probability of competitive exclusion	385	Spatial scale (Sub-patch)	3.61	0.34	174.35	<0.001
			Age class (Juvenile)	-1.32	0.32	18.38	<0.001

For each model, reference categories are as follows: Age Class (Adult), Troop (J), and Year (2012).

At the sub-patch scale, the influence of dominance rank on scrounging was dependent on age class (Fig. 1b; Table 1, SP_{ps}). As predicted, there was a strong positive relationship between social dominance and scrounging for adults. The lowest ranked adults had <1% probability of scrounging when entering a new sub-patch, while mid-ranked and top-ranked adults did so approximately 2.5% and 10% of the time, respectively. In contrast, there was almost no effect of dominance rank on the probability of scrounging at the sub-patch scale for juveniles. The consequence of this was that low-ranked juveniles scrounged more frequently when entering a new sub-patch than similarly ranked adults did, while the pattern was reversed for high-ranked juveniles.

Social constraints on scrounging behaviour at different spatial scales

At the patch scale, adult individuals scrounged from others regardless of any differences in dominance rank (Table 1, P_{rd}). Within this spread, adults most commonly entered patches occupied by those ranging approximately between 18 rank positions below and 11 rank units above them (first and third quantile, respectively; Fig. 2a). In contrast, juveniles generally scrounged from those higher ranking than themselves (Fig. 2a; Table 1, P_{rd}).

At the sub-patch scale, adults scrounged almost exclusively from those to whom they were dominant (Table 1, SP_{rd}), most typically by 6 to 26 rank units (first and third quantile, respectively; Fig. 2b). In contrast, juveniles scrounged equally from those higher and lower ranked than themselves at the sub-patch scale.

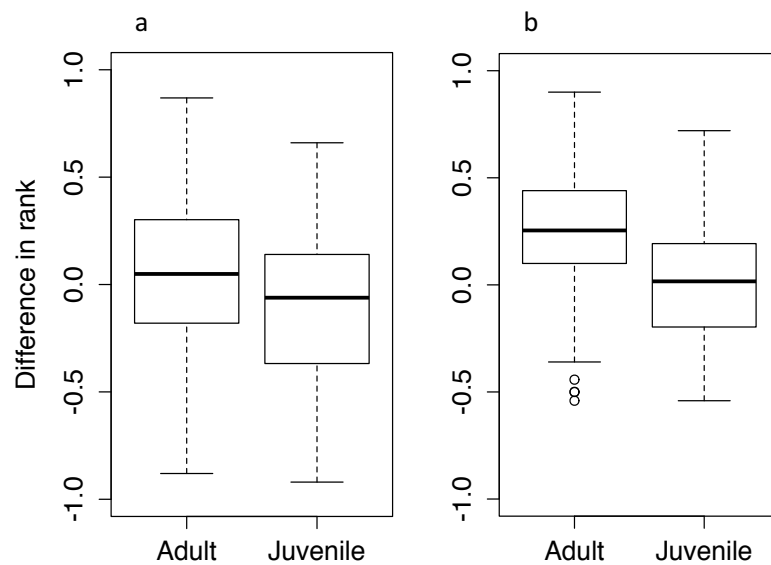


Figure 2. Dominance asymmetry during ‘scrounge’ events at the (a) patch and (b) sub-patch level. Positive values indicate events where the focal individual is dominant to the scrounged individual, while negative values signify the opposite relationship. For each spatial scale, Tukey boxplots are shown both for adult and juvenile focal individuals. Each box is split by the median value, and enclosed by the first and third quartiles; whiskers extend to the most extreme data point which is no greater than 1.5 times the interquartile range from the box edge (any values beyond this extreme are shown as outliers).

Competitive exclusion at different spatial scales

Scrounging caused competitive exclusion at the sub-patch scale much more than it did at the patch scale (Table 1, CE). In adults, scrounging at the patch scale was associated with competitive exclusion in fewer than 10% of cases. This figure increased to over 79% at the sub-patch scale. Scrounging by juveniles was less likely to result in competitive exclusion at both spatial scales (patch: approx. 50%; sub-patch: approx. 2.5%).

Discussion

We provide, to our knowledge, the first empirical support for Barta and Giraldeau's (1998) prediction that scrounging behaviour should be more strongly related to social rank when the competitive asymmetries associated with dominance are stronger. We show that changes in resource monopolisability can mediate this shift in competitive asymmetry through changes in competitive exclusion at different spatial scales. While at the larger patch scale, adults could scrounge from others regardless of their social rank, scrounging at the smaller sub-patch level represented a more exclusive tactic, almost non-existent in the lowest-ranking individuals but increasing in probability with social dominance. When resources are monopolisable, socially subordinate individuals may thus be constrained in their ability to use social information. Since the size of a resource is expected to influence its economic defensibility (Grant 1993), our study supports calls to unify producer-scrounger and resource defence theory in order to better understand the relationship between dominance and socially exploitative behaviours (Barta & Giraldeau 1998; Dubois *et al.* 2003; Dubois & Giraldeau 2005; Giraldeau & Dubois 2008). However, our study also highlights two areas in which our understanding of the evolutionary ecology of animal information use is still lacking, requiring both theoretical and empirical developments.

First, we show an increase in the frequency of scrounging at higher ranks at the sub-patch scale, where single individuals could use their dominance to exclude competitors. However, the pattern we observed was weaker than that predicted by Barta and Giraldeau (1998), who suggested a complete absence of scrounging in all

but the most dominant individuals when resources could be monopolised. We found that even middle- and low-ranking adults can scrounge from others, provided that the others they scrounge from are even lower ranked than themselves. The failure of the producer-scrounger model to predict this pattern likely reflects two of its assumptions. Specifically, the model is built such that any individual playing scrounger can access all the discoveries of others, since (1) resources are assumed to be sufficiently rare that all discoveries occur sequentially and (2) scroungers can access perfect social information and so detect each discovery (Vickery *et al.* 1991b; Giraldeau & Caraco 2000; see Ohtsuka & Toquenaga 2009 for exception). When resources can be monopolised, these conditions mean that only the highest-ranked individuals will benefit from scrounging behaviour. However, in reality many social foragers tend to discover multiple patches at the same time (and this will likely be true for other resources too). As such, scrounging individuals will be unable to access all resource discoveries even if they have perfect social information. Furthermore, since individuals within social groups are unlikely to be in close proximity of each other at all times (see Krause & Ruxton 2002 for a general review; see Castles *et al.* 2014 for characterisation of social networks in these study troops), scrounging individuals are unlikely to possess perfect social information regarding all discoveries occurring at the group level (Barta *et al.* 1997; Hirsch 2007).

Under the conditions of simultaneous discoveries and imperfect access to social information, the most dominant individuals will be unable to monopolise all resource discoveries, regardless of the economic defensibility of single resource patches. Instead, as shown here, the difference in rank between individuals should

play an important role in mediating scrounging behaviour. For instance, if the highest ranking animals do not detect a particular patch discovery, and/or are occupied at another discovery, then middle and lower ranking animals have the freedom to scrounge, provided that the producers from whom they are scrounging are lower ranking than themselves. Individuals may also benefit from positioning themselves in space so as to maximise such scrounging opportunities (Barta *et al.* 1997; di Bitetti & Janson 2001; Hirsch 2007). Our result that scrounging at the sub-patch level still increases with social rank likely reflects the fact that higher ranked individuals have more competitors subordinate to them. The most dominant individual should thus be unconstrained in its ability to act upon opportunities to scrounge, and constraints should increase down the dominance hierarchy. Furthermore, dominant individuals may be able to secure more central positions in the group which, in addition to providing safety from predation, may maximise their probability of detecting the discoveries of others and minimise their average distance from such discoveries (Barta *et al.* 1997; King *et al.* 2009).

Second, we show that the relationship between social dominance and scrounging behaviour at the sub-patch level is strongly influenced by age class. In stark contrast to adults, juvenile baboons showed no general relationship between social dominance and scrounging at this spatial scale. Indeed, juvenile scrounging behaviour accounted for almost all instances where a subordinate joined a higher-ranking individual. There are two likely explanations for this pattern. Firstly, rank acquisition in chacma baboons is mediated primarily through aggressive maternal behaviours that establish a juvenile's dominance to competitors subordinate to its

mother (Cheney 1977; Holekamp & Smale 1991; Lea *et al.* 2014). Consequently, social rank during early life may be particularly vulnerable to context-dependence, such that local maternal absence may permit social interactions between juveniles that are inconsistent with differences in their maternal ranks. Secondly, there is evidence that juvenile baboons, like the juveniles of several other primate species (Janson 1985), are more frequently tolerated at feeding sites than adults. The presence of co-foraging juveniles may impose only a minimal direct cost to adults, but permitting close kin access to resources may provide inclusive fitness benefits. In particular, it has been shown in chacma baboons that father-offspring relationships afford juveniles access to high-quality feeding sites (Huchard *et al.* 2013). Such tolerance may mean that, in addition to better access to monopolisable resources, low-ranked juveniles may not be constrained in their ability to use social information in the same way that similarly ranked adults will be. The near complete lack of competitive exclusion enforced by juvenile scrounging behaviour at the sub-patch scale observed in our study suggests that tolerance was a more important mechanism for allowing juveniles to scrounge up the dominance hierarchy than was the instability of juvenile rank.

Our study demonstrates the way in which the monopolisability of resources may drive social constraints on a subordinate individual's ability to use scrounging behaviour to access them. We also show that such constraints may be relaxed in juveniles, perhaps due to the tolerance of dominant individuals towards them at feeding sites. However, since resources generally show some uncertainty in their distribution through space and time, information use is also likely to play a key role

in resource acquisition. Scrounging behaviour is generally associated with the use of social information, but our study illustrates how competitive processes might facilitate or constrain an individual's ability to benefit from collecting social information when its use requires scrounging behaviour. An important step in future research will be to develop frameworks that consider how resource distributions simultaneously underpin the strength and type of competition between individuals, the benefits of collecting information socially versus personally, and the rate at which such information becomes out-dated. This approach will elucidate the environmental conditions that should generate interdependencies between contest competition and social information use. By better characterising the ways in which competition can modulate relationships between an individual's ability to use information and its access to resources, we should gain an improved understanding of the evolutionary ecology of both animal information use and social dominance.

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Chapter 3

Information use and resource competition: an integrative framework

A version of this chapter is in review as follows:

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Information use and resource competition: an integrative framework. *Proceedings of the Royal Society B: Biological Sciences*.

Abstract

Organisms may reduce uncertainty regarding how best to exploit their environment by collecting information about resource distribution. We develop a model to demonstrate how competition can facilitate or constrain an individual's ability to use information when acquiring resources. Since resource distribution underpins both selection on information use and the strength and nature of competition between individuals, we demonstrate interdependencies between the two that should be common in nature. Individuals in our model can search for resources either personally or by using social information. We explore selection on social information use across a comprehensive range of ecological conditions, generalising the producer-scrounger framework to a wide diversity of taxa and resources. We show that resource ecology – defined by scarcity, depletion rate, and monopolisability – determines patterns of individual differences in social information use. These differences suggest co-evolutionary processes linking dominance systems and social information use, with implications for the evolutionary demography of populations.

Introduction

Organisms must secure resources such as food, mates, and safety from predation to ensure survival and reproduction. Variability in the spatiotemporal distribution of these resources means that individuals face uncertainty regarding how best to exploit them. Individuals can thus acquire resources more efficiently by collecting uncertainty-reducing information (Dall *et al.* 2005; McNamara & Dall 2010).

However, resource distribution also underpins the strength and nature of competition between individuals (Milinski & Parker 1991; Parker 2000; Stillman *et al.* 2000a). Despite this convergence in resource distribution as a selective force, very little is known about how competition might facilitate or constrain information use. In this study, we present a general model to predict how resource competition will affect individual information use across a comprehensive range of ecological conditions, generating novel insights into the behavioural processes underlying the evolution of social systems.

Information can be gathered either personally, by direct interaction with the environment, or socially, by observing the behaviours of others (Danchin *et al.* 2004; Rieucau & Giraldeau 2011). The majority of research into information use has focussed on two key ways that the costs and benefits of ‘personal’ versus ‘social’ information can differ. First, empirical and theoretical studies have shown that if gathering personal information involves long search times, trial-and-error sampling, or risk-taking, collecting social information can reduce these costs by exploiting the efforts of others (Kendal *et al.* 2004; Giraldeau & Dubois 2008; Rendell *et al.* 2010). Second, the usefulness of one type of information over the other will depend on how

rapidly each becomes outdated (Boyd & Richerson 1985; Kameda & Nakanishi 2002; van Bergen *et al.* 2004). The resultant cost/reliability trade-off between personal and social information suggests that selection should favour strategies that balance adaptively an individual's reliance on each source (Kendal *et al.* 2009b; Rieucou & Giraldeau 2011).

Individuals may nonetheless be constrained in their ability to use information due to competition with others over resources, but such interactions have received little attention. An individual may be free to *collect* reliable social information at a relatively low cost, yet its ability to *use* it may be mediated by certain phenotypic factors, such as competitive ability. For example, if food patches or breeding territories are both limited and monopolisable, then the advantages of using social information may be restricted to socially dominant individuals (e.g., Piper *et al.* 2000; Stahl *et al.* 2001; King *et al.* 2009). Since social information has been variously implicated as a regulator of population growth (Coolen *et al.* 2007), a benefit of group living (Clark & Mangel 1984), and a facilitator of learning and culture (Laland 2004; Whiten *et al.* 2011), constraints on its use may have important ecological and evolutionary consequences.

The producer-scrounger model represents a useful game theoretical framework for exploring the influence that competition over resources can have on the evolutionary dynamics of social information use (Barnard 1984; Giraldeau & Dubois 2008). The model considers groups of individuals searching for and consuming discrete resource patches by using either personal information ('producing') or social

information ('scrounging'). When playing 'producer', an individual searches for its own resources; when playing 'scrounger', it looks for and exploits the discoveries of producers (Vickery *et al.* 1991). A well-established insight from producer-scrounger games, relating to one element of resource distribution, is that the 'finder's share' should influence optimal levels of social information use within a group (Barnard & Sibly 1981). When producers can fully deplete a discovery before the arrival of any scroungers – at which point social information becomes outdated – there is no benefit to scrounging behaviour. In contrast, when depletion time is longer, the finder's share is lower, and scrounging becomes more prevalent. Consistent with this, Giraldeau and Livoreil (1998) experimentally demonstrated a positive relationship between the finder's share and scrounging behaviour in nutmeg mannikins (*Lonchura punctulata*).

Two further elements of resource distribution can readily be incorporated into producer-scrounger games, but have received limited attention. First, almost all producer-scrounger models assume that resources are so hard to find that they are only discovered singly and successively, regardless of the number of individuals searching for them as producers. However, it is clear that many organisms inhabit environments in which simultaneous resource discoveries are likely. Those few studies that have varied the difficulty of resource discovery such that simultaneous resource discoveries can occur (Beauchamp & Giraldeau 1996; Ohtsuka & Toquenaga 2009) propose that social information use should decrease as finding resources using personal information becomes easier. Second, only one model (Barta & Giraldeau 1998) has explored the effects of resource monopolisability on scrounging

behaviour, while others have assumed scramble-like competition between a producer and any scroungers at its discovery. Barta & Giraldeau (1998) demonstrated a positive link between dominance and scrounging behaviour when resources were monopolisable.

No study to date has attempted to combine the three elements of resource distribution outlined above to better understand how their influences on the strength and nature of competition might interact to impact individual information use. Such an approach should be of general interest given the range of ecological conditions that different taxa experience when exploiting resources in nature. Here, we expand the producer-scrounger game to develop a general model for how resource ecology should affect individual information use in a social context. We define resource ecology along three axes of variation: 1) the 'scarcity' of resource patches, which quantifies how difficult they are to discover using personal information; 2) the 'depletion rate' of resource patches, which quantifies how rapidly social information becomes outdated following discovery; and 3) the 'monopolisability' of resource patches, which quantifies the degree to which competitors can exclude one another based on differences in competitive ability (Parker 1974). Within this framework, the classic producer-scrounger game is represented by a specific subset of the environmental conditions considered.

Using this framework, we investigate how individual decisions to use personal or social information may be affected or constrained by ecological conditions and individual phenotype. By considering the interactive effects of three dimensions of

resource ecology, we provide general insights into how the relative costs of not just collecting, but also using, personal versus social information should influence individual information use. Furthermore, we demonstrate that the individual benefits of high competitive ability are dependent on more than just resource monopolisability when individuals face uncertainty about the spatiotemporal distribution of resources. As such, patterns of resource ecology may have previously unexpected influences on the character of social systems across taxa.

The Model

We model groups of N individuals searching for and consuming resource patches. Patches contain F resource units. Individuals can choose to search for patches using one of two mutually exclusive tactics: producing or scrounging. Producers collect and use personal information, sampling their environment asocially. The *per capita* resource discovery rate for producers is determined by λ – the probability of discovering a resource in a single time step – which ranges from 0 to 1 and represents ‘scarcity’. The lower the value of λ , the more difficult resources are to find. Scroungers, in contrast, collect and use social information. They do not contribute to the group’s resource discovery rate, but exploit patches produced by others. The proportion of the group producing and scrounging is denoted by q and $(1-q)$, respectively. Patches are fully depleted in the same time step that they are discovered.

The total number of patches discovered per time step is given by λqN – the probability of an individual producer discovering a patch multiplied by the number of

producers in the group. Simultaneous resource discoveries occur if $\lambda qN > 1$, but individual scroungers can only access a maximum of one discovered patch per time step. Therefore, when $\lambda qN \geq 1$, λ represents the ratio of the costs of collecting social versus personal information, since a scrounger can access a patch each time step, whereas a producer discovers a patch only every $1/\lambda$ time steps. When $\lambda qN < 1$, however, scroungers only access a patch every $1/(\lambda qN)$ time steps. In this case, the ratio of the costs of collecting social versus personal information will be $1/qN$, since scroungers access each producer's discovery, while producers only benefit from their own discoveries. Because our parameters and variables do not change across time steps for a given group composition, all resource consumption formulae given below represent rates (i.e., $T = 1$).

A producer discovering a patch gains a finder's advantage of a resource units before any scroungers arrive (Barnard & Sibly 1981). The finder's share is thus defined by a/F , representing the 'depletion rate' of a resource patch. The remaining $(F-a)$ resource units, defined as A , are divided between the producer and any scroungers present in proportion to their relative competitive weights. An individual's competitive weight is defined as

$$CW_i = (1 + N - i)^c,$$

where i denotes an individual's ranked competitive ability relative to others in the group (expressed as an integer, ascending from 1 to N ; hereafter 'social rank'), and c defines the degree to which patches can be monopolised (Barta & Giraldeau 1998).

The exponent c represents resource ‘monopolisability’, and may be best considered patch size. When $c = 0$, an individual cannot monopolise a patch regardless of social rank; CW_i is the same for all individuals, and competition at patches is scramble-like. However, as c increases, resources become more defensible and the degree to which social rank influences competitive asymmetry between individuals increases following a power law. When $c = 100$, the highest-ranking individual in a patch essentially monopolises A .

If $\lambda qN \leq 1$, scroungers are able to access each patch discovery. In this case, the rate of resource consumption for producers and scroungers is equivalent to that given in Barta & Giraldeau (1998). When, in addition to this, $c = 0$, the model becomes equivalent to the classical producer-scrounger game (Barnard & Sibly 1981; Vickery *et al.* 1991). The rate of resource consumption for the i th-ranking producer with competitive weight CW_i when $\lambda qN \leq 1$ is given by

$$I_{P,i} = \lambda T \left(a + A \frac{CW_i}{CW_i + \sum_{j \in S} CW_j} \right),$$

where S is the set of social ranks for all $(1-q)N$ individuals playing scrounger, and CW_j is the competitive weight of the j th scrounger in the set, making $\sum_{j \in S} CW_j$ the summed competitive weight of all scroungers in the group. The rate of resource consumption for the i th-ranking scrounger, in contrast, is

$$I_{S,i} = \lambda T A \sum_{k \in P} \left(\frac{CW_i}{CW_k + \sum_{j \in S} CW_j} \right),$$

where P is the set of social ranks for all qN individuals playing producer, making CW_k the competitive weight of the k th producer in the set. The summation operator describes a scrounger accessing the discoveries of all qN producers in the group.

When $\lambda qN > 1$, scroungers cannot access all discoveries, since some are occurring simultaneously. As such, we assume that the probability of a scrounger exploiting a given producer's discovery in each time step is determined by the total number of discoveries in the group (i.e., λqN). For example, if four producers simultaneously discover separate patches (i.e., $\lambda qN = 4$), the likelihood of a scrounger exploiting a given producer will be 0.25, since there are four patches to choose from. The probability of a scrounger not exploiting a given producer, in contrast, will be 0.75. More formally, this process can be defined as a Bernoulli trial with a $1/\lambda qN$ probability of 'success'.

A given producer is at risk of being exploited by a total of $n = (1-q)N$ scroungers, where the likelihood of each of these scroungers being present is $1/\lambda qN$. The probability of a given producer being scrounged by a certain number, l , of the n scroungers is drawn from a binomial distribution:

$$\binom{n}{l} \left(\frac{1}{\lambda qN} \right)^l \left(1 - \frac{1}{\lambda qN} \right)^{n-l}.$$

However, the identities of the l scroungers exploiting a producer will influence the cumulative competitive weight of the individuals within a patch. We thus define all possible combinations of scroungers that can occur at a given producer's discovery, and calculate the probability of occurrence and cumulative competitive weight for each combination. The total number of possible combinations of scroungers at any given discovery is given by

$$Y_p = \sum_{l=0}^n \binom{n}{l}.$$

We define a $Y_p \times n$ matrix, \mathbf{S}_p , which defines the absence (0) or presence (1) of each scrounger for each combination. The probability of occurrence for each of these combinations is given in a $Y_p \times 1$ matrix, \mathbf{B}_p , the elements of which are calculated as follows:

$$\frac{1}{\lambda q N} \left(1 - \frac{1}{\lambda q N}\right)^{n-l}.$$

To calculate the cumulative competitive weight of scroungers for each combination, we multiplied \mathbf{S}_p by an $n \times 1$ matrix, \mathbf{C}_p , of competitive weights for each individual scrounger, to produce a $Y_p \times 1$ matrix, \mathbf{W}_p , of competitive weights summed across scroungers for each possible combination of individual scroungers present.

As such, when $\lambda qN > 1$, the rate of resource consumption for the i th-ranking producer is given by

$$I_{P,i} = \lambda T \left(a + \sum_{m=1}^{Y_P} b_{p,m} A \frac{CW_i}{CW_i + w_{p,m}} \right),$$

where $b_{p,m}$ and $w_{p,m}$ represent the m th elements (i.e., rows) of the \mathbf{B}_P and \mathbf{W}_P matrices, respectively, and m ranges from 1 to Y_P .

To calculate the rate of resource consumption for a given scrounger, we must define all of the possible contexts in which it can be when exploiting producers. For each context, we calculate its probability of occurrence and the cumulative competitive weight of individuals present. A scrounger will always exploit one producer when $\lambda qN > 1$. This may occur alone or in conjunction with a certain number, $(l-1)$, of the remaining $(n-1)$ scroungers. The total number of possible combinations of other scroungers occurring alongside a given focal scrounger is, therefore, given by

$$Y_S = \sum_{(l-1)=0}^{(n-1)} \binom{n-1}{l-1}.$$

We define a $Y_S \times (n-1)$ matrix, \mathbf{S}_S , which records the absence (0) or presence (1) of the $(n-1)$ remaining scroungers for each of the Y_S possible combinations. The likelihood of any individual scrounger exploiting a given producer is $1/\lambda qN$, making

the probability of a given scrounger sharing a resource with a given combination of the remaining scroungers

$$\frac{1}{\lambda q N} \left(1 - \frac{1}{\lambda q N}\right)^{(n-1)-(l-1)}.$$

Since the focal scrounger will itself only have a $1/\lambda q N$ chance of being present at a given producer's discovery, the probability of each of these combinations occurring at a given discovery will be

$$\frac{1}{\lambda q N} \left(1 - \frac{1}{\lambda q N}\right)^{(n-1)-(l-1)} \frac{1}{\lambda q N},$$

simplified as follows:

$$\frac{1}{\lambda q N} \left(1 - \frac{1}{\lambda q N}\right)^{(n-l)}.$$

We calculate this probability for each of the Y_S possible combinations to produce a Y_S x 1 matrix, \mathbf{B}_S .

The identity of a given focal scrounger will influence the cumulative competitive weight of the $(n-1)$ remaining scroungers. As such, we define, for each focal scrounger, a separate $(n-1)$ x 1 matrix, \mathbf{C}_{Si} , of competitive weights for the remaining scroungers, where i is the rank of the focal scrounger. The cumulative competitive

weight of remaining scroungers for each of the Y_S combinations is calculated for the i th-ranking scrounger by multiplying the matrices \mathbf{S}_S and \mathbf{C}_{S_i} , to generate a $Y_S \times 1$ matrix, \mathbf{W}_{S_i} .

When $\lambda qN > 1$, therefore, the rate of resource consumption for the i th-ranking scrounger is given by

$$I_{S,i} = \lambda T \left(\sum_{k \in P} \sum_{m=1}^{Y_S} b_{s,m} A \frac{CW_i}{CW_k + CW_i + w_{si,m}} \right),$$

where $b_{s,m}$ and $w_{si,m}$ represent the m th elements (i.e., rows) of the \mathbf{B}_S and \mathbf{W}_{S_i} matrices, respectively, and m ranges from 1 to Y_S . The competitive weight of a given producer, CW_k , is defined as above.

We analysed the model – for fixed values of N , a/F , λ , and c – by allowing individuals to switch between the producer and scrounger tactic in an attempt to improve their relative rate of resource consumption, or relative fitness. This was calculated for the i th-ranking individual as $P_i = I_i / ((\sum_{r=1}^N I_r) / N)$ – its fitness relative to the group's average. In this way, we searched for Nash equilibria: stable group compositions where no individual could increase its payoff by switching tactic. We generated results numerically for groups of size 2, 4, 8, and 16, but our equations are applicable to groups of any size.

We began each model run by defining a group as a vector of zeros and ones of length N , where the value at position i represents the tactic (0 = producer; 1 = scrounger) of the i th-ranking individual. Initial group composition was generated such that each individual had a 50% chance of starting as a producer or scrounger. The group was then perturbed by randomly selecting one individual to switch tactic. If this individual's payoff increased, the new tactic would be maintained; otherwise it would revert to its previous tactic. This perturbation was repeated until a Nash equilibrium was reached. Model runs for a given parameter set were replicated up to 10,000 times in order to account for multiple Nash equilibria. We thus calculated – for each group and each individual in each parameter set – the probability of scrounging based on average tactics in the stable group compositions of model replicates. All model analysis was conducted in R version 3.0.2 (R Core Team 2013).

Results

Increasing the producer's resource discovery rate (λ) reduced the relative cost of collecting personal information. However, the impact of this relationship on the decision to produce or scrounge was dependent upon resource monopolisability. When individuals were unable to monopolise resources (i.e., $c = 0$), scrounging became less common if patches were easier to find (higher λ) (Fig. 1). Under these conditions, there was no between-individual variation in scrounging behaviour (Fig. 2a). Scrounging ultimately disappeared from the population (i.e., producing became fixed) when resources were sufficiently easy to find using personal information that the associated costs of resource sharing were no longer economical.

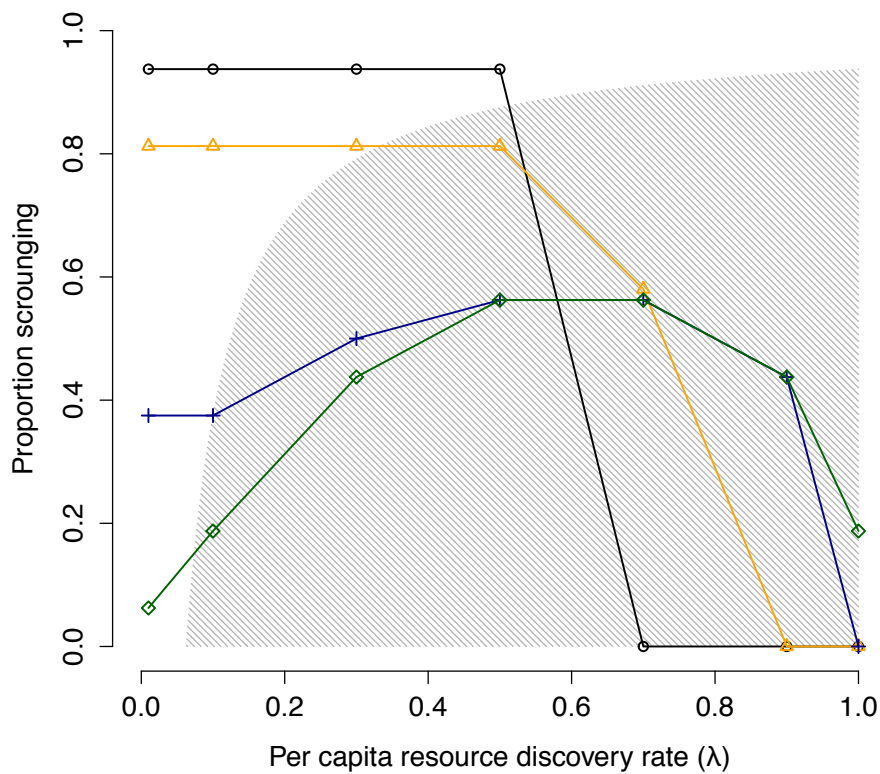


Figure 1. The combined influence of resource scarcity and monopolisability on levels of scrounging in a group. Simultaneous resource discoveries occurred only within the shaded region (i.e., where $\lambda qN > 1$). Values of c as follows: 0 (black circles); 1 (orange triangles); 10 (blue crosses); 100 (green diamonds). Data only shown for $N = 16$ and $a/F = 0.05$, but results for other values were qualitatively similar.

As resources became monopolisable (increasing c), the relationship between the discovery rate and the proportion of scrounging in a population changed dramatically. First, when the discovery rate was low, such that no more than one patch was being discovered per time step ($\lambda qN \leq 1$), scrounging became less common at higher values of c (Fig. 1). This occurred because the more effectively every discovery could be monopolised by a single, top-ranked individual playing scrounger, the less profitable this tactic became for others (Fig. 2a-d, far-left

columns). Rather, other individuals would benefit more from playing producer: even though patch discoveries would be rare, and would be largely appropriated by the dominant scrounger, producers would at least secure a finder’s advantage.

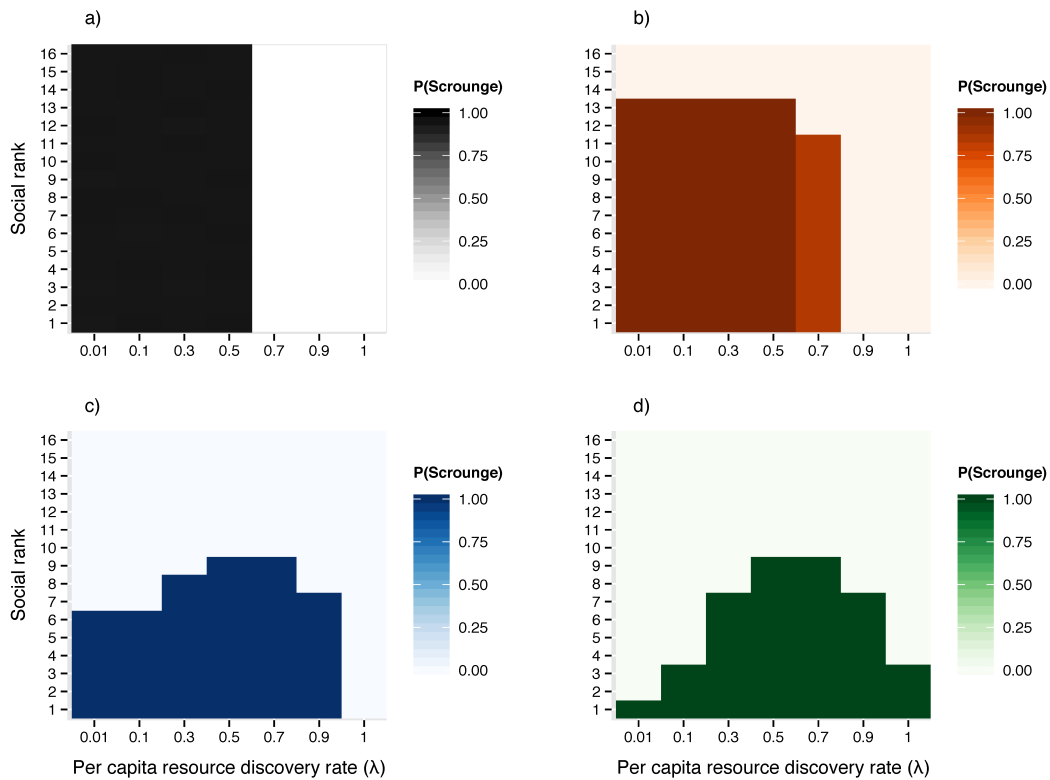


Figure 2. The combined effect of resource scarcity and monopolisability on the probability of scrounging for individuals of different social rank. Resource monopolisability for each panel as follows: a) $c = 0$ (black); b) $c = 1$ (orange); c) $c = 10$ (blue); d) $c = 100$ (green). Colour coding corresponds to that given in Figure 1. Data only shown for $N = 16$ and $a/F = 0.05$, but results for other values were qualitatively similar. Note that social rank ranges highest to lowest from 1 to N .

Second, under conditions of strong monopolisability ($c \geq 10$), intermediate discovery rates promoted higher levels of scrounging despite the lower relative cost of

collecting personal information (Fig. 1). This was because simultaneous resource discoveries (i.e., $\lambda qN > 1$) could occur more easily as λ increased. Simultaneous resource discoveries precluded complete monopolisation by single individuals, freeing up resources for other individuals to scrounge. Due to the higher competitive weights of higher-ranking individuals, however, scrounging remained tightly linked to social rank despite more individuals being able to utilise the tactic (Fig. 2c-d). Finally, scrounging began to decline once resources became so easy to find that even the highest-ranked individuals would benefit more from producing – thus gaining a finder’s advantage – than from monopolising the discoveries of others (Fig. 1). The overall result when $c \geq 10$ was thus a ‘peaked’ relationship between resource discovery rate and population levels of scrounging.

Scrounging was less common when the finder’s share was high (Fig. 3). Individuals were less likely to scrounge as those producing benefited from consuming greater portions of their discoveries, leaving less for scroungers to exploit. The strength of this effect, however, was influenced by both resource discovery rate and monopolisability. While at very small finder’s shares the levels of scrounging were usually lower when monopolisability was high, the rate of decline of scrounging with increasing finder’s share was actually slower at higher levels of monopolisability (Fig. 3a-d). This reflects the fact that scroungers able to monopolise patches were more robust to the losses associated with a higher finder’s share, because they still secured large proportions of the remaining A resource units. In contrast, the general effect of a higher resource discovery rate was to accelerate the decline in scrounging

associated with the finder's share (Fig. 3a-d). When resources could be discovered more easily, individuals benefited from producing when the finder's share was high.

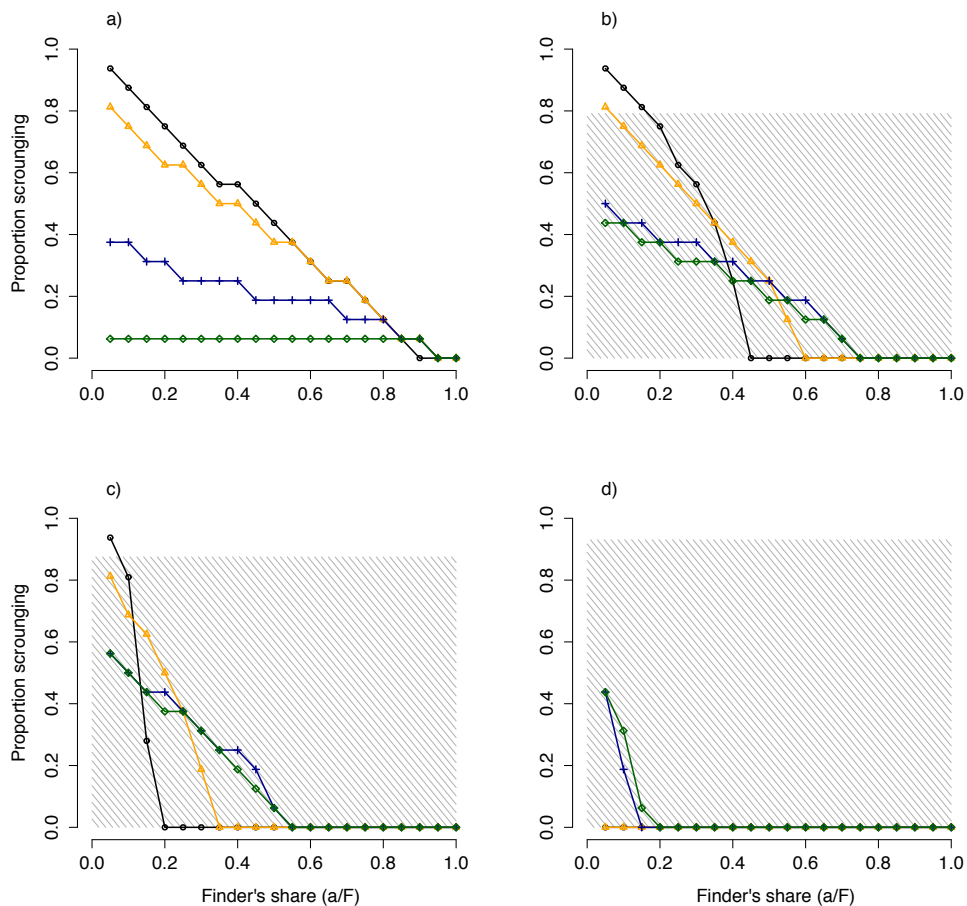


Figure 3. The effect of the finder's share on levels of scrounging in a group depends on interactions between resource scarcity and monopolisability. Panels show data for different values of per capita resource discovery rate (λ) as follows: a) 0.01; b) 0.3; c) 0.5; d) 0.9. Values of c as follows: 0 (black circles); 1 (orange triangles); 10 (blue crosses); 100 (green diamonds). Simultaneous resource discoveries occurred only within the shaded regions (i.e., where $\lambda q N > 1$). Data only shown for $N = 16$, but results were qualitatively similar for all group sizes.

Finally, high resource monopolisability allowed scrounging to persist at intermediate values of the finder's share when it would otherwise disappear from the population (Fig. 3b), although this effect persisted only at progressively smaller values of the finder's share as discovery rates increased (Figs. 3c-d). This was caused by a combination of simultaneous resource discoveries and the robustness of scrounging for individuals of high social rank described above.

The interactive effects of resource discovery rate and monopolisability on scrounging behavior had important fitness consequences. The exclusivity of scrounging to individuals of high rank when resources were monopolisable but extremely rare resulted in a strong skew in fitness favouring dominant individuals. This increased in proportion with c , and tended towards a single, top-ranked scrounger with a very high relative fitness (Fig. 4d, far left column). As resources became easier to find, however, this fitness skew became less dramatic (Fig. 4d). This was primarily due to the occurrence of simultaneous resource discoveries, which made scrounging behaviour and its benefits more evenly shared across more individuals of relatively high social rank, and lower-ranked producers less prone to being in direct competition with the highest-ranked individuals. Low-ranked producers also benefited from more frequent discoveries, and the resulting finder's share benefits, when the discovery rate was high.

The fact that a fitness skew emerged whenever resources were monopolisable and scrounging persisted meant that the population did not reach an evolutionarily (or behaviourally) stable state (ESS) of producers and scroungers. This was in stark

contrast to the outcome when resources could not be monopolised ($c = 0$). In these cases, there was no variation in scrounging propensity between individuals, leading the population to an ESS mix of producers and scroungers where all individuals had equal fitness irrespective of social rank or resource scarcity (Fig. 4a).

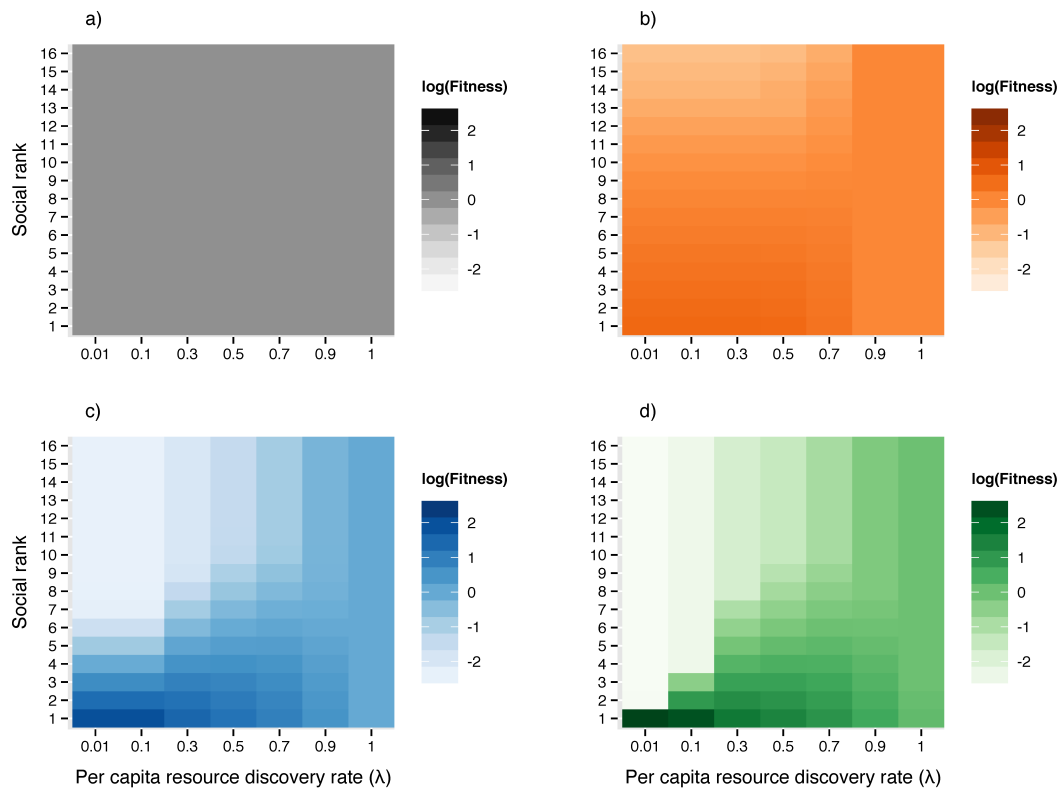


Figure 4. Resource scarcity and monopolisability interact to determine both the skew and strength of the fitness benefits of social rank. Resource monopolisability for each panel as follows: a) $c = 0$ (black); b) $c = 1$ (orange); c) $c = 10$ (blue); d) $c = 100$ (green). Colour coding corresponds to that given in Figure 1. Data only shown for $N = 16$ and $a/F = 0.05$, but results for other values were qualitatively similar. Note that social rank ranges highest to lowest from 1 to N .

Since scroungers do not contribute to resource discovery, they can reduce a population's average individual resource consumption rate, potentially impacting on various demographic processes. When resources were rare (i.e., low λ), higher values of c resulted in fewer scroungers and therefore greater average intake rates (Fig. 5). However, as resources became more common this pattern reversed: high values of c led to more scroungers and thus lower average intake rates relative to when c was low.

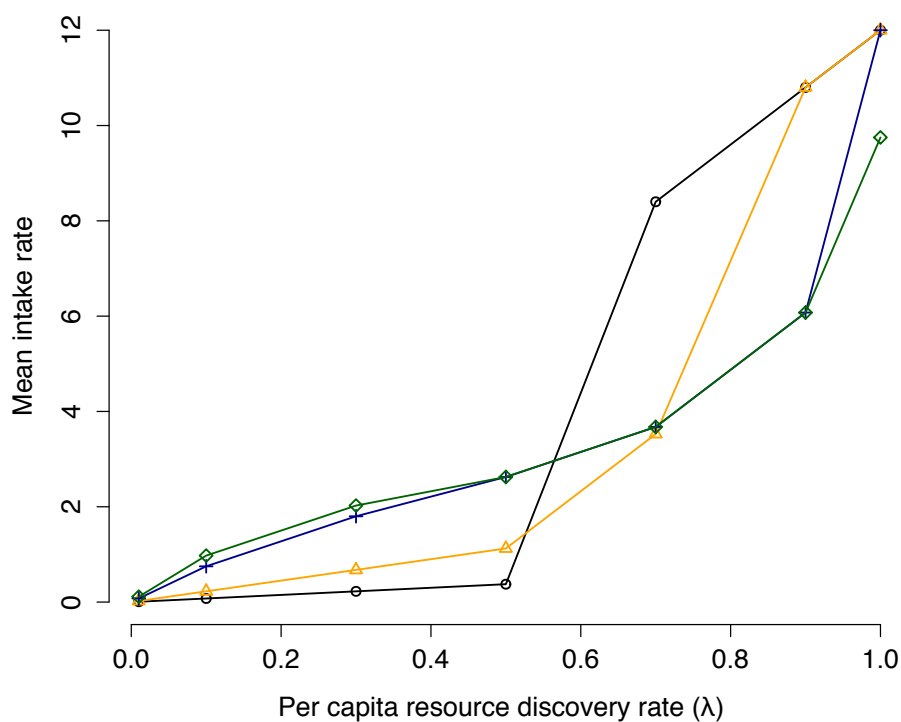


Figure 5. Resource scarcity and monopolisability affects a group's average resource consumption rate through their influence on scrounging behaviour. Values of c as follows: 0 (black circles); 1 (orange triangles); 10 (blue crosses); 100 (green diamonds). Data only shown for $N = 16$ and $a/F = 0.05$, but results for other values were qualitatively similar.

Discussion

Our aim was to explore the interdependencies between information use and competition over resources, driven by resource distribution as a shared selective force. To do this, we investigated how three key aspects of resource ecology – scarcity, depletion rate, and monopolisability – interact to promote or constrain the use of social information when acquiring resources in an uncertain environment. Further, we asked how such influences might lead to variation in fitness between individuals through differential access to resources. Our findings generated two key predictions. First, the effects of resource scarcity on social information use should depend strongly on resource monopolisability. Second, the potential benefits of social dominance should be closely linked to social information use in uncertain environments, determined not just by monopolisability, but all three aspects of resource ecology. Below, we discuss these predictions in the context of previous work and propose avenues for future research. We then raise an important theoretical consideration for the study of social information use, and conclude by outlining the potential evolutionary demographic implications of our research.

Previous producer-scrounger models have proposed that individuals should rely more on social information when the costs of collecting personal information are high, i.e., scrounging increases as valuable resources become harder to find (Beauchamp & Giraldeau 1996; Beauchamp 2008; Ohtsuka & Toquenaga 2009).

Although this relationship seems intuitive, direct experimental support is surprisingly lacking (Kendal *et al.* 2009b), possibly because the true relationship is dependent on the degree of resource monopolisability. Thus, our results confirmed this pattern

when resources were not monopolisable, but predicted a ‘peaked’ relationship when resource were monopolisable, where social information use (scrounging) only increases initially but then declines again as resources become progressively scarcer. Data from Koops & Giraldeau (1996) provides circumstantial evidence supporting this explanation. These authors found that scrounging declined in European starlings (*Sturnus vulgaris*) when novel food patches were more scarce, contrary to conventional wisdom but consistent with the downturn our model predicts at higher levels of resource scarcity and monopolisability. Crucially, starling social groups exhibit a dominance structure (Summers *et al.* 1986), and Koops & Giraldeau (1996) reported that scroungers in their study were primarily socially dominant starlings with a competitive advantage at resource patches. Our findings thus suggest that resource scarcity, depletion rate, and monopolisability should be considered in unison when making predictions about how selection should act on social information use in a given species.

Most research into information use has focussed on how individuals optimise their reliance on social versus personal information based on trade-offs between their collection costs and reliabilities (Laland 2004; Kendal *et al.* 2009b), and their negatively frequency-dependent payoffs (Vickery *et al.* 1991). Very little attention has been given to the constraints that competition imposes on an individual’s liberty to use social information to access resources. Our findings are consistent with the only previous study to explore the relationship between social information use and competitive ability (Barta & Giraldeau 1998): when resources are monopolisable, social information use may become exclusive to dominant individuals, leading to a

positive relationship between social rank and resource acquisition rate. However, our model further demonstrates that resource scarcity is critical in determining the degree of this exclusivity. Specifically, it is only under conditions of sequential resource discovery that a single individual can make exclusive use of social information; when resources are discovered simultaneously social information may be exploited by successively lower-ranked individuals.

Despite the clear influence that social dominance may play in constraining information use, we know of no studies exploring how social information use varies in response to systematic manipulation of resource monopolisability in taxa exhibiting dominance hierarchies. Liker and Barta (2002) showed that dominant house sparrows (*Passer domesticus*) scrounged more than subordinates when searching for spatially clumped seeds, but did not investigate conditions where resources could not be monopolised. A number of other experimental producer-scrounger studies in birds and primates have reported either a positive relationship or no relationship between social rank and scrounging (di Bitetti & Janson 2001; Stahl *et al.* 2001; Beauchamp 2006). Consistent with our findings, observational studies in chacma baboons have shown that dominance-linked scrounging increases when food patches are monopolisable (King *et al.* 2009; Marshall *et al.* 2012a). Our model suggests that predictions (and associated experimental designs) regarding the relationship between social dominance and information use for a given taxon should be guided by an appreciation of resource scarcity, depletion rate, and monopolisability. Further empirical work is needed to experimentally test the predictions that resource monopolisability constrains an individual's use of social

information according to dominance, leading to differential access to resources, and that the patterns of these constraints is dependent on resource scarcity.

The fact that resource monopolisability influences the benefits of dominance is well established (Parker 1974; Vehrencamp 1983; Vahl *et al.* 2005). However, since there is expected to be uncertainty associated with the spatiotemporal distribution of most resources, our model highlights a crucial role for social information use in capturing the benefits of dominance. As such, selection pressures on dominance will depend on multidimensional aspects of resource ecology (e.g., scarcity, depletion rate, and monopolisability) that influence both the benefits of social information use and competition between individuals. This does not mean that we predict the ecology of any single resource to lead to any particular information use phenotype or social system, since organisms must exploit many different resources to survive and reproduce. Overall selection on these phenotypes and systems will be driven by the combined pressures of multiple resources' ecologies through space and time (Botero *et al.* 2015).

Our findings also highlight an important theoretical issue that requires development if we are to fully understand the evolutionary ecology of social information use. We only consider the acquisition of ephemeral resources that are fully depleted upon discovery. Like most previous theory, we thus assume that any information generated by the discovery of a resource becomes useless upon its depletion. Yet it is clear that many organisms exploit resources that exhibit at least some spatiotemporal predictability, such that previous experience, or prior information,

can be used to inform future decisions (Kendal *et al.* 2004; Valone 2006; Marshall *et al.* 2013; Amaya-Márquez *et al.* 2014). When information is reusable or generalisable in this way, the relationship between social information use and competition over resources may change dramatically. Specifically, social information use may be decoupled from the context in which it was collected in a way that would not be possible with unpredictable, ephemeral resources (where information must be used as soon as it is collected). For example, an individual may be able to collect social information in a highly competitive situation and then use it in a less competitive one. In this way, competitive constraints on social information use may be relaxed or altered. Since the fitness benefits of information use are generally expected to be associated with improvements in resource exploitation, research is needed to more formally define the links between information acquisition and resource acquisition, and to explore how these links can vary.

Our model may have important evolutionary demographic implications. Coolen *et al.* (2007) showed that social information use can regulate population dynamics. They argued that, because individuals forgoing personal information in favour of social information (i.e., scroungers) do not contribute to per capita food discovery rates, higher levels of scrounging could reduce average population birth rates (Coolen *et al.* 2007). Our results thus suggest that demographic rates may differ for different systems of social dominance – ranging from egalitarian to despotic – driven by differences in levels of scrounging behaviour within groups, in turn driven by differences in resource ecology. For example, when simultaneous resource discoveries occur, we predict scrounging to be more prevalent if resources are

monopolisable, resulting in lower average resource consumption rates. We predict the opposite pattern when resources are discovered sequentially. It is widely accepted that population-level processes such as density-dependence and trait-mediated interference are often driven by underlying behavioural mechanisms (Stillman *et al.* 2000b; Sutherland & Norris 2002; Bolnick *et al.* 2011). Better understanding of the relationships between resource ecology, information use, social dominance, and fitness should thus strengthen our understanding of the differences in population dynamics across environments and taxa, and improve our ability to predict population responses to environmental change.

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Chapter 4

Social constraints on social information use depend on resource distribution

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Abstract

Animals are expected to collect and use social information in favour of personal information when the former facilitates more efficient acquisition of resources. However, the heterogeneous and uncertain nature of resource distribution that promotes social information use will also generate competition between individuals. Such competition may act to constrain or facilitate an individual's ability to use social information, but has received limited attention in studies of animal information use. We conducted a feeding experiment using wild chacma baboons (*Papio ursinus*) to investigate how an individual's ability to access resources can affect its ability to use social information. We demonstrate that constraints on an individual's ability to use social information, driven by low social rank, can have a strong impact on its performance relative to others. However, we also show that when resources exhibit some stability in their spatiotemporal distribution, individuals with low competitive ability can decouple their use of social information from the competitive context in which it was collected. Our experiment stresses the importance of considering the levels of competition and uncertainty faced by individuals as distinct but interdependent processes, underpinned by the spatiotemporal distribution of resources. Taking this approach will allow us to understand both the causes and consequences of individual constraints on social information use.

Introduction

Organisms may improve their decision-making by gathering information to reduce uncertainty (Dall & Johnstone 2002; Dall *et al.* 2005; Kendal *et al.* 2009a; Schmidt *et al.* 2010). An individual can accrue information by personally sampling its environment, or by collecting information generated by the behaviour of others (Valone & Templeton 2002; Danchin *et al.* 2004). Both empirical and theoretical studies have demonstrated that individuals can benefit from favouring social information over personal information to make decisions when the former is less risky or reduces uncertainty more efficiently (Kendal *et al.* 2004; King & Cowlshaw 2007; Rendell *et al.* 2010; Rieucau & Giraldeau 2011). However, decision-making may also be constrained by competition between individuals over limited resources. An individual's ability to access resources may thus affect its ability to use any collected information when making decisions. For example, northern wheatears (*Oenanthe oenanthe*) collect social information regarding the breeding success of conspecifics to assess territory quality, but are only able to use this information to improve their own success if the territory holder leaves (Pärt *et al.* 2011). While similar constraints appear to operate in common loons (*Gavia immer*), a minority of individuals are able to overcome them, freely using the social information they collect regarding breeding performance by usurping the territories of successful competitors (Piper *et al.* 2000, 2006). The idea that competitive processes may modulate an individual's ability to use information has received little attention, but may have important implications given the widespread expectation that individual information use will have far-reaching ecological and evolutionary consequences (Danchin *et al.* 2004; Coolen *et al.* 2007; McNamara & Dall 2010; Schmidt *et al.* 2010;

Whiten *et al.* 2011). In this study, we demonstrate experimentally how individuals can be constrained in their ability to use social information due to their low social dominance, and challenge prevailing theoretical frameworks by investigating how such constraints might be strengthened or relaxed depending on resource distribution.

An individual's ability to access resources – such as food, mates, breeding sites or territories, or safety from predation – is fundamental to its ability to survive and reproduce. However, social constraints on access to resources can arise when asymmetries in competitive ability facilitate the monopolisation of limited resources by some individuals at the expense of others (Schneider 1984; Parker & Sutherland 1986; Grant 1993; Vahl *et al.* 2005; Cotton *et al.* 2006). Such between-individual variation in access to resources is referred to as contest competition (Nicholson 1954; Parker 2000), and is expressed as social dominance (Bernstein 1981; Kaufmann 1983; Moore 1993). If the spatiotemporal distributions of certain resources are such that both individual uncertainty is high and contest competition can operate, it follows that socially dominant individuals may be able to suppress the ability of competitors to use information to access those resources.

Only two theoretical studies have explored the limiting effect that social dominance can have on an individual's ability to use information for resource acquisition (Barta & Giraldeau 1998; Lee *et al.* in review). Both studies developed game theoretic models in which group-living individuals search for rare, patchy resources using one of two tactics: 'producer' or 'scrounger'. Individuals playing producer search for

resources personally, while scroungers exploit producers by joining them at their discoveries. Crucially, producers incur search costs while actively sampling the environment, whereas scroungers avoid these costs by using the social information generated by producers. The models demonstrated that when individuals differ in their ability to monopolise resources, scrounging should become exclusive to individuals of high social rank (Barta & Giraldeau 1998; Lee *et al.* in review). This is because socially dominant individuals monopolise resources through a combination of social information use and competitive exclusion. Despite these predictions, there has been little attempt to test empirically for a relationship between social dominance and the ability to use social information that results in differential success in resource acquisition (but see Stahl *et al.* 2001).

The degree to which social dominance will constrain informed decision-making is also likely to depend on the timescale over which collected information remains pertinent. Current theoretical frameworks for studying the evolutionary ecology of social information use in a competitive context primarily consider animals searching for ephemeral resources unpredictably distributed through space and time (Giraldeau & Caraco 2000; Giraldeau & Dubois 2008; Afshar & Giraldeau 2014; Lee *et al.* in review), originally inspired by the foraging behaviour of many flocking passerines (Barnard & Sibly 1981; Clark & Mangel 1984). Once discovered, these resource patches are continually exploited until depletion or disappearance, at which point any associated information becomes out-dated. Social information use is thus tightly coupled with social interaction in this framework: individuals can only use social information through ‘scrounging’ behaviour, which involves interaction at

a resource and so can be limited by social rank (Barta & Giraldeau 1998; Lee *et al.* in review).

However, it is clear that many organisms exploit resources that exhibit some degree of spatiotemporal predictability (Valone 1991; Dall *et al.* 2005; McNamara *et al.* 2006). Increased predictability will allow individuals to learn by collecting reusable, or prior, information to exploit their environment more efficiently (Dall *et al.* 2005; McNamara *et al.* 2006; Valone 2006; Marshall *et al.* 2013; Amaya-Márquez *et al.* 2014; Noser & Byrne 2015). When information remains relevant after its initial collection in this way, individuals may have the opportunity to use it in a social context that differs from the one in which it was collected. For instance, a frugivorous individual may observe the success of a conspecific to locate a rich fruiting tree, but could delay its use of this social information to preferentially feed from it in the future once it has re-fruited and is unoccupied. This potential for social information use to be decoupled from interactions with the information generator likely has two important consequences. First, traditional frameworks such as ‘producer-scrounger’ may be poorly suited to predicting or detecting individual information use in relatively predictable environments, since observable behaviours may actually contradict the underlying information that is utilised. Second, socially subordinate individuals may benefit from collecting social information from dominant competitors if they are able to delay or generalise its use for contexts where competition is less intense, acting to reducing the overall strength of contest competition.

We conducted a social foraging experiment using a population of wild chacma baboons (*Papio ursinus*) to test three hypotheses regarding the interplay between information use and access to resources. First, we tested the theory that an individual's ability to use information should be dependent on its ability to access resources (i.e., social dominance), and that this could lead to between-individual differences in resource acquisition rate (Hypothesis 1, H1). Second, we asked whether the ability of individuals to acquire prior information about their feeding environment could decouple social information use from 'scrounger' interactions (H2). Finally, we tested the hypothesis that any such decoupling should allow subordinate individuals to benefit from collecting social information from dominant individuals by delaying its use for contexts with reduced competition (H3).

Materials and Methods

Study Site and Species

Fieldwork was conducted at Tsaobis Nature Park, Namibia (22°23'S, 15°45'E) from May to October 2013. We studied two troops of wild chacma baboons, hereafter referred to as 'troop J' (58 individuals) and 'troop L' (62 individuals). All baboons were individually recognisable and habituated to the presence of observers at close proximity.

The social foraging dynamics of baboons represent an excellent model system for this study. Baboons forage in large, stable social groups in which linear dominance hierarchies are clear (Altmann & Altmann 1973), and while foraging, individuals exhibit producer-scrounger-like social interactions (King *et al.* 2009; Marshall *et al.*

2012a; Carter *et al.* 2013), have been shown to use social information (Carter *et al.* in prep), and can learn socially (Carter *et al.* 2014). Furthermore, their natural foraging environment – consisting of a mixture of large and long-lived fruiting trees, and smaller, ephemeral food patches (see Marshall *et al.* 2012a for further details) – is such that they are likely to have experienced through their evolutionary history both conditions in which social information use and social interaction are tightly coupled and conditions in which they could be decoupled. The fact that some low-ranked individuals may not be strongly associated with more dominant competitors in space (Castles *et al.* 2014; Carter *et al.* 2015) may also provide opportunities for social information to be used in less competitive contexts than that in which it was collected.

To estimate individual social ranks, we used pairwise agonistic interactions occurring outside of the experimental arena during the study period, analysed using Matman 1.1.4 (Noldus Information Technology 2003). Linearity was supported for both hierarchies (Landau's corrected linearity index: $h'_J = 0.18$; $h'_L = 0.15$, $p < 0.001$ in both cases). To control for differences in group size, all absolute ranks (ranging from 1 to the group size, n) were standardised to between 0 (lowest rank) and 1 (highest rank) following $1 - ((1-r)/(1-n))$, where r is the absolute rank of an individual.

Experimental design

We conducted a field experiment to explore the three hypotheses outlined above, generating a set of associated predictions detailed in this section. A feeding arena with artificial patches was established in the home range of each study troop from

June to July 2013 (Appendix 1, Fig. S1.1). Maize kernels were used as bait because the study subjects were familiar with this food from previous field experiments (e.g., Marshall *et al.* 2013).

Each arena comprised 48 circular patches (4 m diameter), sized such that socially dominant individuals could competitively exclude subordinates. All patches were numbered, and their perimeters were clearly defined with large, white-painted rocks. They were arranged in a diamond-shaped lattice to make constant the shortest distance (10 m) between neighbouring patches (Fig. 1). The maize kernels were buried in the sandy substrate, so that individuals could not use long-distance visual cues to assess patch quality. Individuals could thus collect information about patch quality either by trial-and-error sampling (personal information) or by observing the decisions and performance of conspecifics (social information). This designed allowed us to simulate conditions in which collecting social information might be less costly than collecting personal information.

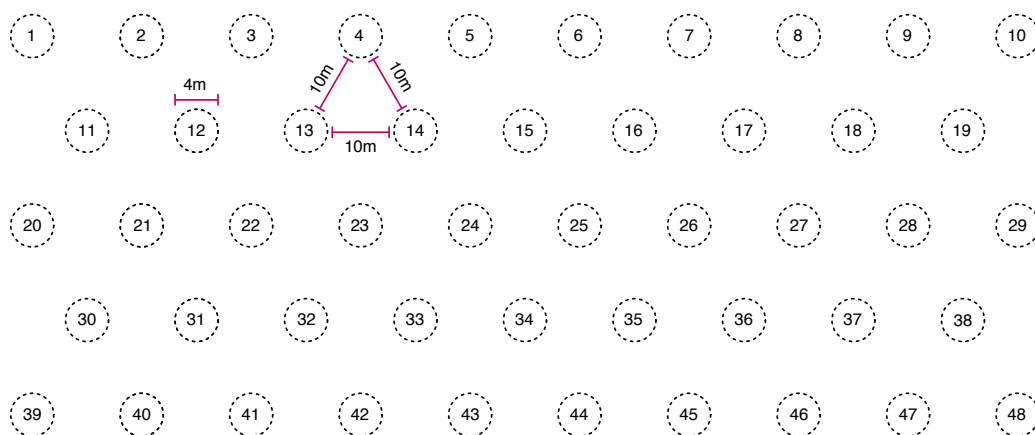


Figure 1. Schematic of the feeding arena design used in this feeding experiment.

Within this basic setup, the troops were presented with two experimental feeding environments – high and low variability in patch quality – designed to change the spatial distribution of resources in a realistic way that would manipulate the value of information in decision-making. The high variability environment included 12 patches for each of 4 different qualities ('1': empty; '2': low [120 ± 1 g; 405 ± 5 kernels]; '3': medium [277 ± 1 g; 939 ± 3 kernels]; '4': high [574 ± 3 g; 1944 ± 9 kernels]; values are mass and count \pm standard errors). The distribution of these qualities was randomised each day to ensure that individuals could not accumulate prior information about their feeding environment across experimental trials, making them naïve at the start of each trial. As a consequence, individuals employing trial-and-error sampling under these conditions should access a top quality patch every one in four attempts. We therefore identified those individuals benefitting from using social information as those who located the highest quality patches at a rate higher than 25%. However, since the number of top quality patches was severely limited relative to group size, we predicted that use of social information in this way should be limited to dominant individuals who could monopolise these patches.

We used the low variability environment as a control treatment to corroborate both any use of social information and its associated benefits detected in the high variability environment. As such, in the low variability environment, all patches were equivalently provisioned using the average quantity provided in the high variability environment (232 ± 1 g; 822 ± 4 kernels). This homogeneity meant that there would be relatively little value in using information to make decisions. Further, since the

total number of patches was not severely limited relative to group size, socially dominant individuals had little opportunity to monopolise access to resources. We randomly assigned 12 patches in each trial of the low variability environment as nominally 'top quality', predicting that there should be no individual biases towards entering these patches at a rate above or below 25%.

Based on this overall setup, we were able to test our three hypotheses. Our first prediction for hypothesis H1 (P1.1) was that using social information to access top quality resources should be positively related to social rank in the high variability environment, while accessing 'top quality' patches in the low variability environment should be unrelated to social information use. Our second prediction for H1 was that feeding success would increase with social rank in the high variability environment – facilitated by social information use – but not in the low variability environment (P1.2).

During each experimental trial, the entire troop would normally enter and forage in the feeding arena. Troop members would move rapidly between patches as they reached their marginal value, were displaced by dominant animals, or relocated to dominate others elsewhere, such that patches would often be left unoccupied while they still contained food. However, over time, individuals' marginal values declined as the feeding arena depleted, and patches were re-entered until all patches were totally depleted (>60 minutes from the start of the trial). Consequently, social information was frequently broadcast at patches (i.e., individuals were observed to forage in patches) that subsequently became unoccupied but were not yet depleted.

Our test of hypothesis H2 thus predicted – contrary to standard assumptions in the literature – that the use of social information should not be exclusively coupled to the ‘scrounger’ tactic (P2), meaning that individuals could use social information to enter unoccupied patches (see below for details regarding how we detected such social information use).

For hypothesis H3, we predicted that, if social information use and scrounger interactions were decoupled, lower-ranked individuals should collect social information about patch quality and delay its use to access high quality patches until they became unoccupied (P3.1). Finally, we predicted that subordinate individuals should reduce any deleterious effects of low rank on feeding success by using social information in this way (P3.2), reducing the impact of contest competition by avoiding resource sharing in space and time.

The experimental period lasted 36 days, comprising four alternating 9-day blocks of each treatment. Thus, both troops experienced two consecutive 18-day experimental blocks, each beginning with a 9-day block of the high variability environment followed by a 9-day block of the low variability environment. All feeding trials were carried out at dawn to control for satiation levels. A 10-day training period was conducted prior to the experiment to habituate baboons to the arenas. For each troop, at least four training trials were dedicated to each experimental treatment.

Data collection

To record individual patch entry decisions and feeding rates, we conducted two-minute focal follows on a subset of adults sampled evenly across the hierarchy from each troop. Our sample comprised 36 adults (J troop: 14 females, 6 males; L troop: 11 females; 5 males).

Focal follows were conducted by single observers on foot, using handheld video cameras (Canon EOS 550D Digital SLR) to film focal individuals while dictating behavioural observations. Patch entries were recorded (with associated patch quality) when a focal individual began searching for food in a patch, along with patch exits. To calculate the focal intake rate during patch occupancies, the number of maize kernels eaten during consecutive 10 s intervals was extracted from the videos.

Since we expected the depletion of the feeding arena to affect both intake rates and foraging behaviour, each trial was divided into four time periods of 20 minutes. Time period 1 (T1) commenced on the arrival of the first 10 % of the troop (6 individuals in both cases) at the arena. Individuals were sampled using a pseudorandom process (i.e., across days, they were initially randomly sampled within each period, but were subsequently prioritised if under-sampled for that period) to ensure relatively even coverage through time. Our total sample comprised 2341 focal minutes (minutes per individual, mean \pm s.e.: T1: 13.0 \pm 0.7; T2: 16.3 \pm 0.7; T3: 16.4 \pm 0.7; T4: 19.3 \pm 1.1).

In addition to focal follows, we conducted a series of 'patch focal observations' by filming a sample of patches for the first 10 minutes of T1, recording each patch entry

and exit of all individuals using the patch. By recording the full history of patch occupancies over this period, these focal observations allowed us to determine whether social information use could be decoupled from the ‘scrounger’ tactic. Specifically, we were able to ask whether the probability of entry into an unoccupied or occupied patch was dependent on the amount of time it had been occupied in the past (i.e., how much social information had been generated there). Patch focal observations were conducted for 93 patches in the high variability treatment. The identity of focal patches were selected using a pseudorandom sampling process that ensured even coverage across patch qualities.

Statistical analyses

H1: Dominance rank, social information use, and access to high quality resources

We first asked whether dominant individuals used social information to monopolise access to the highest quality patches in the high variability environment (P1.1). At the beginning of each trial, individuals could learn about their environment either using trial-and-error sampling (personal information) or social information. If favouring the former, we expected individuals to access the highest quality patches (top 25%) with a probability of 0.25. If the latter, we would expect individuals to access the highest quality patches more frequently. We used the low variability environment as a control treatment, defining nominally ‘top quality’ patches to compare patterns of patch entry in a homogeneous environment with the high variability environment. Generalised linear mixed-effects modelling (GLMM) was used to determine the effect of social rank on the probability of entering a top quality patch across experimental treatments. Only decisions during the first time

period (T1) were included in this analysis, since we expected all individuals to be equally motivated to feed during this period, whereas satiation levels may have differed for individuals of different rank in later time periods due to differences in foraging success. Nevertheless, we repeated the analyses for the following two time periods (T2 and T3) and the results were qualitatively equivalent, albeit slightly weaker (see below for analysis of decisions during T4). Our response variable was a binary indicator of patch quality (top quality: yes/no) for each patch entry during T1 focal follows, modelled using a binomial error structure. We initially constructed a global model that contained social rank, treatment (high/low variability), and an interaction between the two, as fixed effects. This model was based on our prediction that social information use to access top quality patches should increase with social rank in the high, but not low, variability environment. We then used an information theoretic approach to determine the relative support for this global model and two other biologically realistic candidate models. The first included only treatment as a fixed effect. This model would receive support if all individuals irrespective of rank used social information to access high quality patches in the high variability environment. The second was a null model (i.e., no effect of rank or treatment). The following control variables were included in all three candidate models: troop, focal ID, focal follow ID, experiment block, and trial number within treatment, block, and experiment. All control variables were included as random intercepts except for troop and block number, which only had two factor levels and so were included as fixed effects (Crawley 2002). We calculated Akaike weights for each candidate model, and generated a 95% confidence set of models which were included in descending order of their Akaike weights (i.e., starting with the model

with the highest weight) until a cumulative Akaike weight of 0.95 was reached (Symonds & Moussalli 2011). If more than one model was contained within this set, we employed a full-model averaging approach (Lukacs *et al.* 2010) to generate a final model.

Second, we asked whether any dominance-dependent use of social information to monopolise high quality resources in T1 permitted dominance-dependent feeding success by analysing how variability in resource quality influenced the relationship between social rank and food intake rate (P1.2). Our response variable was the total number of food items consumed in each T1 patch residency by each focal, modelled as a GLMM with a Poisson error structure. Because this number is likely to be a function of time spent feeding, we included log-transformed patch residency time as an offset, effectively converting our response variable to feeding rate. We began with a global model including the same main effects and control variables as above, as well an additional observation-level random effect to account for overdispersion (Harrison 2014). Again, we had two further candidate models. The first included only rank as a fixed effect, since individuals of higher rank may have achieved higher feeding success regardless of variability in patch quality. The second was a null model. We followed the protocol outlined above to obtain a final model.

H2: Decoupling social foraging interactions from information use

We asked whether individuals used social information to access top quality patches that were unoccupied, decoupling social information use from scrounger interactions (P2). We used our patch focal data to determine whether the probability

of entry into a top quality patch was dependent on its previous occupancy history, expecting that individuals would be more likely to have acquired social information about a patch the more it had been occupied. We divided the 10 minutes of observation for each patch focal into 10 s intervals, and generated our response variable as a binary indicator of whether or not a patch entry occurred during each interval at a given patch. We built a global GLMM including the following fixed effects: (1) the proportion of time since the start of the trial that the patch had been occupied; (2) the absence/presence of an occupant at the start of a 10 s interval (meaning a patch entry that occurred during this interval would be a 'produce' if absent and a 'scrounge' if present); (3) an interaction between the two. Since individuals may not have been using the previous occupancy history of a patch to inform entry decisions, and the presence of another occupant in a patch may or may not systematically affect patch entries, we also built a set of four other candidate models to capture all presence/absence combinations of the two main effects (i.e., presence of both with no interaction, presence of only one of the two, absence of both). We controlled for the effects of time elapsed since the start of the 10 min period by including it as a fixed effect in all models. We also included the following two random intercepts: (1) focal patch ID and (2) a code given to each unique patch occupancy period. This latter variable allowed us to account for resampling the same patch during extended periods of continuity in state, either due to remaining unoccupied or remaining occupied by given individual or set of individuals. For example, long-term monopolisation of a patch by a high-ranked individual may have precluded any other patch entries, and this will have been sampled repeatedly over consecutive 10 s intervals. We also checked for more systematic temporal

autocorrelation across 10 s intervals, discovering that the presence or absence of a patch entry in a given 10 s intervals was not correlated with the presence or absence of an entry in previous time intervals. Finally, we included a random slope that allowed the effect of time elapsed on patch entry to vary across patches, controlling for any effects of differential rates of patch depletion on the likelihood of patch entry. We then proceeded using the information theoretic approach described above to generate a final model from our five candidate models.

H3: Delayed use of social information by low-ranked individuals

We explored whether low-ranked individuals delayed their use of social information regarding high quality patches to access them when unoccupied (P3.1), and asked whether this reduced or removed any relationship between social dominance and feeding success (P3.2). To do this, we reran the first two analyses outlined above (for P1.1 and P1.2), but using focal data from the final time period (T4) instead. The logic behind this decision was that top quality patches were more likely to be unoccupied during this period, since dominant individuals were more likely to be satiated and to have left the feeding arena. To confirm that top quality patches still conferred feeding benefits over other patch qualities in T4, we also asked whether individuals actually gained higher feeding rates by accessing top quality, as opposed to lower quality, patches during T4.

All analyses were conducted in R version 3.0.2 (R Core Team 2013), with the use of the lme4 (Bates *et al.* 2013) and MuMIn (Bartoń 2015) packages.

Results

H1: Dominance rank, social information use, and access to high quality resources

The probability of entering a top quality patch in the high variability environment during the first time period (T1) strongly increased with social rank (Table 1, P1.1).

The highest ranked individuals accessed top quality patches in approximately 80% of their patch entries, well above the 25% success rate achievable through trial-and-error sampling (Fig. 2a). In contrast, the lowest ranked individuals accessed top quality patches in only 2% of their patch entries, while mid-ranked individuals did so approximately 23% of the time (Fig. 2a). In the low variability environment – in which ‘top quality’ patches were randomly allocated patches that had the same quality as all others – there was no effect of social rank on the probability of entering a top quality patch (Table 1, P1.1). Furthermore, the average rate of entry into these patches for all ranks was approximately 25% (Fig. 2a). We thus found strong support for our prediction (P1.1) that high-ranked individuals would use social information to locate and monopolise top quality patches in a high variability environment. This monopolisation prohibited the use of equivalent social information by lower-ranked individuals during T1, constraining their access to top quality patches to rates below that theoretically achievable through trial-and-error sampling.

The consequence of the observed asymmetry in freedom to use social information and access resources was that feeding rate during T1 strongly increased with rank in the high variability environment (Table 1, P1.2). In contrast, social rank had little effect on feeding rate in the low variability environment (Table 1, P1.2; Fig. 2b), providing strong support for P1.2.

Table 1. Factors affecting the probability of entering a top quality patch in T1 (P1.1) and T4 (P3.1), individual feeding rate in T1 (P1.2) and T4 (P3.2), and the probability of entry into a patch in consecutive 10 s intervals (P2).

Prediction	No. models averaged	Response	N	Fixed Effect	β	s.e.	Relative contribution to final model
P1.1	1	Probability of entering highest quality (T1)	477	Intercept	-1.37	0.58	1
				Rank	0.13	0.75	1
				Treatment_HV	-2.57	0.80	1
				Rank * Treatment_HV	5.18	1.13	1
P1.2	2	Feeding rate (T1)	434	Intercept	-0.41	0.16	1
				Rank	0.21	0.20	1
				Treatment_HV	-0.48	0.21	0.93
				Rank * Treatment_HV	0.60	0.27	0.93
P2	1	Probability of patch entry	1342	Intercept	-1.72	0.33	1
				Proportion prior time occupied (PPTO)	2.01	0.71	1
				Currently occupied_Yes	1.01	0.45	1
				PPTO * Currently occupied_Yes	-3.88	0.78	1
P3.1	2	Probability of entering highest quality (T4)	240	Intercept	-1.09	0.41	1
				Rank	0.26	0.54	0.59
				Treatment_HV	0.82	0.55	1
				Rank * Treatment_HV	0.55	0.83	0.59
P3.2	3	Feeding rate (T4)	219	Intercept	-2.00	0.20	1
				Rank	-0.22	0.25	0.61
				Treatment_HV	0.01	0.08	0.08
				Rank * Treatment_HV	-0.01	0.10	0.08

HV: High variability; the reference category for treatment is 'Low variability'.

In model P2, the reference category for 'Currently occupied' is 'No'. Note that any patch entry occurring during an interval where the patch was 'currently occupied' was considered a 'scrounge', while the opposite was considered a 'produce'. See Appendix 1, Table S1.1 for full models included parameter estimates for control fixed effects.

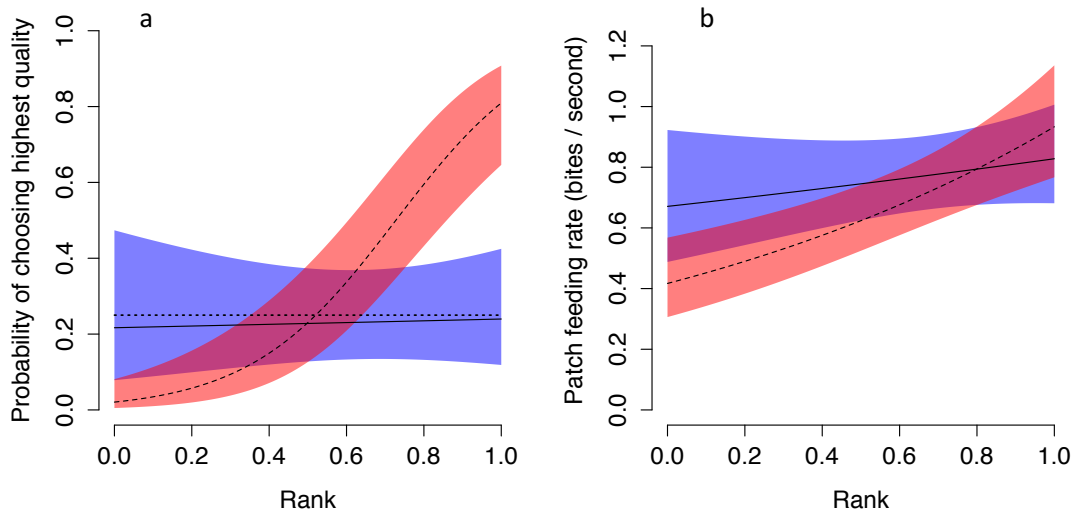


Figure 2. Rank-related social information use and access to resources in T1. (a) The observed effect of dominance rank on the probability of entry into a top quality patch in the high (dashed line, red-shaded 95% confidence intervals) and low (solid line, blue-shaded 95% confidence intervals) variability experimental feeding environments compared with that achievable through trial-and-error sampling (dotted line). (b) Relationships between dominance rank and feeding rate in the high and low variability experimental feeding environments.

H2: Decoupling social foraging interactions from information use

There was a strong positive effect of previous patch occupancy on the probability of patch entry, but only if the patch was now unoccupied (Table 1, P2; Fig. 3). We thus found support for the idea that social information use could be decoupled from the competitive context traditionally associated with scrounger interactions (P2), instead being used in a producer-like context in which no competitors were present at the resource. In contrast, if the patch was still occupied, the pattern was reversed, such

that a patch entry was less likely with a greater history of patch occupancy (Table 1, P2; Fig. 3).

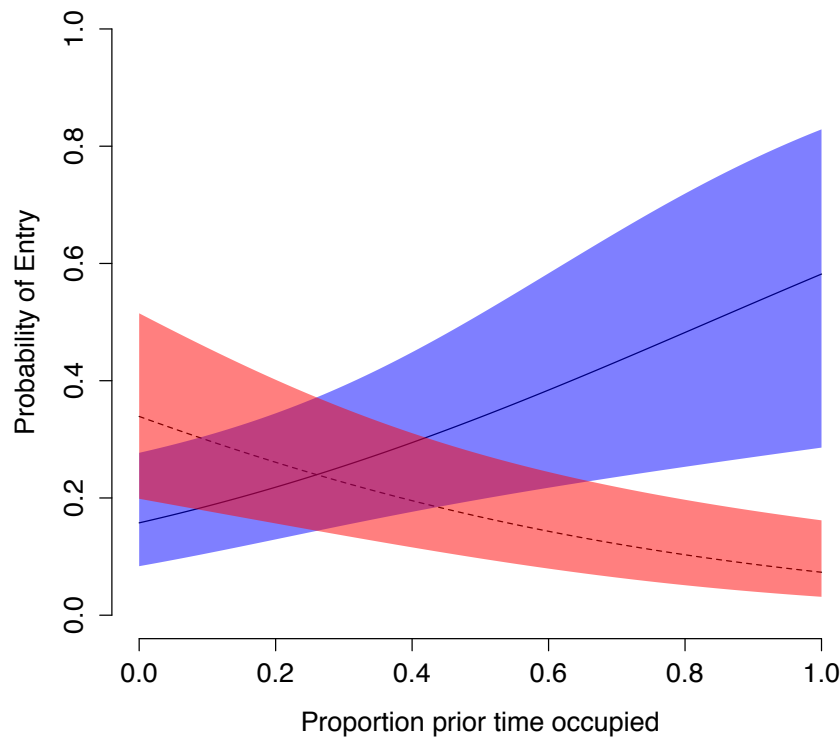


Figure 3. Decoupling social information use from scrounger interactions. The influence of patch occupancy history on the probability of subsequent entry into it when currently unoccupied (solid line, blue-shaded 95% confidence intervals) or occupied (dashed line, red-shaded 95% confidence intervals).

H3: Delayed use of social information by low-ranked individuals

During the final time period (T4), we found little support for any positive effect of social rank on the probability of entering a top quality patch in the high variability environment (Table 1, P3.1). Unlike in T1, all individuals accessed the top quality patches more than would have been achievable through trial-and-error sampling (Fig. 4a). Consistent with our findings in T1, there was still no effect of social rank on

the probability of entering a ‘top quality’ patch in the low variability environment (Table 1, P3.1), with the average probability remaining approximately 25% (Fig. 4a). Together, these findings support our prediction (P3.1) that, due to social constraints on their ability to use the scrounger tactic, subordinate individuals delay their use of social information to access high quality patches once they become vacant.

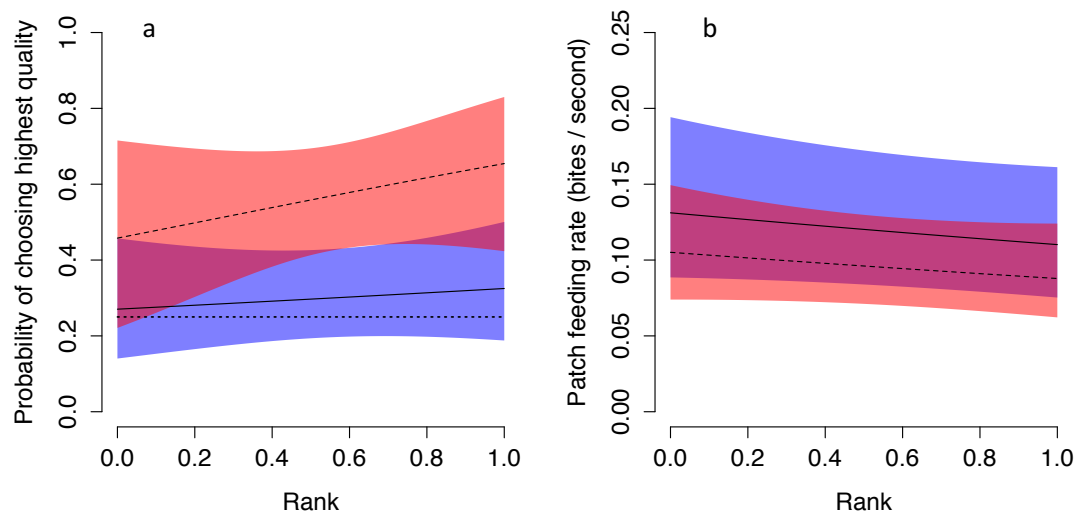


Figure 4. Rank-related social information use and access to resources in T4. (a) The observed effect of dominance rank on the probability of entry into a top quality patch in the high (dashed line, red-shaded 95% confidence intervals) and low (solid line, blue-shaded 95% confidence intervals) variability experimental feeding environments compared with that achievable through trial-and-error sampling (dotted line). (b) Relationships between dominance rank and feeding rate in the high and low variability experimental feeding environments.

There was no clear effect of social rank on feeding rate in T4 in either the high or low variability environments (Table 1, P3.2; Fig. 4b). This similarity in feeding rate between individuals was not due to the effects of patch depletion on variability in

quality: individuals occupying top quality patches during T4 in the high variability environment fed at nearly double the rate of those in lower quality patches (see Appendix 1, Fig. S1.2). We thus found support for our prediction (P3.2) that delayed use of social information by subordinates should reduce the costs of lower competitive ability.

Discussion

Individuals are expected to collect and use social information in favour of personal information when the former facilitates more efficient acquisition of resources. However, the character and uncertainty of resource distribution that promotes social information use will also generate competition between individuals. The purpose of our experiment was to understand how such competition can constrain an individual's ability to use social information and its resultant access to resources. In line with our three hypotheses, we present three important findings regarding the interplay between social information use and resource competition. First, when resources are limited and monopolisable, an individual's freedom to use social information may be determined by its social rank, driven by competitive asymmetries and resulting in differential access to resources. Second, social information need not be used in the context of the scrounger tactic, allowing the former to be decoupled from competitive social interactions. Third, this decoupling can allow subordinate individuals to collect social information in a highly competitive context and then use it in a less competitive one. Below, we discuss these findings with respect to previous research, considering the ecological and evolutionary implications of individual constraints on social information use.

Social dominance systems have long been defined by between-individual differences in competitive ability (Kaufmann 1983; Vehrencamp 1983; Parker & Sutherland 1986). The general consensus has been that the benefits of social dominance arise when the distribution of resources facilitates their monopolisation by individuals with high competitive ability, resulting in an inequitable share of resources across a group or population (Ellis 1995; Humphries *et al.* 2001; Vahl *et al.* 2005; Rands *et al.* 2006; Clutton-Brock & Huchard 2013). Two theoretical studies have proposed that, when individuals face uncertainty over resource distribution, social information use should play a crucial role alongside monopolisation in generating these benefits (Barta & Giraldeau 1998; Lee *et al.* submitted), elucidating some of the behavioural processes that might realistically underpin social dominance. Lee *et al.* (submitted) demonstrated that it is not enough for resources to be monopolisable to generate selection for social dominance: resources must also be relatively scarce. Since organisms are generally expected to face uncertainty regarding the distribution of scarce resources (Dall *et al.* 2005, 2010; McNamara *et al.* 2006; Trimmer *et al.* 2011; Mathot *et al.* 2012), selection will favour individuals that use a combination of social information and competitive exclusion to secure priority of access to resources (Lee *et al.* in review). Our experimental study provides the first empirical test of, and support for, these theoretical predictions, showing that dominant individuals benefit from using social information to improve the efficiency with which they locate high quality, monopolisable resources.

We also show that contest competition with dominant individuals can constrain subordinate individuals in their ability to use social information. Further to the

demonstrated negative impact these constraints exert on an individual's relative rate of resource acquisition, there are at least two important ecological and evolutionary consequences that warrant future investigation. First, social information use has variously been suggested as either a facilitator (e.g., Clark & Mangel 1984) or a regulator (e.g., Coolen *et al.* 2001, 2007) of average resource acquisition rates in group-living animals (Beauchamp & Giraldeau 1996), with predicted impacts on demographic rates. No studies to date have considered the effect that individual differences in the ability to use social information will have on such population level processes. Second, recent developments in social network analysis have facilitated our ability to explore how information flows between individuals that are socially connected (Franz & Nunn 2009; Allen *et al.* 2013; Farine *et al.* 2015). Our findings suggest that attention should be given to social constraints on this information flow. In particular, individuals may be free to collect social information, but may be phenotypically limited in their ability to use it effectively. This will affect information diffusion processes within, and patterns between, groups. Since social information likely plays an important role in a wide range of behaviours, from optimal foraging, mate choice, and space use under uncertainty (Dall *et al.* 2005; Rieucou & Giraldeau 2011), to the learning of novel behaviours (Laland 2004; Dukas 2013) and the evolution of culture (Boyd & Richerson 1985; Derex *et al.* 2013a), the consequences of individual constraints on its use should be far-reaching.

While our findings suggest that individual constraints on social information use should be common and important in nature, they also make clear that such constraints will be dependent on the spatiotemporal distribution of resources, and

might be relaxed if collecting social information can optimise the decoupling of the highest quality resources from positive associations with the strength of contest competition. The prevailing theoretical framework for studying social information use in animals assumes that individuals search for ephemeral resources that are unpredictably distributed and continuously exploited to depletion following discovery (Giraldeau & Caraco 2000). The consequence of these assumptions is that personal and social information use become inextricably linked to the absence and presence, respectively, of social interaction at a resource. Individuals using personal information ('producers') discover resource patches alone, generating novel information regarding its whereabouts that can be collected vicariously by others. Individuals that use this social information ('scroungers') can only do so by accessing the same resource discovery. The social interaction (in this case, co-occurrence at a resource) that necessarily follows as a result of scrounging represents competition between individuals, and can lead to the dominance-dependent use of social information demonstrated in the first time period of our experiment.

However, we feel that this link between the scrounger tactic (akin to 'kleptoparasitic' or 'joining' behaviour; Giraldeau & Beauchamp 1999; McCormack *et al.* 2007; Giraldeau & Dubois 2008) and social information use has led to a framework that can cause confusion by oversimplifying the association between social interaction and social information use in most natural contexts and for most resources. When individuals exploit resources that show some stability in their spatiotemporal distribution or accessibility, such that individuals can generate prior knowledge for future use (e.g., Dall *et al.* 2005; McNamara *et al.* 2006; Valone 2006), there will be

opportunities to decouple social information use from social interaction (as defined above). In our study, we present evidence for such decoupling and, furthermore, demonstrate how it can allow socially subordinate individuals to collect social information in a competitive context and delay its use for a less competitive one. Under natural conditions, this decoupling may weaken the constraints on subordinate individuals' ability to use social information. They may thus use prior (but socially acquired) information to reduce contest competition with dominant conspecifics.

Our experiment stresses the importance of considering the levels of competition and uncertainty faced by individuals as distinct but interdependent processes, underpinned by the spatiotemporal distribution of resources. To our knowledge, there are no current theoretical or conceptual frameworks, or empirical studies, that systematically employ this approach. The producer-scrounger framework – which has generated a large body of empirical research (see Giraldeau & Dubois 2008 for review; David *et al.* 2011; Kurvers *et al.* 2012) – explores social information use in a competitive context, but is appropriate only for environments where social information use is directly linked to social interaction and has generally focussed on acquisition of food as opposed to other vital resources. There has also been intense study over the past decade regarding social information use in the context of social learning, focussing on the spread of behavioural innovations through populations and its role in the evolution of cumulative culture. However, much of this research does not consider the distribution of the resource(s) about which behavioural innovations or cultural traits are generally useful, and thus overlook the competitive

environment in which information diffuses and is used (e.g., Rendell *et al.* 2010; Derex *et al.* 2013a; but see Derex *et al.* 2014). We feel that advancements in our understanding of the evolutionary ecology of information use across taxa will thus be dependent on better characterisation of both the information and competitive landscapes experienced by individuals. Both will be influenced by the spatiotemporal distribution of resources, while information landscapes may also involve search through fitness landscapes associated with the character of different behavioural innovations (e.g., Derex *et al.* 2013b). As demonstrated in our experiment, the effects of competition may constrain individuals in their use of social information regardless of the shape of information landscapes. Taking this approach will also lead to an information-driven framework for studying competition in biology more generally, with important implications for our understanding of eco-evolutionary processes and patterns across taxa.

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Chapter 5

The eco-evolutionary dynamics of social dominance

A version of this chapter will be submitted to *Nature*, as follows:

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Abstract

There is growing recognition that advances in our understanding of ecology and evolution will require a unified approach that addresses the feedback loops that exist between the two. Competition is central to such feedbacks, which have been termed eco-evolutionary dynamics. Here, we present the first consideration of contest competition in an eco-evolutionary framework. Contest competition, or social dominance, occurs when asymmetries in individual competitive ability permit the enforcement of an unequal resource share across a group. We build a simple matrix projection model to derive reproductive values from the expected relationships between dominance rank and survival, reproduction, inheritance, and development. We demonstrate that when rank inheritance is strong, alpha individuals will secure near total contribution to long-term population growth rate, even when the lifetime effects of dominance on survival and reproduction are weak. We then use a game theoretic approach to ask when subordinate individuals should benefit from leaving their parent group to increase their dominance in a smaller daughter group more subject to Allee effects. Our findings suggest that strong rank inheritance will lead to evolutionary extinction in all cases except when contest competition is weak. In contrast, when rank inheritance is weaker, fissions are more likely to produce daughter groups with positive growth rate. However, such daughter groups may have lower growth rates than their parent group, leading to conflict between individual- and group-level selective forces. We suggest that such conflicts may provide novel insights into the evolution of cooperative breeding and eusociality.

Introduction

One of the key challenges of modern biology is to understand the causes and consequences of phenotypic variation within populations (Dingemanse *et al.* 2010; Bolnick *et al.* 2011; Dall *et al.* 2012). While the basic rules of Darwinian selection are a well-established natural force, the evolutionary process itself is complex and chaotic, simultaneously acting across multiple levels of biological organisation as well as different spatial and temporal scales (Levin 1992; Pigliucci & Muller 2010). There is a growing recognition that the fundamental demographic processes of birth and death are vital components of the evolutionary process, not just by capturing the strength and direction of selection, but by simultaneously driving population dynamic parameters, such as growth rate and density, that can feed back to influence evolutionary responses on ecological timescales (Kokko & López-Sepulcre 2007; Metcalf & Pavard 2007; Smallegange & Coulson 2013). Considering such feedbacks between evolutionary and ecological change has been termed eco-evolutionary dynamics (Schoener 2011), and despite a precedent set over four decades ago in the context of density-dependent selection (MacArthur 1962; Roughgarden 1971), this approach is still not widespread in the evolutionary or ecological sciences.

Competition is fundamental to eco-evolutionary dynamics, since the relative fitness associated with a given phenotype will be determined by both the distribution of phenotypes in a population and population size (Kokko & López-Sepulcre 2007; Metcalf & Pavard 2007; Bolnick *et al.* 2011). For example, increases in population size coupled with changes in trait means can intensify competition over limited

resources, resulting in density-dependent effects that alter selective regimes (e.g., Coulson *et al.* 2011). Indeed, resource limitation is the basis of all competition. Organisms must secure resources such as food, mates, territories, or safety from predation in order to survive and reproduce, and limits on these resources generate the evolutionary trade-offs that are pervasive across natural systems (MacArthur & Levins 1964). But the distributions of these limited resources through space and time determine the type of competition that can arise between individuals (Milinski & Parker 1991). Specifically, resources may be distributed such that individuals must ‘scramble’ for them, and an increase in competitor density will increase scramble competition for all (Nicholson 1954; Parker 2000). Alternatively, resources may be distributed such that individuals can suppress their competitors’ access to them through monopolisation. This is termed ‘contest’ competition (Nicholson 1954; Parker 2000). To date, there has been no attempt to study contest competition in an eco-evolutionary framework, despite the fact that it is expected to be a widespread biological phenomenon.

Contest competition is manifest as dominance interactions or relationships, where one or more individuals gain from enforcing an inequitable share of resources among competitors. Such interactions are taxonomically widespread (Kaufmann 1983; Weiner 1990; Clutton-Brock 2002; Cotton *et al.* 2006), and occur across the full range of social organisation, from competition between individuals of relatively solitary species (Kaufmann 1983; Moore 1990; Piper *et al.* 2000), through dominance hierarchies in fission-fusion and stable social groups (Kappeler & van Schaik 2002; Aureli *et al.* 2008; Smith *et al.* 2008), to the extreme reproductive skew and division

of labour observed in cooperative breeders (Creel *et al.* 1992; Abbott 1993; Clutton-Brock *et al.* 2001; Clutton-Brock 2002) and eusocial animals (Keller & Reeve 1994; Clarke & Faulkes 1997). In addition, dominance interactions pervade human socio-economic dynamics (Marx 1906), and also occur between competing species, playing an important role in community ecology (e.g., Creel & Creel 1996).

Despite this knowledge of the competitive processes underpinning dominance, and its generality and importance across natural systems, it is a surprisingly poorly understood phenomenon. While ecological studies have focussed on the population-level consequences of contest competition outside of an evolutionary framework (Goss-Custard & Durell 1988; Begon *et al.* 2006), behavioural ecologists have studied the evolution of optimal behavioural strategies underpinning animal contest outside of a demographic framework (Parker & Sutherland 1986; Barta & Giraldeau 1998; Lee *et al.* in review). However, consideration of dominance in an eco-evolutionary framework poses some interesting and unanswered questions. Although the conditions necessary for contest competition are determined by resource distribution, the dominance interactions that mediate this competition are wholly dependent on phenotypic traits that confer asymmetries in competitive ability between individuals (Parker 1974, 1982; Parker & Sutherland 1986). It follows that dominance is an emergent, relational phenomenon: dominance can only exist alongside subordination (Barrette 1993; Moore 1993). However, it also follows that dominance must be an evolutionary phenomenon: for dominance to emerge and persist, the traits underpinning high competitive ability must increase individual fitness and have a heritable component (Moore 1993; Moore *et al.* 2002). Indeed,

the prevalence of morphological, physiological, and behavioural traits that mediate asymmetric contests across taxa (Hardy & Briffa 2013) provide strong evidence for such historic selection and inheritance. The existence of social dominance is thus inextricably linked to its fitness benefits at the expense of the fitness of subordinate competitors. This linkage is echoed by some optimality models of asymmetric contests that have demonstrated a lack of evolutionarily stable equilibria because dominant individuals secure consistently higher payoffs than subordinates (e.g., Barta & Giraldeau 1998; Lee *et al.* in review).

How, then, are dominance asymmetries and hierarchies so commonly maintained across generations in nature, despite positive selection on the traits generating high competitive ability? What are the long-term fitness prospects for subordinate individuals in terms of relative contribution to future generations? It may be true for some taxa that subordinate individuals have evolved mechanisms to reduce the fitness costs of contest competition through avoidance behaviours or strategies to increase the tolerance of dominant competitors (e.g., Smith *et al.* 2007).

Furthermore, some studies have highlighted potential costs to dominance (Packer *et al.* 1995; Frank *et al.* 2002; Muehlenbein & Watts 2010), leading to suggestions that there may be life-history trade-offs associated with high and low competitive ability. However, there is a host of taxa for which lifetime reproductive success increases with social rank, yet dominance hierarchies – or between-individual phenotypic variation in traits mediating asymmetric contests – persist (Moore 1990; Piper & Wiley 1990; van Noordwijk & van Schaik 1999; Clutton-Brock 2002; Piper *et al.* 2006; Hodge *et al.* 2008; Hughes *et al.* 2008; Huchard *et al.* 2014). In this study, we present

a simple matrix projection model that explores the eco-evolutionary dynamics of the relational trait of dominance rank in social groups. By considering not just how social rank affects individual survival and reproduction, but also its mode of inheritance across generations and development within individual lifetimes, we provide novel insight into the evolutionary ecology of dominance. Since socially subordinate individuals may benefit from leaving their group to reduce contest competition, our approach also provides interesting predictions regarding the dynamics and consequences of individual dispersal and group stability, viability, and fission. Our findings suggest that contest competition represents an important and unique force in organismal evolution that has heretofore been understudied.

The Model

To model the evolutionary demography of social dominance, we first needed to generate functions to quantify the relationship between dominance rank and the following four fundamental biological processes: survival, reproduction, inheritance, and development.

Survival and reproduction

Contest competition is dependent on a set of phenotypic traits that mediate dominance interactions (i.e., asymmetry in competitive ability). We thus assume that, under conditions that promote contest competition, there should be at least some positive relationship between dominance rank and survival and/or reproduction. As such, we defined the effect of social dominance on the probability of survival as

$$P(S_i) = \frac{1}{1 + e^{-(a-bi)}},$$

where i denotes an individual's rank expressed as an integer, ranging highest to lowest from 1 to N (group size), and a and b are parameters that determine the slope and intercept of the function. Similarly, the effect of dominance on the probability of reproduction was given by

$$P(R_i) = \frac{1}{1 + e^{-(c-di)}}.$$

For simplicity, we assumed that individuals reproduce asexually, and can do so immediately following recruitment until death.

It is widely accepted that social species evolved to live gregariously because there is some cost to living solitarily or in small groups, such as increased predation risk or reduced ability to find or secure food (see Krause & Ruxton 2002 for review). To account for these processes simply and effectively, we included the following inverse density dependence function (i.e., 'Allee effect', hereafter interchangeable with 'depensation'), impacting all individuals' survival and reproduction probabilities by a factor W , based on group size, N , and two constants f and g :

$$W = 1 - \frac{1}{e^{(f+gN)}}.$$

We explored three different pairs of functions for survival and reproduction – hereafter referred to collectively as ‘contest regimes’ – capturing a variety of the ways that dominance rank might lead to between-individual differences in these vital rates. These ranged from (‘Type 1’) the severe reproductive skew observed in many cooperatively breeding species (Clutton-Brock *et al.* 2006; Hodge *et al.* 2008), through (‘Type 2’) a more moderate reproductive skew combined with a stronger relationship between dominance and survival, to (‘Type 3’) the steadier decline in survival and reproduction with dominance observed in many cercopithecoid and hominid primates (Pusey *et al.* 1997; Wasser *et al.* 2004; Robbins *et al.* 2007) (Fig. 1). For each contest regime, we also considered two inverse density dependence effects: one in which it was costly only to be in groups of very small size (‘A’), and another in which the costs of decreasing group size increased more gradually, affecting a wider range of group sizes (‘B’) (Fig. 2).

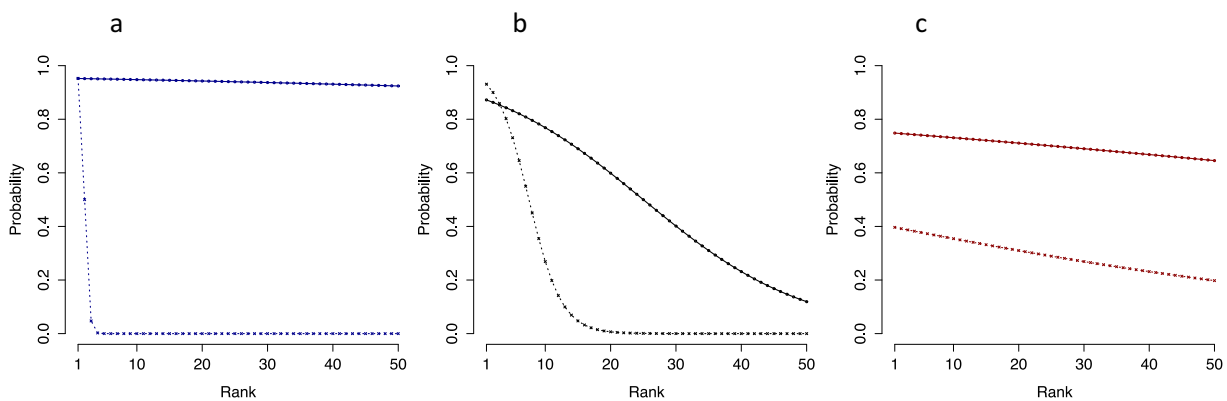


Figure 1. The modelled effects of dominance rank on survival (solid lines, closed circles) and reproduction (dashed lines, crosses). Panels a) – c) show the three different contest regimes explored: ‘Type 1’ ($a = 3$, $b = 0.01$, $c = 6$, $d = 3$), ‘Type 2’ ($a = 2$, $b = 0.08$, $c = 3$, $d = 0.4$), ‘Type 3’ ($a = 1.1$, $b = 0.01$, $c = -0.4$, $d = 0.02$). Note that a low number represents a high dominance rank, such that dominance decreases in each panel from left to right.

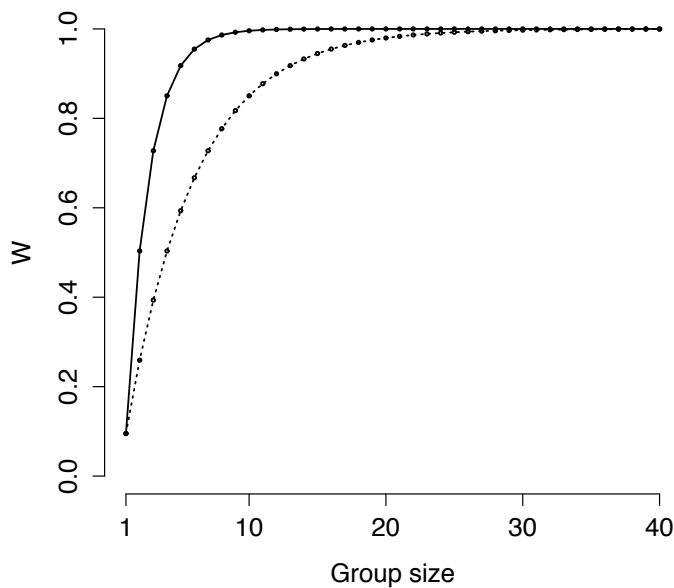


Figure 2. Inverse density dependent (Allee) effects on individual survival and reproduction probabilities. The weighting factor W decreases exponentially as groups become smaller in size, reducing the vital rates of all individuals by the same proportion. The solid line (A) shows an Allee effects that penalises only very small groups ($f = -0.5$, $g = 0.6$), while the dotted line (B) shows conditions where the benefits of larger group size increase more gradually ($f = -0.1$, $g = 0.2$).

Our survival and reproduction functions were defined such that they were not influenced by any scramble effect due to the presence of competitors in addition to the impact of contest competition. As a result, an individual's survival and reproduction probabilities were not weakened by the addition of subordinate competitors to its group. Rather, an individual added to the bottom of the hierarchy would have the lowest survival and reproduction probability, decreasing the group's average but not affecting more dominant individuals directly (Fig. 1). Contest competition thus regulated group size by lowering average survival and reproduction

probabilities at larger group sizes. For each contest regime, the stable group size could thus be calculated as the value of N at which the summed means of the survival and reproduction functions (weighted by the inverse density dependent effect) equal 1. Figure 3 shows how deterministic population growth rate changed with group size for each combination of survival, reproduction, and inverse density dependence.

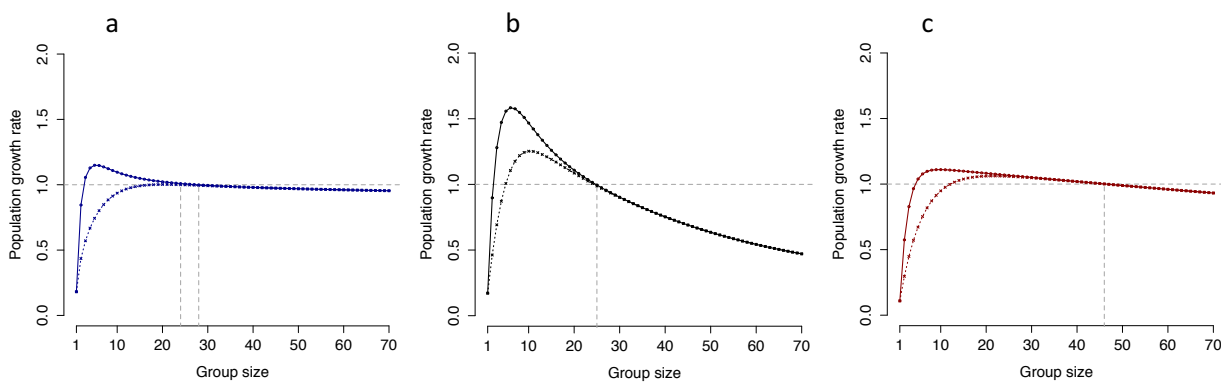


Figure 3. The combined effect of inverse density dependence and rank-mediated survival and reproduction on average population growth rate. Panels a) – c) correspond to the ‘Type 1’, ‘Type 2’, and ‘Type 3’ contest regimes shown in Fig. 1, respectively. Solid curves with closed circles and dotted curves with crosses correspond to the Allee effects ‘A’ and ‘B’, respectively. Vertical dashed lines show the stable group size at asymptotic growth rate for each combination. Note that these curves were unaffected by the shape of the inheritance function.

Inheritance

Because traits can only be subject to the evolutionary process if they show some degree of heritability, and social dominance is such a general phenomenon in nature,

we assumed that dominance status was inherited from parent to offspring. This approach is supported by findings from a wide range of taxa demonstrating the heritability of traits relating to asymmetric contests that predict social dominance status combined with a maintenance of individual variation in competitive ability across generations (Moore 1990; Piper & Wiley 1990; Holekamp & Smale 1991; van Noordwijk & van Schaik 1999; Clutton-Brock 2002; Piper *et al.* 2006; Hodge *et al.* 2008; Hughes *et al.* 2008; Cunningham *et al.* 2013; Huchard *et al.* 2014). We assumed that in each generation individuals adopted an exclusive rank position in the dominance hierarchy. Within these constraints, we modelled rank inheritance in the following two ways to capture some of the diversity documented in nature.

First, inheritance of a rank position one below the parent individual. This ‘maternal’ rank inheritance mechanism is observed in, for example, spotted hyaenas (*Crocuta crocuta*) and many social cercopitheid primates (Holekamp & Smale 1991; Engh *et al.* 2000). Second, we modelled rank inheritance as that of parental rank relative only to those within the same birth ‘cohort’. Thus, offspring A, B, and C would be ranked relative to each other in a way that corresponded with the relative ranks of their parents, but all three would still rank below the parental cohort. This broadly captured the process of age-structured maternal rank inheritance observed in mouflon sheep (*Ovis gmelini*) (Guilhem *et al.* 2002) and equids (Haupt *et al.* 1978; Araba & Crowell-Davis 1994; Weeks *et al.* 2000), and the reproductive queuing that is characteristic of cooperative breeders and primitively eusocial insects (Cant & Field 2005; Cant *et al.* 2006; Clutton-Brock 2009). In meerkats (*Suricata suricatta*) for example, older females tend to acquire the dominant position when a vacancy

arises, but if competitors are age-matched, then the heaviest generally secures dominance tenure (Hodge *et al.* 2008). Some additive genetic variation has been detected for adult body weight, and the offspring of dominant females are generally heaviest (Huchard *et al.* 2014).

A positive correlation has been observed between parental dominance and offspring dominance at adulthood in many mammals, birds, and insects (Clutton-Brock *et al.* 1984; Black & Owen 1987; Moore 1990; Nol *et al.* 1996; Poisbleau *et al.* 2009; Cunningham *et al.* 2013). Since individuals in our model were able to reproduce immediately following recruitment and did not undergo senescence, our two inheritance mechanisms can thus be viewed more generally as the two extreme ends of life-histories in which there is either frequent or no overlap between generations in the adult reproductive stage (i.e., ‘maternal’ or ‘cohort’ dominance inheritance systems, respectively).

Development

The trajectory, or development, of an individual’s rank through its lifetime was dependent on the birth and death of individuals dominant to it, acting either to push this individual down or up the hierarchy, respectively. Since individuals of some species with social dominance hierarchies are known to challenge competitors in an attempt to increase their rank (e.g., Hodge *et al.* 2008), we also explored conditions where this was possible by allowing individuals a 5% chance of moving up a single rank each time step. Modelling with and without this 5% probability produced near equivalent results, so we only present data from the latter conditions here.

Simulation

Probability density functions were generated to quantify transitional probabilities for inheritance and development across generations. For inheritance, this quantified the probability of different offspring ranks given a specific parental rank. For development, this quantified an individual's probability of securing different ranks in generation $t+1$ given its rank in generation t . Since these probability density functions could not be defined analytically, they were approximated using a simple individual-based simulation following the rules for survival, reproduction, inheritance, development, and depensation outlined above. Simulations for all parameter sets (see 'Matrix model' section below for a list of combinations) began at the stable group size (as calculated above, Fig. 3), lasted for 100 generations, and were replicated 10,000 times each.

Matrix model

Survival, reproduction, development, and inheritance functions were generated for a total of twelve different parameter sets, defined according to all possible combinations of our contest regimes (three categories), depensation effects (two categories), and inheritance methods (two categories). For each parameter set, we then used our four functions to build a matrix projection model, which uses the vital rates associated with the states or classes of individuals to make population projections (Merow *et al.* 2014). Such a structured demographic approach has never before been applied to animal behaviour or contest competition (Merow *et al.* 2014), but is particularly valuable in that it facilitates estimation of the reproductive

value – an asymptotic measure of Darwinian fitness (Gardner 2015) – associated with different individual states or classes (see further details below) (Keyfitz & Caswell 2005; Ellner & Rees 2006).

Each demographic projection matrix was calculated as $\mathbf{A} = \mathbf{D}\mathbf{S} + \mathbf{H}\mathbf{R}$, and indicated the probabilities of an individual of a given rank contributing an individual to each rank in the following generation. \mathbf{S} and \mathbf{R} represented diagonal matrices derived from the survival and reproduction functions, respectively, describing the survival and reproduction probabilities associated with each rank. \mathbf{D} and \mathbf{H} represented transition matrices derived from the development and inheritance probability density functions, respectively. Asymptotic population growth rate was determined by the dominant eigenvalue of a given \mathbf{A} matrix. The right and left eigenvectors associated with the dominant eigenvalue determined the stable stage distribution of dominance ranks within a group and the reproductive values associated with a given rank, respectively.

Reproductive values derived from our projection matrices allowed us to determine – based on a given set of conditions for survival, reproduction, inheritance, and development – the expected relative contribution of an individual of a given dominance rank to long-term population growth rate. In doing this, the reproductive value captured the long-term fitness potential associated with each rank, taking into account the probabilities of moving up and down the hierarchy for a given individual and its descendants.

Group size and fission

The stable group sizes identified by our model reflected the balance between depensation effects on fitness at small group sizes and competitive effects at large group sizes. While it is not always clear how increasing group size will change the relative contributions of scramble versus contest processes to resource competition (Sutherland & Parker 1992; Tregenza *et al.* 1996; López-Sepulcre & Kokko 2005; Łomnicki 2009), here population regulation solely reflected the effects of contest competition on low-ranked individuals.

The impact of contest competition on low-ranked individuals meant that they might increase their reproductive value by leaving their group to form a new, smaller group, in which their dominance rank would necessarily be higher. However, this potential benefit would be traded off against the depensation costs associated with small group size. We used a game theoretic approach to explore the dynamics of group fission, determining whether groups were likely to fission prior to reaching their stable size. This approach was employed because the processes of contest and depensation meant that the expected individual fitness benefits associated with staying in versus leaving a group were dependent on the decisions of others. For example, if a second-ranked individual leaves its parent group to form a daughter group, a third-ranked individual will do better to stay behind in the parent group, where it will take-up the second rank position; although this individual could also take-up the second rank position in the daughter group, the daughter group will be smaller than the parent group and thus more vulnerable to depensation effects.

To determine the expected fitness of individuals of different ranks in groups of different sizes, ranging (for a given parameter set) from solitary to the stable group size, we first estimated the probability of a group of each of these starting sizes being viable (i.e., not going to extinction). Using the simulation technique outlined above, we calculated the proportion of 1000 simulations in which a group of given starting size remained viable in its first 50 generations. This probability of population viability was then used as a weighting factor, which we multiplied by the reproductive values from our projection matrix to estimate the expected fitness of an individual of a given rank in a group of given size.

We then asked, for the smallest possible group size (i.e., $N = 2$), whether the subordinate individual would maximise its reproductive value by staying in the group, or leaving it to become the 'dominant' individual in a second 'group' of size 1. If the latter, it follows that group living should not persist under the corresponding conditions of survival, reproduction, inheritance, development, and depensation. If the former, we successively increased group size to search for the smallest possible group at which a 'stable fission' could occur before reaching the stable group size. A stable fission was defined as the generation of a reduced parent group and a new daughter group in which individuals either 'staying' or 'going' could not increase their expected fitness by switching to the other tactic (i.e., a Nash equilibrium; Maynard Smith 1982).

For each parameter set, we searched for stable fissions using the following algorithm. For a given group size, we determined all 2^{N-1} combinations of possible

group fissions (including no fission) in which all individuals except for the top-ranked individual could either 'stay' or 'go'. Each individual's expected fitness was then calculated for each combination, based on its new group size and new dominance rank. Since forming a new group is expected to be a risky or costly activity due to, for example, habitat saturation or quality variability (Koenig *et al.* 1992; Covas *et al.* 2004), we weighted the expected fitness of a leaving individual by 0.99. This also acted to prevent cyclical dynamics in our game theoretic estimation of group fission. We then collated all 'candidate' fissions where all leaving individuals were increasing their expected fitness compared with staying in their current group. To determine the stability of each candidate fission, we asked whether any individuals could increase their expected fitness by switching tactic again, defecting to return to the parent group at a higher rank. If no, the fission was stable. If yes, fissions could still occur, but only if chains of tactic switching were not attracted back to the state of 'no fission' in which all individuals eventually defected to return to the parent group. In cases where our search continued above group sizes of 13, the 2^{N-1} combinations of possible group fissions became so numerous that we employed a heuristic algorithm, searching only the group conformations that were similar in structure to stable fissions at smaller group sizes for other parameter sets.

All model analysis was conducted in R version 3.0.2 (R Core Team 2013).

Results

Social dominance and reproductive value

When the heritability of social dominance status was strong, such that individuals inherited rank positions directly below their parent ('maternal' inheritance), the relationship between social rank and reproductive value was severely skewed compared with what might be expected from the corresponding survival and reproduction functions (Fig. 4). This was caused by the fact that individuals were displaced down the hierarchy during their lifetime due to recruitment by others dominant to them (Fig. 5a and 5c), reducing their survival and reproduction probabilities in the process. Under the two strongest contest regimes ('Type 1' and 'Type 2'), this skew essentially meant that only the top-ranked individual contributed to long-term population growth rate (Fig. 4a-b). When the contest regime was at its weakest ('Type 3'), the skew in reproductive value was still strong, but reduced enough to allow some immediately lower-ranked individuals to contribute to long-term population growth rate (Fig. 4c).

When rank inheritance was broadly age-related, such that individuals secured rank positions consistent with the rank of their parent relative only to the parental rank of others in their birth 'cohort', reproductive value still decreased exponentially with lower social rank (Fig. 4). However, this decrease was more gradual than that seen with 'maternal' inheritance, because individuals were no longer pushed down the hierarchy within their lifetime when more dominant competitors recruited offspring. On the contrary, an individual's rank (and consequently its survival and reproduction probabilities) could actually increase during its lifetime, following the death of more

dominant competitors (Fig. 5b and 5d). The skew in reproductive value (albeit weaker) was maintained by the fact that individuals born to a high-ranked parent were dominant within their cohort, and so the most likely to push highest up the hierarchy within their lifetime. They thus contributed more to long-term population growth rate than individuals born to a lower-ranked parent. As with ‘maternal’ inheritance, the skew was strongest and similar for the ‘Type 1’ and ‘Type 2’ contest regimes (Fig. 4a-b). Under the weakest contest regime (‘Type 3’), the decline in reproductive value with rank was much more gradual, such that all individuals in a group would contribute to long-term population growth rate (Fig. 4c).

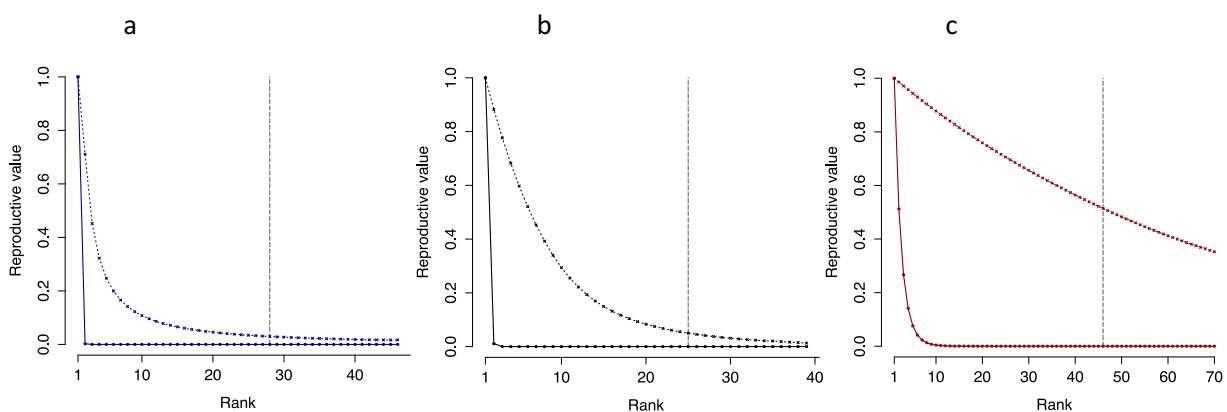


Figure 4. The relationship between social rank and reproductive value. Panels a) – c) correspond to the ‘Type 1’, ‘Type 2’, and ‘Type 3’ contest regimes shown in Fig. 1, respectively. Solid curves with closed circles and dotted lines with crosses correspond to ‘maternal’ and ‘cohort’ inheritance mechanisms, respectively. Vertical dashed lines show the stable group size at asymptotic growth rate. Reproductive values were unaffected by the strength of inverse density dependence, because densation affected each individual’s vital rates by the same proportion. Note that a low number represents a high dominance rank, such that dominance decreases in each panel from left to right.

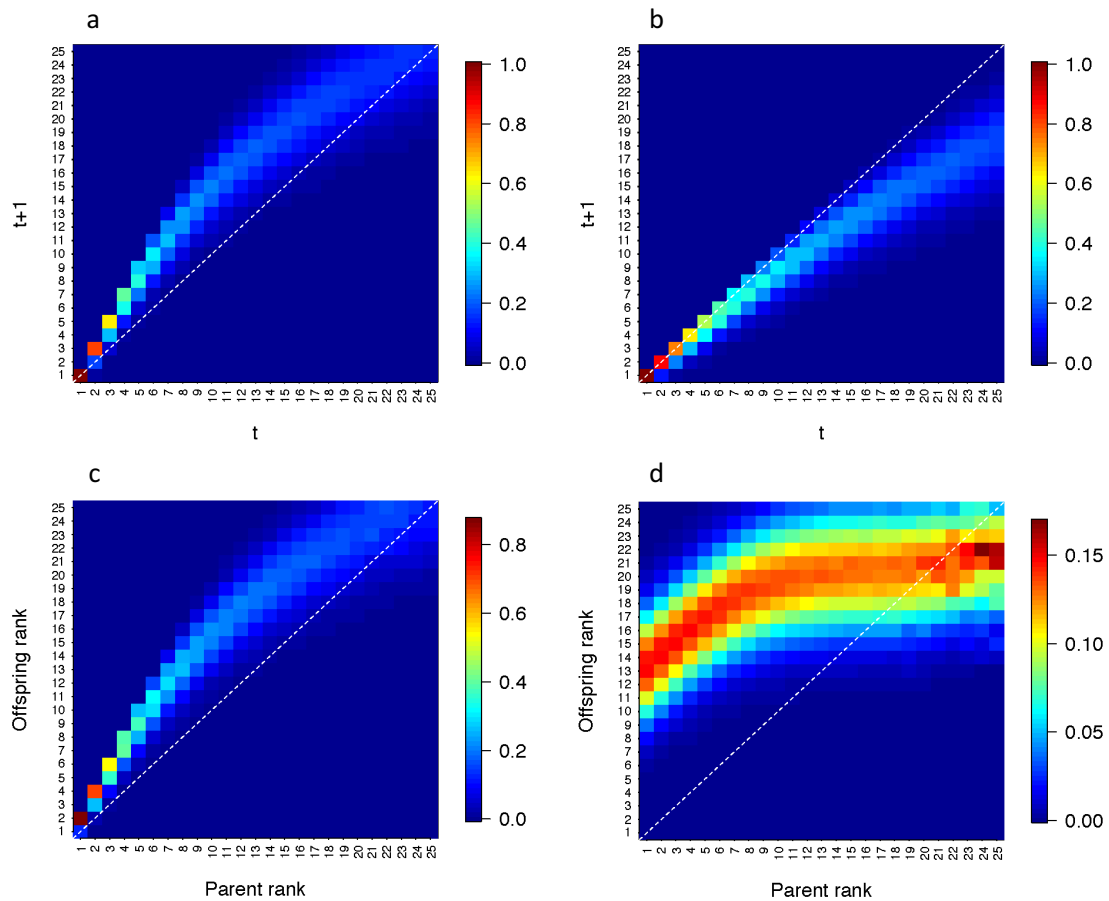


Figure 5. Transition matrices for the development and inheritance of dominance rank.

Colours indicate the probability of transition, generated through simulations to approximate analytical probability density functions. Transitions for development (panels a and b) show the probabilities of changes in an individual's rank across generations, while transitions for inheritance (panels c and d) show the probabilities of offspring rank in relation to parent rank. Panels a) and c) show probabilities for the 'maternal' inheritance mechanism while panels b) and d) show probabilities for the 'cohort' inheritance mechanism, under the 'Med' contest function. Note that a low number represents a high dominance rank, such that dominance decreases in each panel from left to right.

The shape of the densipation function had no effect on the relationship between reproductive value and social rank, since it affected each individual's vital rates by the same proportion.

Group size and fission

The probability of population viability showed a positive sigmoidal relationship with starting group size for all parameter sets (Fig. 6). When it was only costly for individuals to be in very small groups (Allee effect 'A'), population viability increased rapidly with group size (Fig. 6a-c), but when the group size costs were more gradual (Allee effect 'B'), the increase in population viability was also more gradual.

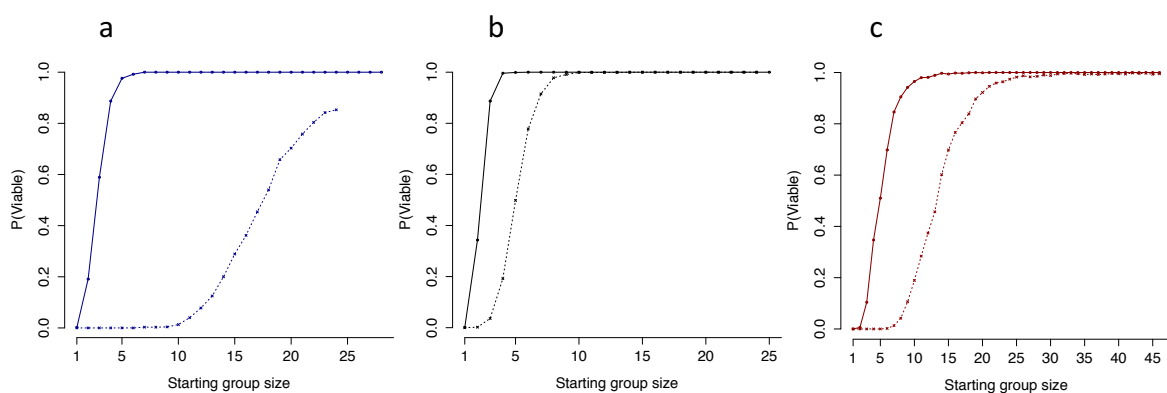


Figure 6. The relationship between the probability of population viability and starting group size. Panels a) – c) correspond to the 'Type 1', 'Type 2', and 'Type 3' contest regimes shown in Fig. 1, respectively. Solid curves with closed circles and dotted lines with crosses correspond to the Allee effects 'A' and 'B', respectively. For each combination, viabilities were calculated for starting groups ranging from 1 to the stable group size. Note that these curves were unaffected by the shape of the inheritance function.

We found selection for stable group fissions to occur before populations reached their asymptotic growth rate in ten of our twelve parameter sets (Table 1). All group fissions were structured such that staying and leaving alternated down the hierarchy, beginning with the most dominant individual staying (Fig. 7). The consequence of this was that the original group split approximately in half and each individual

(except the most dominant one) climbed one rank position. All individuals increased their fitness, except the most dominant one, whose fitness decreased despite maintaining its rank if being in a smaller group resulted in a higher probability of group extinction (Fig. 7).

Table 1. Population dynamic consequences of contest competition, depensation, and rank inheritance. The three processes interacted to determine the group size at asymptotic growth rate, the size at which groups fissioned (indicating the number leaving to form the daughter group), and the sign of the population growth rate (λ) associated with the parent group prior to fission ('Parent'), and the parent ('Stay') and daughter ('Leave') groups following fission.

Model	Contest regime	Allee effect	Inheritance	Stable N	N at fission (no. leavers)	'Parent' λ	'Stay' λ	'Leave' λ
1	1	A	Maternal	28	2 (1)	-	-	-
2	2	A	Maternal	25	5 (2)	+	+	-
3	3	A	Maternal	46	11 (5)	+	+	+
4	1	B	Maternal	24	23 (11)	+	-	-
5	2	B	Maternal	24	7 (3)	+	-	-
6	3	B	Maternal	46	29 (14)	+	+	+
7	1	A	Cohort	28	9 (4)	+	+	+
8	2	A	Cohort	25	8 (4)	+	+	+
9	3	A	Cohort	46	32 (16)	+	+	+
10	1	B	Cohort	24	>24	=	NA	NA
11	2	B	Cohort	24	17 (8)	+	+	+
12	3	B	Cohort	46	>46	=	NA	NA

Note that '=' indicates groups that did not fission, but instead reached asymptotic growth rate.

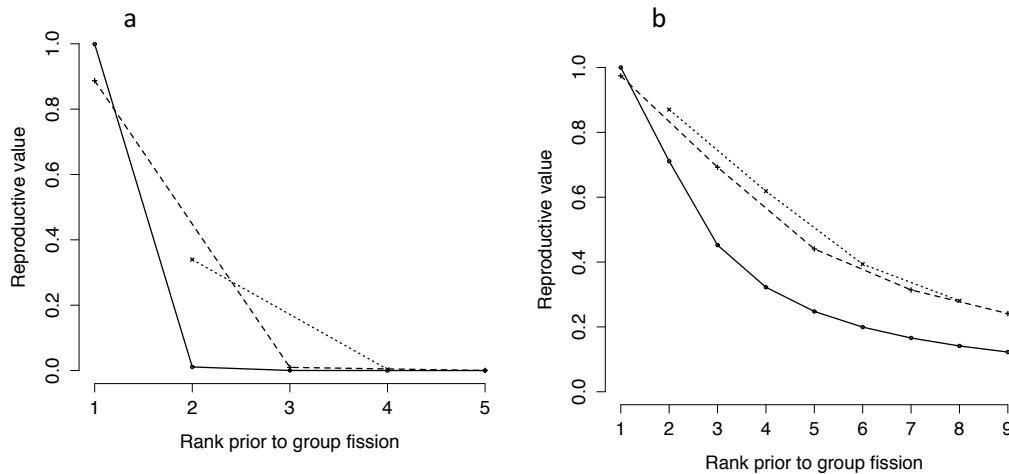


Figure 7. Patterns of stable group fission determined by contest competition and inverse density dependence. Solid lines with closed circles show the expected reproductive value associated with an individual's initial dominance rank prior to group fission. Dashed lines with vertical crosses show expected reproductive values for the individuals that remained in their initial group following fission, while dotted lines with diagonal crosses show expected reproductive values for those that left their group. Note that the sizes of groups after fission are smaller than initial groups, meaning that each (except the most dominant) individual increased in rank due to fission. The benefits of this increase were dependent on the size of their new group (i.e., any Allee effect). Panels a) and b) show the stable fissions for Models 2 and 7 given in Table 1, respectively.

Group fission occurred at larger group sizes when densation affected larger groups (Allee effects 'A' vs 'B', Table 1). Group fission also occurred at larger group sizes when rank inheritance was weak ('cohort') compared with strong ('maternal'), since the impact of contest competition on reproductive value was weaker under the former conditions. Finally, increasing the intensity of contest competition generally reduced group size at fission (Table 1). The exception to this pattern arose when the contest regime was strongest ('Type 1') and densation affected larger groups

(Allee effect 'B'). Under these conditions, the probability of group extinction increased rapidly below the stable group size, either delaying fission until a large group size was attained (for 'maternal' inheritance) or preventing fission altogether (for 'cohort' inheritance).

The severe skew in reproductive value that resulted from a 'maternal' inheritance mechanism drove subordinate individuals to leave their group at such small sizes that fissions frequently generated two new groups tended to extinction due to negative population growth rate (Table 1). Selection on individuals to maximise reproductive value thus resulted in a high probability of evolutionary extinction. Positive population growth rate was only maintained in both groups following fission when the contest regime was at its weakest ('Type 3'). In contrast, fissions always led to two groups with positive growth rates under a 'cohort' rank inheritance mechanism (Table 1). This occurred because the costs of low rank were weaker, meaning that subordinate individuals could not benefit from leaving their group until they reached a large enough critical mass to form a new group with a sufficiently low probability of extinction. However, the groups that followed fission nonetheless had higher extinction probabilities than their larger, parent group (Fig. 6). In two cases, the costs of being subordinate were not sufficient to drive fission, meaning that single groups reached their asymptotic growth rate (Table 1).

Discussion

Social dominance has a widespread taxonomic distribution and is prevalent across all known types of social organisation (Bernstein 1981; Kaufmann 1983; Ellis 1995;

Hughes *et al.* 2008; Clutton-Brock 2009), but its evolutionary importance and consequences are poorly understood. In this study, we modelled the eco-evolutionary dynamics of groups in which asymmetries in dominance rank drive between-individual differences in survival and fertility rates. This approach allowed us to explore the long-term fitness and population dynamic consequences of dominance in novel ways, by quantifying how the combined processes of birth, death, inheritance, and development might interact to determine the distribution of an individual and its descendants in a dominance hierarchy through time.

Our key findings were fourfold. First, between-individual fitness differences associated with dominance result in regulation of population growth with no need for scramble-like density dependence. Second, when dominance rank follows a strict parental inheritance rule, the fitness skew associated with dominance is considerably more severe than would be expected given the corresponding survival and reproduction functions. When dominance rank is less strongly heritable and involves an age-related component, the fitness skew reflects the corresponding survival and reproduction functions more closely. Third, considering social dominance in an eco-evolutionary framework improves our understanding of the relative benefits to subordinate individuals of philopatry versus dispersal to form a new group when the long-term expected fitness associated with social rank is traded off against the costs of new group formation. Fourth, group fissions resulting from selfish individual behaviour can increase the probability of group extinction, such that the 'optimal' group size at the level of individual selection may not persist in the long term. Below, we discuss these findings in the context of previous research into

the evolutionary causes and consequences of social dominance, highlighting directions for future empirical and theoretical study. We propose that studying social dominance in an eco-evolutionary framework demonstrates the fundamental role of contest competition in evolutionary biology. Finally, we suggest that our approach may help to resolve one of the major long-standing controversies in biology: the evolution of cooperative breeding and eusociality.

Individuals have frequently been shown to gain fitness benefits from social dominance, and the traits that give rise to dominance have regularly been proven heritable and predictive of an individual's future rank (Moore 1990; Holekamp & Smale 1991; Hodge *et al.* 2008; Cunningham *et al.* 2013; Huchard *et al.* 2014). In some sense, this is unsurprising, since social dominance is the emergent phenomenon arising from contest competition. Its very existence and maintenance is thus predicated on the heritable benefits of traits that lead to the uneven distribution of resources between individuals: dominance evolves in response to conditions that favour contest competition and necessarily generates subordination, not vice versa. This seemingly philosophical point is crucial and fundamental. Normally, when a novel phenotypic trait has a strong heritable component and confers fitness benefits, there will be an evolutionary response of that trait mean as the heritable component spreads in a population. Yet the incompatibility of this conclusion with the maintenance of social dominance asymmetries has been largely overlooked (but see Moore *et al.* 2002; Wilson *et al.* 2011; Sartori & Mantovani 2012; van der Kooij & Sandi 2015). Our findings indicate that, indeed, dominant individuals will provide the greatest genetic contribution to future generations.

When rank inheritance was strong, the contribution of one or a few top-ranked individuals was near total, even when the positive relationship between dominance and survival and fertility was weak. The genetic component of the morphological, physiological, and behavioural traits underlying socially dominant phenotypes must thus spread through a population, eroding additive genetic variation.

Our model was built such that dominance hierarchies had to persist across generations. This constraint was introduced because hierarchies are clearly maintained in many taxa for which the benefits and heritability of dominance have been demonstrated (Moore 1990; Piper & Wiley 1990; van Noordwijk & van Schaik 1999; Clutton-Brock 2002; Piper *et al.* 2006; Hodge *et al.* 2008; Hughes *et al.* 2008; Huchard *et al.* 2014). It is not enough to argue that this maintenance is driven by the logical constraint that contests must always have a winner and a loser (Moore *et al.* 2002; Wilson *et al.* 2009, 2011). Rather, the persistence of a hierarchy must reflect persistence in the conditions for contest competition through time (i.e., the opportunity to monopolise some limited resource to net fitness benefit is constant). Given these conditions, there are two (non-mutually exclusive) ways that between-individual asymmetries in phenotypic traits relating to dominance can persist, generating and maintaining hierarchies as a consequence.

First, constancy in resource distribution that promotes contest competition could drive unrelenting directional selection for the exaggeration of traits relating to dominance. For example, individuals may fight physically for mates, food, or territories, and increasing body size, weaponry, or aggression may be under

selection (Kaufmann 1983; Andersson & Simmons 2006). However, such selection might lead to evolutionary limits on the exaggeration of traits relating to dominance if the benefits associated with increasingly extreme phenotypes are eventually counterbalanced by costs (Fisher 1930; Knell *et al.* 2004). Furthermore, the evolutionary dynamics that follow unrelenting directional selection might be expected to lead to fluctuations in variation in competitive ability through evolutionary time as beneficial mutations emerge and spread to fixation. At points of fixation, there may be little variation in competitive ability between individuals, and so no clear dominance hierarchy. As such, this process may be a poor candidate for the maintenance of competitive asymmetries, and thus dominance hierarchies, through time.

Second, the resource monopolisation that characterises the emergence of a socially dominant individual might cause or permit the suppression of its descendants from generating the socially dominant phenotype despite underlying genetic similarities. Such suppression may reflect simple condition-dependence (Cotton *et al.* 2006), or may be driven by active suppression through, for instance, aggressive behaviours (Holekamp & Smale 1991; Clarke & Faulkes 1997; Korb *et al.* 2009; Holman *et al.* 2010; Clutton-Brock & Huchard 2013). Rather than representing additive genetic variation between individuals, phenotypic variation in traits relating to dominance would thus reflect differential gene expression caused by the absence or presence of suppression in dominant and subordinate individuals, respectively.

Most empirical evidence points towards some form of suppression as playing a key role in maintaining phenotypic variation in competitive ability within groups or populations, stabilising hierarchies in the process. First, plastic developmental trajectories across different life-history stages in response to shifts in dominance status have been shown to involve changes in morphology, physiology, and behaviour in a number of vertebrate and invertebrate taxa (e.g., Clutton-Brock *et al.* 2006; Korb *et al.* 2009; Huchard *et al.* 2014). For example, experimental queen removal in the eusocial naked mole-rat (*Heterocephalus glaber*) results in increased body weight and aggression as well as the onset of reproductive activity in adult females competing to become the next queen (Clarke & Faulkes 1997). Second, age is possibly the most common mediator of dominance in nature, and is the ordering system usually observed in reproductive queues (Post 1992; Clutton-Brock & Huchard 2013). Age-based dominance may represent an effective mechanism to facilitate phenotypic suppression if older individuals are able to exploit the natural ontogenetic asymmetry in competitive ability between adults and young to maintain later adult asymmetries in competitive ability. Although senescence has the potential to weaken covariance between competitive ability and age as adults grow older, asymmetries may be reinforced if older individuals may gain relatively more from escalating in contests compared with younger ones due to lower future reproductive opportunities (Korona 1991).

An individual's ability to respond plastically to opportunities to increase dominance status by filling vacancies that arise in a hierarchy is usually framed as an adaptation to some lifetime probability of such opportunities arising that remains reasonably

reliable through evolutionary time (Shreeves & Field 2002; Field *et al.* 2006).

However, our model suggests that this plasticity may be better understood in the context of its origins. Specifically, if contributions to long-term population growth rate are overwhelmingly provided by dominant individuals, the ability of subordinate individuals to respond plastically to dominance vacancies is likely to be a consequence of the removal of the conditions causing phenotypic suppression (e.g., Korb *et al.* 2009). Subordinate individuals may then be driven to favour philopatry over dispersal due to the future fitness benefits associated with queuing when suppression is relaxed, although our study suggest that queuing prospects will be strongly dependent on the mechanism of dominance inheritance from parent to offspring.

Our findings suggest that the skew in reproductive value towards top-ranked individuals will be stronger under strict parental rank inheritance than when inheritance is broadly age-based. As such, we might predict there to be positive selection for strict parental rank inheritance in nature. The difference in skew occurs because subordinate adults are prevented from migrating up the dominance hierarchy within their lifetime when inheritance is strict, and are instead pushed down the hierarchy due to recruitment by more dominant adults. Such inheritance is observed in many cercopithecoid primates and the spotted hyaena (Holekamp & Smale 1991), where mothers use aggressive behaviours to establish their offspring's dominance over subordinate adult competitors. Nonetheless, mothers will still ensure dominance over their own offspring, and it is this subtle suppression that should maintain asymmetries in dominance status and generate the severe skew in

reproductive value predicted by our model. Interestingly, our model thus predicts that the erosion of additive genetic variation for traits relating to dominance should be strongest when rank inheritance is strict. Accordingly, phenotypic variation in such traits should be maintained through the evolution of mechanisms involving ‘broad-sense’ heritability, such as environmental or maternal effects, that mediate plastic developmental trajectories. This is consistent with the maternal enforcement of rank acquisition observed in cercopithecoid primates and the spotted hyaena (Holekamp & Smale 1991).

However, we show that such a strong inheritance mechanism may make groups particularly vulnerable to extinction unless the effects of contest competition on vital rates are relatively weak. The reason for this vulnerability is that strict inheritance of rank will lead to a severe skew in reproductive value even when contest competition is relatively low, and will become even more severe as the effect of dominance on survival and/or reproduction strengthens. The result is that subordinate individuals will abandon groups at very small group sizes under strict inheritance, which will lead in some cases to negative growth rate and a strong Allee effect. In contrast, we show that groups with a weaker rank inheritance mechanism, in which there is an age-based component to dominance (our ‘cohort’ mechanism), are much less vulnerable to extinction. This is because even with near total complete reproductive suppression (our ‘Type 1’ contest regime), the skew in reproductive value towards dominant individuals will not be strong enough to drive subordinates to leave to form new groups that have negative growth rate. Perhaps counter-intuitively, the skew in reproductive value towards the alpha individual when dominance

inheritance was strict and contest competition was relatively weak was actually stronger than when dominance inheritance was cohort-based and there was near total reproductive suppression. Consistent with this, traits strongly predicting the acquisition of dominant status in cooperatively breeding meerkats (which, broadly, fit the latter category) have been shown to have some, albeit low, additive genetic variance (Hodge *et al.* 2008; Huchard *et al.* 2014).

These patterns of group size, fission, and extinction may explain why we do not see maternal rank inheritance mechanisms in cooperative breeders, which are characterised by near total reproductive suppression. Indeed, maternal rank inheritance is a rare phenomenon, only observed in the females of some societies in which reproductive skew is relatively low (e.g., Wasser *et al.* 2004). Instead, the relative resilience of groups with cohort-based dominance inheritance may provide insight as to why age is such a prevalent mediator of dominance across taxa (Post 1992; Clutton-Brock & Huchard 2013). However, further insight into the relationships between the strength of contest competition and dominance rank inheritance mechanisms will require more extensive modelling of species life histories. For example, the eco-evolutionary dynamics of social dominance may be influenced by intergenerational overlap within reproductive stages, or broods with multiple offspring, and this will in turn affect the dynamics of group fission and its demographic consequences.

Our eco-evolutionary approach to exploring how contest competition can drive group fission may also provide key insight into long-standing debates regarding the

evolution of ‘altruistic’ helping behaviours that are characteristic of cooperative breeders and eusocial species. It is widely accepted that group living may evolve due to the costs associated with being solitary or dispersing (see Krause & Ruxton 2002 for review; Clutton-Brock 2009). Our findings are consistent with this view, and further show that sociality or philopatry also persists in the presence of dominance hierarchies, provided that contest competition is relatively weak or there is a probability of future increases in dominance status (i.e., through reproductive queuing). When reproductive skew is very high and the probability of acquiring dominance is minimal, researchers have generally invoked inclusive fitness benefits to explain why subordinate individuals remain in their natal group (see Clutton-Brock 2002, 2009; Nowak *et al.* 2010; Abbot *et al.* 2011). This is apparently supported by the wealth of ‘helping’ behaviours and divisions of labour that aid the fitness of related dominant individuals in species with such skew (Koenig *et al.* 1992; Clarke & Faulkes 1997; Cant & Field 2005; Wilson & Hölldobler 2005; Clutton-Brock 2009).

However, others have argued that kin selective benefits may be a consequence, rather than a cause, of eusociality (Nowak *et al.* 2010), and there is a general recognition that individuals in cooperatively breeding groups aren’t systematically more closely related than those in other types of social group (Clutton-Brock 2002). Our findings demonstrate that grouping can form under conditions of severe reproductive skew without the need for inclusive fitness benefits when there is some cost to dispersal, but only if offspring inherit dominance rank within their age cohort rather than directly below their parent. Consistent with this result, comparative studies in birds, mammals, and Hymenoptera have shown that cooperative breeding

and eusociality have exclusively evolved from socially monogamous lineages (Arnold & Owens 1998; Hughes *et al.* 2008; Lukas & Clutton-Brock 2012). While heightened relatedness in monogamous groups has generally been the assumed driver of cooperative breeding or eusociality (Lukas & Clutton-Brock 2012; Young & Bennett 2013), our study suggests that social monogamy provides suitable conditions for dominance asymmetries to be maintained under contest conditions through the suppression of younger individuals in a broadly age-based rank inheritance system. Once this suppression emerges, driven in part by the costs of dispersal leading to higher levels of competition in the natal territory, individuals might increase their fitness through kin-selected behaviours, such that inclusive fitness benefits might be a consequence rather than a cause of such social structure.

In our model, we also show that when stable or growing groups fission based on decisions that maximise individual fitness measures (which take into account the probability of group extinction), the resultant two daughter groups may have negative growth rate or be vulnerable to negative impacts of demographic stochasticity. However, in many cases, their large, parent group, was characterised by a higher, positive growth rate, and was thus less vulnerable to extinction. Therefore, one implication of our model is that these parent groups may outcompete daughter groups by virtue of their higher growth rate. This would result in the evolution of groups containing some individuals that do not disperse despite costs to their own reproductive value (i.e., their reproductive value would actually be higher if they left the group). Multi-level selection process (in this case at the individual and group level) may thus also play a role in the maintenance of large groups with severe

reproductive skew. Rather than requiring the presence of cooperative or altruistic individuals, or even direct fitness benefits to subordinate individuals through group augmentation (e.g., Kokko *et al.* 2001; Clutton-Brock 2002), the persistence of such groups may merely reflect a ‘demographic trap’ with respect to subordinate individuals, in which group-level selective forces outweigh individual-level ones.

To conclude, we propose that contest competition represents a distinct and fundamental force in the evolutionary process, underlying a wide range of biological phenomena with far-reaching consequences. Contest is manifest as social dominance, driven by conditions permitting monopolisation of limited resources. Unlike scramble, its action is thus dependent on the presence of phenotypic asymmetries between individuals. The importance of considering evolution in a demographic framework has long been recognised (MacArthur & Levins 1964; Levins 1969; Roughgarden 1971), but has only recently started to be formally incorporated in the modern evolutionary synthesis (Metcalf & Pavard 2007; Schoener 2011). Such an eco-evolutionary approach highlights the importance of competitive forces in the evolutionary process. However, research conducted in an eco-evolutionary framework to date has generally focussed on scramble-like effects. None have considered contest competition, which necessarily involves animal behaviour. Our study suggests that developing theory that incorporates contest competition and animal behaviour into this framework will prove fruitful in generating testable hypotheses regarding the evolutionary causes and consequences of the phenomenon of social dominance, and the population-level effects of individual variation in behaviour.

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Chapter 6

Discussion

The acquisition of resources – such as food, mates, breeding sites, territories, or safety from predation – is fundamental to an individual's ability to survive and reproduce. Given the expectation that individuals will generally face some level of uncertainty regarding the distribution of these resources through space and time (Barnard & Sibly 1981; Clark & Mangel 1984; McNamara *et al.* 2006; McLinn & Stephens 2010; Trimmer *et al.* 2011), a large body of recent research has focussed on how individuals might gain fitness benefits from collecting information about their environment to improve the efficiency of resource acquisition (see Danchin *et al.* 2004; Dall *et al.* 2005; Kendal *et al.* 2009b; McNamara & Dall 2010; Rieucou & Giraldeau 2011). However, this research has generally overlooked the competitive processes that might systematically facilitate or constrain an individual's ability to use any information that it has collected. Such competitive forces are likely to be general, given that the heterogeneous resource distribution that drives individual uncertainty is likely to covary strongly with resource limitation, the basis of biological competition.

In the main body of this thesis, I have developed a conceptual framework for considering the causes and consequences of interdependencies between the individual benefits of information use and competition between individuals over limited resources (*Chapter 2-4*). This has led in particular to insights regarding the potential importance of social information use as a key behavioural mechanism underpinning contest competition when individuals face uncertainty over resource distribution. Under these conditions, individuals with high competitive ability may need to collect and use social information to facilitate the phenomenon of social

dominance. Given this framework, and the widespread empirical evidence in support of the expected fitness benefits of dominance (see Ellis 1995 for review; van Noordwijk & van Schaik 1999; Field *et al.* 2006; Clutton-Brock & Huchard 2013), I proceeded to develop a model exploring the eco-evolutionary dynamics of dominance (*Chapter 5*). This was the first attempt to date to use an eco-evolutionary approach – in which feedback loops between ecological and evolutionary processes are explicitly considered (Schoener 2011; Smallegange & Coulson 2013) – to study the consequences of between-individual variation in behaviour on long-term evolutionary and population dynamics. In this Discussion, I briefly summarise how the findings contained within this thesis combine to improve our understanding of the evolutionary ecology of animal information use and social dominance.

The evolutionary ecology of animal information use in a competitive context

While early studies investigating how individuals might benefit from collecting and using information to reduce environmental uncertainty did so in an explicitly competitive context (Barnard & Sibly 1981; Clark & Mangel 1984), the proliferation of research into animal information use over the past decade has generally overlooked competitive processes. The result has been that, despite rapid developments in our understanding of the importance of social information in the spread of behavioural innovations and the trade-offs between the efficiency of relying on personal versus social information, we know very little about how general competitive forces might facilitate or constrain an individual's ability to use information. In this thesis, I have proposed that a more systematic consideration of the spatiotemporal distribution of the resources about which individuals collect

information should provide insight into the influence of competition on patterns of individual information use across taxa.

I began with an observational study demonstrating that individual baboons with low competitive ability are limited in their ability to carry out behaviours normally associated with the use of social information when resources can be monopolised by dominant competitors (*Chapter 2*). Following from this finding, I developed a general model to explore animal information use in a competitive, social context in which individuals face uncertainty regarding resource distribution (*Chapter 3*). This study was a generalisation of the producer-scrounger model (Barnard & Sibly 1981; Vickery *et al.* 1991; Giraldeau & Caraco 2000), showing how three elements of ‘resource ecology’ – scarcity, depletion rate, and monopolisability – could interact to determine both within- and between-individual variation in social information use. The general effect of resource scarcity was to increase the strength of scramble competition between individuals. Provided that producers were not able to deplete their resource discoveries rapidly, social information about such discoveries remained relevant and cheaper to collect than personal information, such that all individuals benefitted from using social information regularly. When resources were less scarce, scramble competition was weaker, and individuals benefitted less from using social information. Under these conditions, finding resources personally was not much more difficult than attending to the discoveries of others, and didn’t necessitate resource sharing, due to the incidence of simultaneous resource discoveries at the group level.

In this model, the potential for contest competition arose when resources were monopolisable, provided that producers could not deplete their resource discoveries rapidly. Because contest competition occurs when individuals with high competitive ability are able to enforce inequity in access to resources across a group, it can lead to fundamentally different outcomes to conditions in which only scramble can occur (Milinski & Parker 1991; Sutherland & Parker 1992; Łomnicki 2009). As such, when resources were monopolisable, the effect of resource scarcity on patterns of social information use was changed. Specifically, when resources were scarce, only the alpha individual could benefit from social information, using it to locate resources which it could then monopolise in a despotic fashion. In this way, contest competition was maximised, and subordinate individuals were constrained in their ability to use social information. As resources became less scarce, such that simultaneous discoveries could occur, social information use actually increased because the alpha individual could not possibly monopolise all resource discoveries. Instead, other individuals were able to use their dominance in combination with social information in a similar way to the alpha individual. The consequence of this was that the individual benefits of contest competition were less skewed, decreasing more gradually with competitive ability in the fashion of a linear dominance hierarchy. Finally, when resources were common, social information use declined again, because relatively dominant individuals could no longer make contest competition effective by combining their high competitive ability with social information use. Instead, individuals of all ranks benefitted the most from discovering resources themselves, and contest competition disappeared.

The framework that emerged provided predictions regarding how resource scarcity, depletion rate, and monopolisability should combine to determine both average levels of, and consistent between-individual differences in, social information use within a group. To test the predictions of the model regarding important linkages between social information use and dominance, I conducted a feeding experiment with wild chacma baboons (*Chapter 4*). Specifically, I was able to show that, when individuals face uncertainty regarding the distribution of monopolisable resources, exclusivity of social information use to dominant individuals is vital to generating the asymmetric payoffs that characterise contest competition and are fundamental to the phenomenon of social dominance. Interpreted on a shorter ecological timescale, these same insights suggest that resource distribution can modulate an individual's ability to use social information based on its competitive ability, and this may impede information flow through a group. Such flow is important for the spread of behavioural innovations, and vital to the evolution of cumulative culture (Allen *et al.* 2013; Hoppitt & Laland 2013), so understanding individual constraints on social information use should be a primary goal of future research into social learning.

Resource predictability affects linkages between information use and competition

The framework outlined thus far was based upon the producer-scrourer model (Barnard & Sibly 1981; Vickery *et al.* 1991), generalised to capture a wider diversity of environmental conditions to facilitate the study of social information use across a broader range of resource types and taxa. This approach provides an ideal platform for developing testable predictions regarding how resource distribution should modulate interdependencies between competitive processes and the benefits of

using social information. However, the producer-scrounger model has some key assumptions that warrant further exploration, since their violation may make empirical tests of the model's predictions difficult or invalid, confounding our understanding of animal information use and how it can be affected by competition over resources. Specifically, the producer-scrounger model is set up such that all individuals are assumed not to have perfect information about the distribution of limited resources in their environment (Barnard & Sibly 1981; Vickery *et al.* 1991). This uncertainty makes new information – which requires search effort – valuable, and thus vulnerable to cheaters (i.e., scroungers in this case; Barnard 1984; Giraldeau & Dubois 2008). However, once a resource discovery is depleted, the game is assumed to restart, such that there is no accumulation of 'prior' information by individuals through time.

The consequence of this set-up is that the scrounging of a producer's discovery necessarily reflects social information use – the exploitation of information produced by others in order to access resources. This coupling between scrounging and social information use will not be a necessity in many natural environments, yet theoretical predictions that follow from producer-scrounger models are based upon an assumption of such coupling. For instance, if there is some predictability in resource distribution through time and space, individuals might be able to generalise socially acquired information to use it outside of its original context in time and/or space. This will allow individuals to accumulate prior information about their environment that can be utilised to acquire resources in both a 'producer' or 'scrounger' context. At its most extreme (a completely predictable environment in which individuals have

perfect information), we should expect convergence with models of the ideal free distribution (e.g., Fretwell & Lucas 1970; Parker & Sutherland 1986; Humphries *et al.* 2001; Krivan *et al.* 2008), reminding us that competitive processes are an integral part of access to limited resources.

The feeding experiment presented in this thesis (*Chapter 4*) represents the first empirical study to explore these concepts, demonstrating the importance of considering when social information use should and should not be tightly coupled to competitive interactions between information generators and exploiters. At the start of each experimental trial, individual baboons were naïve to the heterogeneous distribution of food across an arena of monopolisable patches. Under these initial conditions, immediate opportunities to use social information generally represented detecting a competitor's discovery and exploiting it in the presence of that competitor (i.e., 'scrounging' behaviour). Only socially dominant individuals were able to benefit from this approach to access the top quality patches with efficiency. Low-ranked individuals were constrained in their ability to use social information and competitively excluded from high-quality resources. This dynamic acted to maximise contest competition across a group, and supported the predictions of the model presented in *Chapter 3*.

However, the movement of baboons between patches prior to their full depletion meant that occasional opportunities arose for individuals to collect social information generated by a competitor occupying a resource patch, and then use this information to enter this patch once unoccupied. This acted to illustrate how the

competitive restrictions associated with social information use might be relaxed by decoupling it from scrounging behaviour. As dominant individuals vacated patches, the consequence of this decoupling was that subordinate individuals were able to reap some benefits from using previously collected social information to preferentially enter unoccupied, high-quality patches.

There is an important distinction, then, between scrounging behaviour, which represents an observable social interaction between individuals at a resource that has also been termed ‘joining’ or ‘kleptoparasitism’ (Giraldeau & Beauchamp 1999; Vahl *et al.* 2005; McCormack *et al.* 2007; Giraldeau & Dubois 2008), and social information use, which may or may not be manifest as scrounging behaviour. While an individual’s ability to scrounge will be strongly influenced by contest competition when resources are monopolisable to some degree (*Chapter 2 and 4*), its ability to use social information may depend on whether the spatiotemporal distribution of resources forces a strong linkage between social information use and scrounging. The degree to which the removal of this linkage will actually allow subordinate individuals to reduce contest competition may then further depend on whether dominant individuals also possess such information. If some level of environmental predictability means that information can be reused or generalised in time and space, it follows that dominant individuals may also benefit from holding on to it. The difference should be that dominant individuals would be able to use any information freely without regard to the competitive context. In contrast, subordinate individuals must first collect information that can be generalised and then evade dominant competitors in time and space in order to use it effectively.

The results of the feeding experiment presented in *Chapter 4* provide some insight into the challenges that subordinate individuals might face in terms of evading dominant individuals in time and space. The study showed that social information use could be decoupled from scrounging behaviour, but subordinate individuals were only able to act on this opportunity to increase their feeding success once dominant individuals had vacated the high-quality patches. The consequence was a reduction in the strength of contest competition towards the end of a feeding trial, but this had little effect on the overall disparity in resource access associated with dominance across a whole trial. Earlier in each trial, when the majority of the available food was consumed, any decoupling did not allow subordinate individuals to access high-quality patches, since such patches were severely limited in number and high-ranked individuals used social information and their dominance to locate and monopolise them. However, the overall purpose of the experiment was to illustrate how some level of spatiotemporal predictability in resource distribution should allow prior information to be collected (see Valone 1991; Dall *et al.* 2005; Trimmer *et al.* 2011; Marshall *et al.* 2013), and how this might permit the decoupling of social information use from competitive social interactions.

Under natural conditions, opportunities to evade dominant individuals in time and space to use prior, socially collected, information may be more likely. It is clear that individuals living in either ephemeral or stable social groups will not always be in each other's presence. Furthermore, studies of animal social networks have demonstrated how societies are generally dynamically structured, such that different pairs of individuals will vary in their association strengths through time, both in

terms of their probability of being in close proximity or of socially interacting (Sih *et al.* 2009; Wilson *et al.* 2013, 2014; Castles *et al.* 2014; Carter *et al.* 2015). Therefore, subordinate individuals may be able to secure benefits akin to the ‘finder’s share’ associated with resource discoveries in the producer-scrounger model if they are able to use social information to efficiently access valuable resources before the arrival of any dominant competitors.

The degree to which this process might be able to weaken the effects of contest competition will likely depend on whether dominant individuals also possess such information, as well as the overall scarcity of resources. Hirsch (2007) generated a qualitative model of feeding competition predicting that dominant individuals should position themselves at the front of a foraging group when they know the location of rapidly depleting, monopolisable resources. This prediction was corroborated by a feeding experiment in chacma baboons, showing that when all individuals had been given the opportunity to learn about the location of a high-quality feeding site, the alpha male baboon became the group leader, reaching the site first each day and monopolising it (King *et al.* 2008). In contrast, when the baboons were naïve to the location of such feeding sites, the alpha male was less likely to be the group leader. This finding is consistent with studies suggesting, under conditions of resource uncertainty, dominant individuals should optimise their detection of social information to exploit competitors by adopting a more central group position (Barta *et al.* 1997; di Bitetti & Janson 2001; Hirsch 2007; King *et al.* 2009). Future research might consider systematically how the predictability of resource distribution through space and time interact with the other elements of resource ecology considered in

this thesis to influence the relationships between information use and competition. At present, these ideas have received no research attention. However, they may prove important in understanding and predicting both constraints on information flow within groups, and the role of social information use in the enforcement of contest competition.

Behavioural mechanisms underpinning the eco-evolutionary dynamics of dominance

Social dominance is a widespread and familiar biological phenomenon, occurring across a broad taxonomic distribution and associated with all types of social organisation (Bernstein 1981; Kaufmann 1983; Ellis 1995; Moore *et al.* 2002; Hughes *et al.* 2008; Clutton-Brock 2009). The prevalence of dominance structures in natural systems is suggestive of a positive relationship between dominance and fitness, and this has been confirmed in the vast majority of cases studied (see Ellis 1995 for review; van Noordwijk & van Schaik 1999; Field *et al.* 2006; Clutton-Brock & Huchard 2013). Resource monopolisation, or contest competition, is fundamental to such benefits (Moore 1990; Clarke & Faulkes 1997; Cotton *et al.* 2006; Piper *et al.* 2006; Holman *et al.* 2010). Because resource monopolisation represents an enforced inequity in access to resources across a group or population, the mechanisms underlying contest competition are fundamentally different to scramble competition. Scramble represents the general effects of resource limitation on an individual's survival and reproduction (Nicholson 1954; Parker 2000), which might influence individuals differently depending on various genotypic or phenotypic factors under selection (Kokko & López-Sepulcre 2007; Schoener 2011). In contrast, contest competition relies explicitly on the maintenance of between-individual

differences in those morphological, physiological, and behavioural traits that generate and mediate asymmetric contests (e.g., Clarke & Faulkes 1997; Hodge *et al.* 2008; Korb *et al.* 2009; Giles *et al.* 2015).

Population ecologists have long expected important population dynamic processes such as density dependence and the Allee effect to be underpinned by processes at the level of individual behaviour (Sutherland 1996; Łomnicki 1999; Sutherland & Norris 2002), but these links have often been difficult to establish (Stillman & Goss-Custard 2010; Evans 2012; Marshall *et al.* 2012b). However, the reliance of contest competition on behavioural interactions that mediate dominance relationships provides a uniquely simple, but biologically general, opportunity to explore such links. Specifically, dominance can only exist through between-individual variation in behaviour, and its effects on fitness are relatively straightforward. In *Chapter 5*, I built a simple demographic model to study the evolutionary and population dynamic consequences of social dominance hierarchies, founded on these basic, but well-supported, assumptions. This study suggested that regulation of population growth rate could emerge simply from the effects of contest competition on individual survival and reproduction. By building this model in an eco-evolutionary framework, I was then able to explore the consequences of social dominance on long-term multigenerational fitness. This generated insights into (1) the potential roles of developmental plasticity and suppression in maintaining between-individual variation in phenotypic traits associated with differences in dominance rank; (2) the dynamics of dispersal versus philopatry; and (3) the evolutionary ecology of cooperative breeding and eusociality. These insights were discussed in detail within

Chapter 5. Consequently, I instead focus below on the insights generated elsewhere in this thesis regarding the possible behavioural mechanisms underpinning social dominance, and how these mechanisms should be influenced by the ecology of resources.

In order for dominance to emerge from individual variation in competitive ability, resources must be economically defensible (e.g., Grant 1993). That is, the benefits accrued by an individual with high competitive ability by defending a resource must outweigh any costs associated with such defence. This trade-off is the basis of resource defence theory (Grant 1993), and empirical tests of its predictions have frequently shown that individuals with relatively high competitive ability will outcompete others when resources are clumped but not when dispersed (Theimer 1987; Grant & Guha 1993; Robb & Grant 1998; Vahl *et al.* 2005). However, the experimental settings in which such resource monopolisation has generally been studied present individuals with an environment in which resources are presented freely and there is little or no uncertainty associated with their distribution. Similarly, studies of the ideal free (and despotic) distribution that consider individual variation in competitive ability assume that animals have perfect knowledge of their environment (Fretwell & Lucas 1970; Milinski & Parker 1991; Krivan *et al.* 2008). These approaches do not consider the potential importance of resource scarcity in the benefits of monopolisation, and are at odds with the widespread expectation that individuals will often face uncertainty about the spatiotemporal distribution of vital resources.

The model presented in *Chapter 3* of this thesis provided a framework in which to consider resource monopolisability and scarcity in unison when attempting to understand the ecological conditions that should permit individuals with high competitive ability to exert contest competition. This model suggested a crucial role for social information use in generating the fitness advantages of dominance alongside competitive ability, building on previous developments in the integration of resource defence theory and social information use (Barta & Giraldeau 1998; Dubois *et al.* 2003; Dubois & Giraldeau 2005). Specifically, the model predicted that in order for despotic systems to evolve under conditions of resource uncertainty, resources need to be monopolisable, scarce, and not rapidly depleted, such that alpha individuals can combine social information use and competitive exclusion to generate severe conditions of contest competition. As monopolisable resources became less scarce, simultaneous resource discoveries meant that contest competition was less skewed, such that multiple individuals could use a combination of social dominance and social information use to gain fitness benefits relative to subordinate competitors. Eventually, when monopolisable resources became extremely common, there was no benefit to using social information, and dominant individuals were unable to exert contest competition.

Empirical support for these predictions regarding the importance of social information use in the benefits of dominance was provided experimentally in *Chapter 4*, as outlined above. Elsewhere, field studies in common loons (*Gavia immer*) have shown that individuals collect social information about the past breeding success of competitors, but only some use this information to usurp the

best breeding territories (Piper *et al.* 2000, 2006). The fact that others do not may reflect their lower social rank, although these studies lacked the data to establish this relationship.

Social information use may be less important for dominance when there is less uncertainty associated with resource distribution. Nonetheless, resource monopolisability alone should still be insufficient to drive contest competition when individuals differ in competitive ability: such resources should also be relatively scarce (*Chapter 3*). As shown in the feeding experiment presented in *Chapter 4*, intermediate levels of predictability in resource distribution through space and time may allow social information use to be decoupled from the competitive context in which it is collected. The degree to which this might allow individuals with low competitive ability to delay their use of such social information for a context with no competitive constraints in the real world is unclear. For example, such information may be useless if individuals with higher competitive ability also possess it, or if contexts with no competitive constraints are unlikely to arise (Piper *et al.* 2000, 2006; e.g., King *et al.* 2008; Pärt *et al.* 2011). More research is required to fully understand the interdependencies between information use and competitive processes when some level of predictability in resource distribution means that individuals have the opportunity to accumulate prior information. Doing so will help to elucidate the ecological conditions and behavioural mechanisms that must combine to underpin social dominance, a general biological phenomenon with far-reaching consequences.

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Appendix 1

Supplementary material for Chapter 4



Figure S1.1. Satellite photograph showing the naturally flat, cleared site (dashed box) in which a feeding arena was set up within one of the two study troops' home ranges.

Table S1.1. Factors (including control variables) affecting the probability of entering a top quality patch in T1 (P1.1) and T4 (P3.1), individual feeding rate in T1 (P1.2) and T4 (P3.2), and the probability of entry into a patch in consecutive 10 s intervals (P2).

Prediction	No. models averaged	Response	N	Fixed Effect	β	s.e.	Relative contribution to final model
P1.1	1	Probability of entering highest quality (T1)	477	Intercept	-1.37	0.58	1
				Rank	0.13	0.75	1
				Treatment_HV	-2.57	0.80	1
				Troop_L	0.38	0.30	1
				Block_2	-0.22	0.31	1
P1.2	2	Feeding rate (T1)	434	Rank * Treatment_HV	5.18	1.13	1
				Intercept	-0.41	0.16	1
				Rank	0.21	0.20	1
				Treatment_HV	-0.48	0.21	0.93
				Troop_L	-0.05	0.08	1
P2	1	Probability of patch entry	1342	Block_2	0.07	0.07	1
				Rank * Treatment_HV	0.60	0.27	0.93
				Intercept	-1.72	0.33	1
				Proportion prior time occupied (PPTO)	2.01	0.71	1
				Currently occupied_Yes	1.01	0.45	1
P3.1	2	Probability of entering highest quality (T4)	240	Interval	0.00	0.00	1
				Troop	0.10	0.27	1
				PPTO * Currently occupied_Yes	-3.88	0.78	1
				Intercept	-1.09	0.41	1
				Rank	0.26	0.54	0.59
P3.1	2	Probability of entering highest quality (T4)	240	Treatment_HV	0.82	0.55	1
				Troop_L	-0.05	0.28	1
				Block_2	0.24	0.29	1
				Rank * Treatment_HV	0.55	0.83	0.59
				Intercept	-2.00	0.20	1
P3.2	3	Feeding rate (T4)	219	Rank	-0.22	0.25	0.61
				Treatment_HV	0.01	0.08	0.08
				Troop_L	-0.17	0.14	1
				Block_2	-0.09	0.13	1
				Rank * Treatment_HV	-0.01	0.10	0.08

HV: High variability; reference category for treatment is 'Low variability'. Reference category for troop and block is 'J' and '1', respectively. In model P2, the reference category for 'Currently occupied' is 'No'. Note that any patch entry occurring during an interval where the patch was 'currently occupied' was considered a 'scrounge', while the opposite was considered a 'produce'.

Feeding benefits of top quality patches in T4

We asked whether individuals still gained higher feeding rates during T4 by accessing patches that had been provisioned as top quality ('Quality 4'), as opposed to lower quality. We analysed these data following the protocol for analysis of feeding rate described in *Chapter 4*, but including only a single fixed effect: whether or not the patch was top quality or not. This effect was assessed using a likelihood ratio test. We removed all data from 'Quality 1' patches from this analysis, since these were never provisioned.

Consistent with our predictions, individuals had a higher feeding rate during T4 in top quality patches than in lower quality patch types ($N = 86$, $\chi^2 = 11.49$, $p = <0.001$; Fig S1.1).

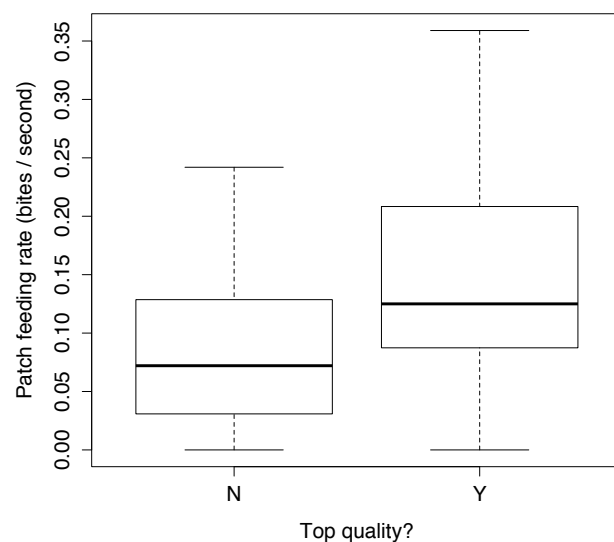


Figure S1.2. Differences in individual feeding rate in top quality ('Y') versus lower quality ('N') patches in T4. Each box is split by the median value, and enclosed by the first and third quartiles; whiskers extend to the most extreme data point in each direction.

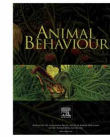
Appendix 2

Co-authored publications



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Commentary

Social networks created with different techniques are not comparable

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The recent application of social network analysis to animal populations has provided a tool to quantify group dynamics and individual social positions, which may enhance our understanding of the costs and benefits of sociality and the evolution of behavioural strategies within societies. Despite this, uncertainties remain about whether comparisons can be drawn between studies in which different sampling techniques have been used. We compared social networks constructed from two interaction and three proximity techniques that are frequently used in the literature, at both the ego network and global network levels, using data collected annually for two troops of chacma baboons, *Papio ursinus*, over 3 years. We obtained very different results at both the global and individual levels, demonstrating the clear distinction between networks built using different interaction and proximity techniques. While interaction techniques may be comparable at the whole global level, proximity techniques were not, and we found the opposite at the ego network level: proximity techniques could be compared whereas interaction techniques could not. As there was a clear distinction between the networks created, caution should be taken when using proximity as a proxy for social interactions (and vice versa) in social network studies. Further, our results showed high variation between troops and study seasons, reemphasizing the importance of incorporating temporal change in the analysis of social networks. Researchers should consider the effects of sampling technique on the networks produced when comparing networks created from different techniques.

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Sociality has played an important role in the ecology and evolution of many species and vice versa (Croft, James, & Krause, 2008; Krause & Ruxton, 2002; Silk, 2007). The patterns of interactions and the relationships that individuals form can have important fitness consequences by affecting, for example, longevity (Silk et al., 2010), reproductive success (Cameron, Setsaas, & Linklater, 2009) and offspring survival (Silk et al., 2009). These patterns of interaction also underpin the overall structure of society which can determine the transmission of disease (Hamede, Bashford, McCallum, & Jones, 2009) and the flow of information (Voelkl & Noë, 2008). By understanding individual behaviour, patterns of association and

population-level structure, biologists can unlock the function, evolution and implications of social living (Croft et al., 2008).

Despite the importance and fitness implications of an individual's social network position, little attention has been given to how the connections between individuals that make a social network are defined (but see Lehmann & Ross, 2011). Ideally, all interactions between individuals would be recorded; however, this is extremely difficult to achieve in wild populations (Croft et al., 2008). Instead, an array of techniques has been developed to sample social interactions in populations (Altmann, 1974; Whitehead & Dufault, 1999). These techniques can be grouped into two overarching categories. First, 'interaction methods' comprise techniques based on observed physical contact or behavioural interactions between individuals (e.g. grooming in chacma baboons, *Papio ursinus*; Henzi, Lycett, & Weingrill, 1997). Second, 'proximity' or 'association methods' are used when interactions cannot be observed, such as with aquatic animals (e.g. dolphins, *Tursiops* spp.; Lusseau, 2003) or 'undemonstrative' species (e.g. kangaroos,

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Macropus giganteus: Carter, Macdonald, Thomson, & Goldizen, 2009). Under this category, a connection is assumed through spatial proximity or shared resource use. Although these two broad techniques may suit the study species or purpose of the research in question, they may present a different perspective of the network. For example, there may be many reasons for individuals to associate that do not relate to a positive social relationship (Pinter-Wollman et al., 2014). These include periods of shared resource use (e.g. shade) or for exploitation of information (Barton & Whiten, 1993), and each aspect may affect individuals' social environment in different ways. Consequently, comparing populations or species for which different techniques have been utilized is unlikely to be justified without an investigation of different sampling effects in the same population.

Few studies have attempted social network comparisons within species using different data collection techniques. This is a potential oversight, as comparisons could lead to better understanding of the aspects of social life determining an individual's fitness and hence the evolutionary forces shaping social behaviour (Davies, Krebs, & West, 2012). Better understanding of how different techniques affect the resulting network will make comparisons more robust and powerful. To our knowledge, only three studies have directly compared networks constructed using different data collection techniques. Lehmann and Ross (2011) used multiple behavioural interactions to determine networks in a troop of olive baboons, *Papio anubis*. The behaviour used to create a network strongly affected its shape and the position of individuals within the network, leaving the authors to conclude that the use of multiple types of social interactions was necessary to gain the most accurate understanding of the network. Further, Madden, Drewe, Pearce, and Clutton-Brock (2011) studied behavioural connections in meerkats, *Suricata suricatta*, and came to a similar conclusion. However, both of these studies compared only networks based on interactions. A study by Hobson, Avery, and Wright (2013) utilized interaction and association techniques in a captive setting to examine how networks form over time and found a clear difference between the two techniques. However, no studies have yet explicitly compared weighted networks that have been constructed using both proximity and interaction techniques in a wild population. This is an important comparison as, in a large proportion of wild species and systems, proximity data are often used as a substitute where interactions cannot be directly observed.

We aimed to make a thorough comparison of the two broad categories of techniques used to gauge sociality in animal populations, namely proximity and interactions between individuals. We calculated ego- and global-level network metrics to compare these techniques when applied to proximity and interaction data from chacma baboons, collected over 3 years. Chacma baboons are an ideal study system as the social environment of baboons is well studied (Henzi, Lusseau, Weingrill, Schaik, & Barrett, 2009; King, Clark, & Cowlshaw, 2011; King, Douglas, Huchard, Isaac, & Cowlshaw, 2008; Silk et al., 2010), social relationships are highly differentiated (Silk, Alberts, & Altmann, 2006) and have significant consequences for individual fitness (Silk, Alberts, & Altmann, 2003; Silk et al., 2009). Importantly for this study, chacma baboons allow for the simultaneous collection of both proximity and interaction data, facilitating direct comparison between these two widely used sampling techniques. As the overall (global) network structure and individuals' positions (local network) within it determine the characteristics of a population (Croft et al., 2008), we aimed to address two specific questions regarding these network levels. (1) Do different proximity and interaction techniques for defining a connection create structurally similar networks at the global level? (2) Do individuals exhibit similar local positions in both types of network?

METHODS

Field Site and Study Species

We studied wild baboons in Tsaobis Nature Park, a semiarid environment on the edge of the Namib Desert in the Erongo region, Namibia (22°22'S 15°44'E; for detailed information on the landscape and climate see Cowlshaw, 1997). We collected data on two habituated troops of baboons, 'L' and 'J', over 3 years (2010–2012; Table 1). In all years only adult and subadult individuals were recorded. Baboons younger than 4 years (infants and young juveniles) were not included, as infant baboons and other primates maintain a social environment similar to that of their mothers' which extends into their early juvenile years (for example, rhesus macaques, *Macaca mulatta*, Berman, 1982). Numbers of adults and subadults in the group ranged from 22–23 and 27–31 individuals in L and J troops, respectively. Females made up 74–77% of the adult population in L troop and 52–63% of J troop. Females were not chosen as focal subjects while they were in oestrus owing to documented changes in the behaviour and social connections of chacma baboons and other closely related species at these times (Kawai, 1979; Nyakudya, Fuller, Meyer, Maloney, & Mitchell, 2012). They were, however, recorded when they were involved in an interaction or connection with other individuals under observation.

Observers followed the troops from dawn until dusk collecting data on social connections using both continuous focal and scan sampling methods (Altmann, 1974). Data were collected from May to September 2010, June to August 2011 and May to October 2012 (Table 1) using Hewlett-Packard iPAQ 112 and 114 Personal Digital Assistants (Bracknell, Berkshire, U.K.) and Motorola MC35 and ES400 (Libertyville, IL, U.S.A.) with the sequence-based data entry program CyberTracker3 (<http://cybertracker.org>) and a customized spreadsheet in SpreadCE version 2.03 (Bye Design Ltd 1999), respectively. All adult and subadult baboons were individually identifiable.

Individual baboons were observed for 15–30 min periods using continuous focal sampling. Focal observations that lasted under 15 min were discarded. Individuals were sampled in a semirandom manner, balancing cumulative focal time recorded for each individual to ensure even sampling over four time periods in each day (0600–0900, 0900–1200, 1200–1500 and 1500–1800 hours). We avoided sampling the same individual within 6 h of a previous observation to maximize the independence of observations. Over the 3 years, we recorded 718 h of focal observation data for L-troop individuals and 942 h for J-troop individuals. If any individual was not present with its troop for the entire data collection season within a year, that individual was removed from the analyses for that field season. In the majority of cases, such losses of individuals were due to adult male emigration (2010: $N = 3$; 2011: $N = 1$);

Table 1
The sample sizes for each of the five sampling methods and two troops over the 3 years of data collection

Year	Troop	<i>N</i>	Chain rule scans	Distance rule scans	Nearest neighbour	Affiliative interactions	Grooming interactions
2010	L troop	23	370	394	272 h 16 min	318	7 h 43 min
	J troop	30	433	458	346 h 37 min	454	5 h 27 min
2011	L troop	23	174	247	122 h 43 min	135	4 h 31 min
	J troop	27	233	283	142 h 37 min	212	3 h 48 min
2012	L troop	22	346	412	210 h 46 min	335	11 h 20 min
	J troop	31	467	583	274 h 57 min	291	9 h 47 min

Presented are the number of individuals (*N*) and the counts of chain rule scans, distance rule scans and affiliative interactions. The nearest neighbour and grooming interactions are presented as a total time. Note that the nearest-neighbour time represents the total focal time.

however, in 2012 an adult male and female died. Our observational protocols were assessed and approved by the Ethics Committee of the Zoological Society of London, and approved by the Ministry of Environment and Tourism in Namibia (Research/Collecting Permits 1486/2010, 1486/2011 and 1696/2012).

Methods of Determining a Connection between Two Individuals

Proximity techniques for defining a connection

We recorded data using three methods to define an association using proximity techniques. First, once during every focal observation period, a distance rule scan (Ansmann, Parra, Chilvers, & Lanyon, 2012; Croft, Krause, & James, 2004; Shorrocks & Croft, 2009; Silk et al., 2003) was employed where all individuals within a 10 m threshold of the focal individual were recorded as associating. Second, during the focal observation, the nearest neighbour (Henzi et al., 2009) within 5 m of the focal individual was recorded continuously. If the focal baboon had no neighbour within 5 m, it was recorded as 'alone'. Third, a chain rule scan (Carter et al., 2009; Gazda, Connor, Edgar, & Cox, 2005) was conducted once during the focal observation period, where all individuals within 5 m of another individual were recorded as associating (see Fig. 1 for details). Scans were not recorded if all baboons could not be identified with certainty, such as when baboons were in thick vegetation, although this occurred very rarely.

Interactions used to define connections

We created two definitions for a connection via an interaction: nonaggressive social interactions and grooming interactions. Lehmann and Ross (2011) found a correlation between networks built from 'mounting' and 'presenting' interactions in olive baboons whereas the networks based on grooming differed. We therefore combined mounting and presenting with other related, nonaggressive interactive behaviours to define a connection (behaviours are described in Table 2). We refer to this combination of behaviours as 'positive interactions' for simplicity. We analysed grooming interactions separately, recording the identity of interacting individuals and the length of time for each grooming bout. Interactions were recorded as events or states during the focal observation period. Both interactions given and received were recorded; however, we analysed only interactions given (outgoing).

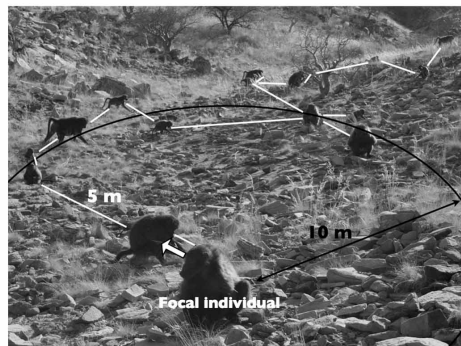


Figure 1. A visual representation of proximity methods used to define a connection. The arrow represents a connection via the 5 m nearest-neighbour rule, the white line, connections via the 5 m chain rule and the black circle represents the 10 m threshold distance for a connection via the distance rule (measures not to scale).

Table 2
Description of behaviours used to define a 'positive interaction'

Behaviour	Description
Present	An individual presents its hindquarters to another baboon
Mount	An individual mounts the hindquarters of another individual, excluding copulation
Lip-smack	An individual slaps its lips together making a 'clicking' sound in the direction of another individual
Come-hither face	An individual raises its eyebrows and pulls its ears flat against its skull in the direction of another individual
Embrace	An individual initiates and maintains contact with another individual using its arms. This is usually accompanied by other positive interactions

This is because incoming, long-distance interactions (such as come-hither faces, see Table 2 for a definition) may have been missed by the observer. Outgoing interactions were, therefore, more likely to be an accurate representation of the baboon's network given the sampling method used (Altmann, 1974). While this sampling issue does not occur with grooming interactions we chose to use only grooming given to remain consistent across all interaction techniques. We recognize that negative (agonistic) interactions are an important component of an individual's social experience; however, as we are comparing interaction techniques with three proximity techniques that are assumed to measure affiliation (for example Carter et al., 2009) we chose to limit our scope to positive interactions in this study.

Data Manipulation

Creation of matrices

We built valued, asymmetric dyadic matrices for each of the years, troops and interaction techniques and symmetric dyadic matrices for each of the years, troops and proximity techniques resulting in a total of 30 matrices. Proximity technique matrices were symmetrical because connections were recorded as undirected scans of the proximity between the focal and other baboons whereas the direction of interactions could be recorded. Each year and troop was analysed separately to account for (potential) temporal variation between years that can result from the addition or loss of individuals (Carter et al., 2009), changes in climate (Ebensperger, Rivera, & Hayes, 2012; Lusseau et al., 2004) and physiological changes in individuals (Brent, MacLarnon, Platt, & Semple, 2013; Hobson, Avery, & Wright, 2013). We calculated matrices for (1) positive interactions, (2) grooming and (3) nearest neighbour from the focal observation data. The strength of connection between dyads was calculated as (1) a proportion of the total interactions observed, (2) the proportion of the total time observed that each focal individual spent grooming another or (3) the proportion of the total time observed that each focal individual spent with a nearest neighbour within 5 m. Matrices for chain scans and distance scans were created using the MATLAB extension, SOCPROG 2.4 (Whitehead, 2009). As our sampling protocol meant that baboons may not have had enough time to show new association preferences between scans we used SOCPROG 2.4 to pool subgroups over a 2 h period (a time period based on the observed frequency of subgroup change events) discarding any repeated connections between two individuals in the same time period before applying the Twice Weight Index (TWI: Cairns & Schwager, 1987). The TWI is given by:

$$TWI_{ab} = \frac{X}{X + 2Y_{ab} + Y_a + Y_b}$$

where X equals the number of times two individuals (a and b) were observed together, Y_a denotes the number of times individual a was

observed in a subgroup (as defined by the sampling method used) while individual *b* was not (vice versa for Y_b) and Y_{ab} denotes the number of times both individuals were observed but in different subgroups (Croft et al., 2008). For each dyad, a TWI of zero represents no connection (they were never observed in the same group) while a TWI of one represents a dyad that was always seen together. This index gives double the emphasis to baboons recorded as alone to reduce the bias caused by individuals being more likely to be sighted when associating (Cairns & Schwager, 1987). We chose not to filter our edge data as we wished to analyse all edges, including rare edges (Laughlin & Sejnowski, 2003). While rare edges are weak, they may be important to the network structure and understanding of positions of individuals within it (Lusseau, Whitehead, & Gero, 2008; Voelkl, Kasper, & Schwab, 2011).

Calculation of network metrics

Using the network software UCINET 6.501 (Borgatti, Everett, & Freeman, 2002), we calculated global and ego network metrics, to examine the overall network characteristics and position of individual baboons in these networks, respectively. To describe each network's global structure for all 30 matrices, we calculated the basic and commonly used network descriptor weighted density. This is calculated as the mean strength of the connections between all dyads based on the number of interactions or times recorded together. Weighted density will equal zero when there are no connections between any individuals and one only when all individuals are connected as strongly as possible; however, a density of one is rarely recorded owing to the nature of interactions in large populations (Lehmann, Korstjens, & Dunbar, 2007; Lehmann & Ross, 2011).

Next, we assessed three aspects of an individual's centrality (position) in the network that are commonly used in animal social network analysis, measure different aspects of an individual's social environment and are biologically relevant to baboons under each data collection technique: (1) an individual's total number of direct connections (degree), (2) the proportion of dyads whose shortest path passes through the individual (Freeman's betweenness) and (3) the distance of an individual to all others through all possible paths of connection (information closeness). As we analysed only out-directed interactions (given by the focal to another individual) we used outgoing directed metrics (i.e. out-degree); the proximity associations were assumed to be undirected and as such we used undirected metrics.

Statistical Analysis

Testing for differentiated social relationships

As dyadic data are not strictly independent, we used permutation tests to determine whether social relationships within the groups were nonrandom. In these tests, we randomly permuted the observed data 5000 times and compared the distribution of the random data sets with our observed data (Lehmann & Ross, 2011). To our knowledge a permutation test for nonrandom association is not available for weighted association data, so we compared the weighted data for each network with a randomly generated set of fully connected networks (density = 1). A significant deviation from 1 demonstrates that animals are unevenly spreading their time among others, creating a global network structure. We achieved this using the two-tailed bootstrap method provided by UCINET, which is available for weighted interaction and association data and has been applied in previous studies (Lehmann & Ross, 2011). This analysis creates a random distribution of connections for permutations by sampling random subsets of the observed nodes within the network after redistributing the edges between them. We ran 5000 permutations to build the random sampling distribution.

Question 1: do different techniques create structurally similar networks?

To determine whether there were significant structural differences between networks collected from the same troop and year based on the different data collection techniques, we ran two-tailed bootstrap equivalents of the paired sample *t* test provided by UCINET using 5000 permutations. We analysed weighted data as this provides the most accurate representation of the relationships in the group (Kasper & Voelkl, 2009). This analysis compares the mean connection strengths of the two related sets of associations to determine whether there is a significant difference between them. Owing to the large number of correlations performed within each metric for each year, we used a Bonferroni correction to alter the alpha level from $P = 0.05$ to $P = 0.0125$ (0.05/4) based on four correlations per metric-year and troop; e.g. for J troop in 2010, the degree calculated by the distance rule would be tested for a correlation with the degree calculated from the (1) nearest neighbour, (2) chain rule, (3) positive interaction and (4) grooming data.

Question 2: do individuals exhibit similar local positions across networks?

We used nonparametric Spearman rank correlations in Genstat15 (Payne, Murray, Harding, Baird, & Soutar, 2012) to investigate whether individuals maintained similar rank order positions for degree, betweenness and information centrality across networks based on the different connection techniques. As for question 1, we used a Bonferroni correction to adjust the alpha level to $P = 0.0125$.

For simplicity of presentation, in our analyses we pooled the individual metrics from both troops, assuming that the relationships that we described existed in both troops. As this may not have been the case, we also analysed each troop separately to ensure that the reported correlations were not a result of between-troop variation; these results can be found in the [Supplementary material, Table S1](#).

RESULTS

Overall, our results showed that proximity and interaction measures lead to markedly different networks within the same troops and years at both the global and ego network levels. While not the focus of our study, we also observed a large amount of temporal variation between study years. First, we describe some general network characteristics generated from the different data collection techniques before addressing our two research questions.

General Network Characteristics

Each of the networks was significantly different to a theoretically fully connected network (bootstrapped *t* test: all $Z < -50$, all $P < 0.001$); thus significant network structure was present (see [Fig. 2](#) for examples of the networks built).

Globally, there was a clear distinction between proximity and interaction techniques. In general, proximity measures led to networks with a larger number of connections than networks made from interaction data, as would be expected given that individuals must be associating to interact. Proximity techniques also had the highest weighted density values in all cases (distance rule and chain rule) except for J troop in 2012 in which positive interactions led to the network with the highest weighted density ([Table 3](#)). The network based on the nearest neighbour had the lowest values in all years and for both troops, with a maximum of 0.041 (L troop 2012). This was due to individuals having a large number of connections with very weak strength as they moved among the troop.

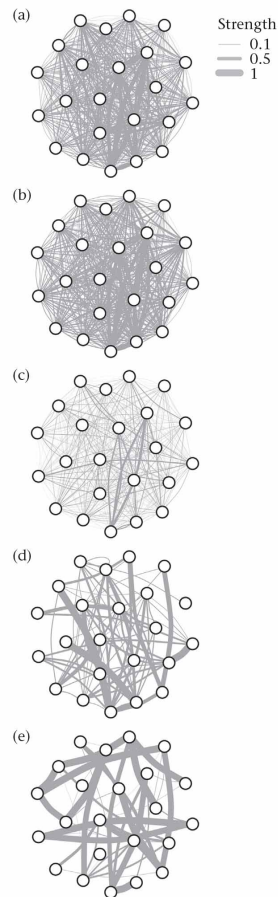


Figure 2. An example of the structure of networks for L troop in 2010 based on (a) 10 m distance scans, (b) 5 m chain rule scans, (c) 5 m nearest neighbour, (d) positive interactions and (e) grooming interactions (all other networks can be found in [Supplementary Fig. S2](#)). Nodes represent individual baboons and lines represent interactions or proximity connections between them. Connection strength is indicated by the thickness of the line, where a thicker line indicates a stronger connection (see key).

Question 1: Do Different Techniques Create Structurally Similar Networks?

The comparison of weighted data from each data collection technique showed that in all troop-year combinations few networks remained structurally nonsignificantly different (t tests; [Table 4](#)). The UCINET equivalent t tests showed that the structure of grooming and positive interactions networks were the only pair that remained consistent (i.e. nonsignificantly different) in all troop-year combinations, whereas nearest-neighbour networks were always significantly different from distance rule networks.

Table 3
Global network weighted density (average interaction frequency) for the five methods analysed (values range from 0 to 1)

Year	Method	J troop	L troop
2010	Distance rule	0.063	0.088
	Chain rule	0.076	0.095
	Nearest neighbour	<i>0.025</i>	<i>0.032</i>
	Positive interactions	0.032	0.068
	Grooming interactions	0.028	0.069
2011	Distance rule	0.064	0.073
	Chain rule	0.068	0.083
	Nearest neighbour	<i>0.023</i>	<i>0.028</i>
	Positive interactions	0.035	0.065
	Grooming interactions	0.052	0.066
2012	Distance rule	0.058	0.109
	Chain rule	0.050	0.095
	Nearest neighbour	<i>0.026</i>	<i>0.041</i>
	Positive interactions	0.059	0.079
	Grooming interactions	0.054	0.080

Values in bold indicate the highest value across the five methods in each year and italics indicate the lowest.

With respect to group-specific patterns, in J troop, chain rule and nearest neighbour were always significantly different in structure. In L troop, grooming interactions and chain rule networks were never significantly different whereas nearest neighbour and grooming interactions were. While these were the most consistent patterns, other one-off significant differences occurred across the troops and methods ([Table 4](#)).

Overall, the results suggest that interaction measures create global networks that may be comparable to other interaction measures, whereas networks built from proximity measures vary structurally from other proximity networks and interaction networks. Statistically, we found that grooming and positive interactions were not significantly different in their network structure ([Table 3](#)) whereas proximity measures varied both in their differences from interactive networks and in other proximity measures. There was also a clear trend towards proximity measures creating networks that were similar to each other with a high number of connections, whereas interaction measures were similar to each other with fewer connections. Nearest-neighbour networks stood out the most from other networks, more often than not differing from other proximity measures as well as interaction measures. Variation in the network for each troop was recorded across the years, which reflects the dynamic nature of wild populations and relationships between individuals.

Question 2: Do Individuals Exhibit Similar Local Positions Across Networks?

Spearman rank correlation analysis of the three individual-based network variables (degree, information closeness and betweenness) indicated that measures of individual centrality tended to be correlated for proximity measures, but more variable both between different interaction measures and between interaction measures and proximity measures ([Fig. 3](#), [Supplementary Table S2](#)).

Here we consider the patterns of consistency for each of the three ego network variables in turn. In the case of degree, the individual scores were largely well correlated across different techniques. In 2012, all methods led to degree positions that were correlated, with the strongest correlations occurring between proximity measures. There were fewer correlations in 2011 and 2010. In 2011, individual degree was correlated across all pairs of techniques with the exception of the correlation between positive interactions and both distance rule and nearest-neighbour

Table 4
Results of permutation *t* tests between weighted density measures of networks based on different data collection methods for L troop and J troop

Year and troop		Distance rule	Chain rule	Nearest neighbour	Positive interactions	Grooming interactions
2010 J troop	Distance rule	—	—	—	—	—
	Chain rule	2.86 (0.0040)*	—	—	—	—
	Nearest neighbour	11.90 (0.0002)* ^a	13.90 (0.0002)* ^b	—	—	—
	Positive interactions	4.90 (0.0002)*	13.90 (0.0002)*	-2.69 (0.0070)*	—	—
	Grooming interactions	4.55 (0.0002)*	5.76 (0.0002)*	-1.42 (0.1506)	-0.58 (0.5437) c	—
2011 J troop	Distance rule	—	—	—	—	—
	Chain rule	2.86 (0.4049)	—	—	—	—
	Nearest neighbour	12.63 (0.0002)* ^a	8.94 (0.0002)* ^b	—	—	—
	Positive interactions	3.87 (0.0008)*	3.7277 (0.0010)*	-1.86 (0.0614)	—	—
	Grooming interactions	1.3369 (0.0009)*	1.81 (0.0730)	-0.0284 (0.0016)*	-1.8557 (0.0610) c	—
2012 J troop	Distance rule	—	—	—	—	—
	Chain rule	3.32 (0.0014)*	—	—	—	—
	Nearest neighbour	12.66 (0.0002)* ^a	-7.72 (0.0002)* ^b	—	—	—
	Positive interactions	0.36 (0.7181)	-0.95 (0.3325)	-5.01 (0.0004)*	—	—
	Grooming interactions	0.47 (0.6306)	1.04 (0.2943)	4.22 (0.0002)*	-0.13 (0.8830) c	—
2010 L troop	Distance rule	—	—	—	—	—
	Chain rule	-1.68 (0.0930)	—	—	—	—
	Nearest neighbour	10.14 (0.0002)* ^a	9.79 (0.0566)	—	—	—
	Positive interactions	2.02 (0.0452)*	2.59 (0.0240)*	-3.60 (0.0012)*	—	—
	Grooming interactions	1.44 (0.1448)	1.93 (0.0540) d	-3.52 (0.0012)* ^b	-0.03 (0.9716) c	—
2011 L troop	Distance rule	—	—	—	—	—
	Chain rule	-1.59 (0.1116)	—	—	—	—
	Nearest neighbour	8.69 (0.0002)* ^a	6.19 (0.0002)*	—	—	—
	Positive interactions	0.84 (0.3929)	1.46 (0.1396)	-4.31 (0.0004)*	—	—
	Grooming interactions	0.76 (0.4475)	1.69 (0.0896) d	-3.35 (0.0010)* ^b	0.11 (0.9054) c	—
2012 L troop	Distance rule	—	—	—	—	—
	Chain rule	4.17 (0.0002)*	—	—	—	—
	Nearest neighbour	10.25 (0.0002)* ^a	7.65 (0.0002)*	—	—	—
	Positive interactions	3.60 (0.0010)*	1.96 (0.0504)	-5.11 (0.0004)*	—	—
	Grooming interactions	2.53 (0.0132)*	1.26 (0.2068) d	-4.64 (0.0002)* ^b	0.12 (0.8984) c	—

Values represent *t* statistics and *P* values (in parentheses) for comparisons between networks based on a two-tailed bootstrap *t* test with 5000 permutations. Significant differences are indicated by an asterisk. Results that are significantly different in both troops and all years are represented by 'a'. Results that are significantly different in all years for one troop are represented by 'b'. Results that demonstrate no significant difference in both troops and all years are represented by 'c' and results that show no significant difference in all years for one troop are represented by 'd'.

techniques. In 2010 the only correlations were between the three proximity measures, and between nearest neighbour and positive interactions. Similar results were returned for information closeness (Fig. 3). For this metric all ego network scores were significantly correlated in 2012 except those generated using the distance rule and grooming interactions techniques. The number of significant correlations decreased in 2011 and 2010. Again, the only correlations that were constant in all years were those between each pair of proximity methods. These results show that for proximity techniques individuals that were well connected in one network were also well connected in others. In contrast, betweenness was not strongly correlated across the methods in any year (Fig. 3). Thus baboons that were central in one network did not have a similarly central position in most other networks. Overall, for two of the three metrics analysed (degree and information closeness), individuals maintained a similar local position in networks derived from proximity techniques, but their local positions varied in networks derived from interaction techniques.

When metrics for individuals in each troop were analysed separately we obtained qualitatively similar results at the overall level in at least one of either troop in these analyses (see Supplementary Table S1). However, there was variation in the relationships between the troops in some cases. When we considered those correlations that arose in the pooled comparison that were also supported by both troops individually for all metrics, comparisons between the proximity methods were the most robust to between-troop network differences: in the 27 possible pairwise correlations of the proximity methods, 14 (52%) agreed with the pooled findings. When betweenness was not considered because of its general lack of agreement between methods (see above), the proportion of agreement was higher (13/18 comparisons: 72%). This

was less true when comparing other methods within troops: in four of 54 (7%) pairwise comparisons of the proximity and interaction methods there was support in both troops for the pooled finding (this increased to 11% (4/36) when betweenness was removed) but there was no situation in which the pairwise comparisons of the interaction methods showed the same correlation in both troops, further supporting the difficulty with comparing interaction methods at the individual level.

DISCUSSION

In this study we tested whether social networks created using two different techniques comprising five different methods were comparable. We compared networks built from three frequently used proximity measures (chain rule, distance rule and nearest neighbour) and two types of interaction measures (positive interactions and grooming). There was a clear distinction between proximity and interaction networks at both the global and local levels. While all methods depicted a troop of baboons that maintain highly differentiated social relationships, at the global level only interaction measures may be comparable. Additionally, at the local level only proximity measures were comparable. This suggests that proximity and interaction techniques produce different networks capturing different aspects of the social relationships between individuals. Further, while it was not the goal of our study to assess between-year variation in social networks, we observed high temporal variation in the networks between study seasons that further complicated the comparability of the techniques among years. To our knowledge, this is the first study to demonstrate that there is a distinct difference in these techniques and we elaborate on the implications of this below.

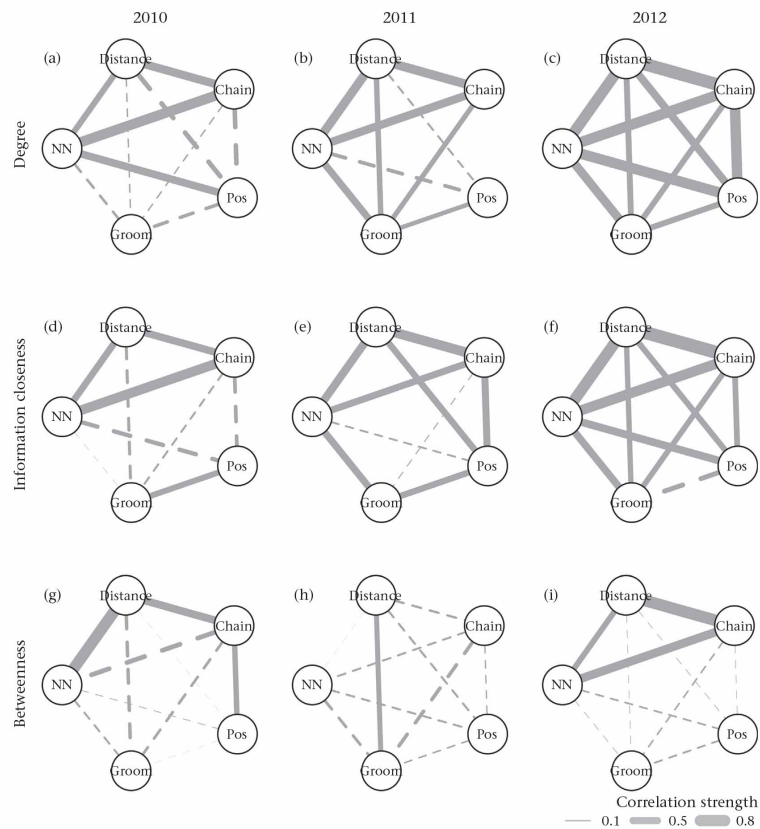


Figure 3. Correlation strengths of individuals' positions among networks constructed from five different data collection techniques for (a, b, c) the social network metrics degree, (d, e, f) information closeness and (g, h, i) betweenness in (a, d, g) 2010, (b, e, h) 2011 and (c, f, i) 2012. Solid lines connecting two methods depict statistically significant correlations ($P < 0.0125$) while dashed lines are nonsignificant correlations. The absolute value of the correlation strength is indicated by the thickness of the line, where a thicker line indicates a stronger correlation (see key); note that correlations can be negative.

Our finding that interaction networks do not differ significantly at the overall network level contrasts with the results of [Lehmann and Ross \(2011\)](#) and [Madden et al. \(2011\)](#). In these previous studies, networks based on different interactive behaviours showed little or no relationship to one another. As a result, these authors suggested that one interactive behaviour alone is insufficient to accurately represent a social network. In these studies, grooming networks were particularly differentiated from other behavioural networks. In contrast, our results suggest that there can be a relationship between the networks built using certain interaction data, specifically in this case between grooming and other positive interactions. While the context of interactions between individuals should be considered when assessing the comparability of any methods, these results highlight the difficulty of making generalizations using different techniques even within populations, let alone from one population to other populations or species.

While interaction techniques may be comparable at the global level, proximity techniques were not, and nearest neighbour stood out as the most different technique. The clear differentiation between proximity and interaction techniques was due to the large difference in the number of connections recorded, which suggests that, although individuals can associate in close proximity, it does not follow that they are necessarily interacting, but in order to interact they must associate in close proximity. Nearest neighbour stood out owing to differences in connection strengths. This occurred with the nearest-neighbour technique because although the baboons had connections with the majority of other troop members, time with each other troop member was minimal; thus the connections were weak in contrast to other techniques, particularly interactions. Therefore, in terms of overall network structure for baboons, nearest neighbour is perhaps the technique that is least comparable to other sampling techniques. We suggest

that this should be tested in other social systems. Further, this result, like those of Kasper and Voelkl (2009), highlights that using weighted connections provides a detailed view of the density of the network and the differences in relationships between the individuals that would be missed if connections are binarized.

At the local level, our findings suggest that centrality metrics based on direct connections (i.e. degree and information closeness) are comparable across proximity networks whereas indirect metrics (i.e. betweenness) are not comparable in any case. Simple metrics such as the strength of connection (degree) and geodesic distance from other individuals (information closeness) were correlated in all proximity comparisons, whereas the more complex measure betweenness, a measure of the number of times an individual connects two others, was only correlated in a few instances. This is in accordance with the findings of Lehmann and Ross (2011) and Madden et al. (2011) who highlighted that the complexity of social networks makes comparison between techniques challenging. Thus until there is better understanding of the complexity of network linkages, comparisons should only be made across direct connection measures rather than indirect connection measures.

The unanimous correlation between direct ego network measures for proximity techniques suggest that proximity techniques produce similar patterns of association and are capturing the same aspect of a baboon's social environment. However, interaction techniques were not correlated in all years or both troops and the local positions based on proximity techniques did not correlate with positions generated from interaction techniques. This calls into question the validity of the use of proximity measures in lieu of social interactions to determine social relationships as seen in studies on, for example, guppies, *Poecilia reticulata* (Croft et al., 2004), dolphins, *Tursiops truncatus* (Gero, Bejder, Whitehead, Mann, & Connor, 2005), killer whales, *Orcinus orca* (Beck, Kuningas, Esteban, & Foote, 2012) and zebras, *Equus spp* (Sundaresan, Fischhoff, Dushoff, & Rubenstein, 2007), among others. While proximity measures may be a useful proxy to define a connection between individuals in studies that are interested in social information or disease transmission, our results suggest that they are not a proxy for a social connection based on rates of affiliation, and researchers should use caution when inferring a 'social bond' between individuals frequently co-occurring in proximity. Our analysis excluded agonistic and incoming interactions so it may be the case that proximity methods do correlate with interaction methods that are based on all interactions (both positive and negative, incoming and outgoing) and further testing should examine this. However, it should not be assumed that proximity in space would give rise to interaction. There may be many reasons why individuals associate in space other than to develop a social bond (Barton & Whiten, 1993; Pinter-Wollman et al., 2014).

Our results add to the growing evidence that social networks are only a snapshot of a particular group at a particular time (Brent et al., 2013; Faust & Skvoretz, 2002; Pinter-Wollman et al., 2014) and should not be extrapolated across time, groups, populations or species. While general trends were apparent in the data, temporal variation between and within the troops was also clear and further analyses highlighted that the trends we observed were not always supported by both the study groups. For example, we recorded an increased number of ego network metric correlations in both troops in 2012 and while this may be an artefact of increased sampling we believe it is more likely to be a result of changed environmental conditions after a particularly wet season. We suggest that inferences about social systems or social evolution in a population should be triangulated across multiple networks representing different techniques, time periods and groups. Further, as

different techniques and metrics capture different aspects of the social structure, researchers should decide which aspects are important for their study and focus on these throughout the research.

A further consideration when comparing networks is the multitude of choices that a researcher makes not only at the data collection stage, which we have explored in detail here, but also at the analytical stage. For example, we chose not to binarize or filter the metrics, as not doing so presented a more detailed picture of the network connections (Kasper & Voelkl, 2009; Lusseau et al., 2008; Voelkl et al., 2011). As a result, however, inaccurate or insignificant ties may have been included (Croft et al., 2008).

The patterns of social connections and extent to which an individual is embedded in its society can have far-reaching consequences for its overall fitness (Cameron et al., 2009; Silk, 2007; Silk et al., 2003, 2010). Social network analysis allows the examination of social interaction and network characteristics to improve understanding of the social dynamics of a group and the individual roles within it. However, the decisions made by researchers at the data collection and analysis stages have clear effects on the networks that are produced. In particular, our analyses have demonstrated that at both the global and local levels, proximity and interaction techniques do not produce comparable metrics, at least in the baboons of our study population, and both temporal and between-troop variation can change the shape of a network. Thus, to gain the best understanding of the social environment of social animals, we suggest a combination of proximity and interaction measures should be applied to a population at multiple time periods. Further, as social networks vary both temporally and between social groups within the same population, caution must be used when generalizing results beyond a particular group of individuals at a particular time.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2014.07.023>.

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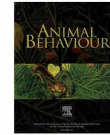
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Forum

Research questions should drive edge definitions in social network studies

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Recently we published a study (Castles et al., 2014) that compared social network metrics that were created from two methods for defining connections (edges) among wild baboon, *Papio ursinus*, individuals (nodes): proximity and interactions. We found that in many (but not all) cases individuals' positions in the proximity networks were not predictive of their positions in the interaction networks and we cautioned researchers about assuming that one is a proxy for the other, which is frequently done in social network studies (e.g. Carter, Macdonald, Thomson, & Goldizen, 2009). In his Forum article, Farine (2015, this issue; henceforth 'Farine') outlines several assumptions that researchers make about how to define edges among individuals that may affect the results of social network studies, before presenting new empirical findings from wild thornbills (genus *Acanthiza*) that he concludes contrast with ours. We are excited that our research has generated such interest, and this new article adds to a growing body of empirical studies that consider sampling issues in social network studies (Castles et al., 2014; Hobson, Avery, & Wright, 2013; Lehmann & Ross, 2011; Madden, Drewe, Pearce, & Clutton-

Brock, 2011; see Whitehead, 2008 for a comprehensive summary of sampling considerations). We agree that the 'gold standard' in social network studies should be for researchers to incorporate multiple networks using different methods to determine edges into their analyses. However, while Farine usefully highlights assumptions that are important to consider when choosing how to collect and analyse one's network data, several aspects of his article require further consideration before we extend the discussion to broader issues in social network studies.

First, Farine presents empirical data from mixed-species flocks of thornbills, collected over a 6-week period, in which there are correlations between individuals' network positions in proximity and interaction networks. Farine states that this pattern was in contrast to our general conclusion, and so suggests that our findings are not generalizable across species and that in some cases proximity can be used as a proxy for interactions. We feel the first assertion is misplaced, and we caution against the second. Our results were in agreement with those of the thornbills in some years for some social network metrics, where we also found correlations between some proximity and interaction methods (see Figure 3 and supplementary material in Castles et al., 2014). However, the correlation between the two methods was not found in other years. Thus, our results from two study groups over 3 years suggest that findings from one time period may not be generalized

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to the same group(s) in a different time period, let alone to other groups of a particular study species. Had we measured the social network in one particular year (or group) and found a correlation between the methods, we may have erroneously concluded that we can use proximity as a proxy for interaction in all future studies. To return to Farine's first assertion, we are not seeking to generalize patterns from our study but rather the principle that consistency between groups/years should not be assumed until it has been demonstrated. Thus, with respect to Farine's second assertion, we would reiterate our conclusion from [Castles et al. \(2014\)](#): because of the dynamic nature of social networks, we recommend that researchers take care when assuming that proximity can be a proxy for interactions. This is distinct from the suggestions that (1) proximity can never be a proxy for interactions and (2) proximity cannot be used to create social networks, generalizations that we do not advocate.

Second, Farine explores some methodological considerations that were not addressed in our study. We focused on one decision a researcher could make at the data collection stage, specifically, the behaviours that could be used to create edges in a social network. Yet, as we mentioned in our study ([Castles et al., 2014](#)), there are many considerations after the data collection stage, as highlighted by Farine) and outlined in detail elsewhere ([Whitehead, 2008](#)). We appreciate that Farine is using our study to illustrate some general points, and agree that had we analysed our data differently (e.g. by using rates, rather than proportions, of dyadic grooming interactions) we may have obtained different results. However, this simply further supports our conclusion that social networks measured (and analysed) using different techniques are not necessarily comparable and care should be taken when generalizing research findings. These considerations in data collection and analysis also highlight more general issues of research design which have perhaps been overlooked in the largely descriptive studies of social networks thus far ([Whitehead, 2008](#)). The definition of an edge connecting nodes in a network should first and foremost depend on the research question, and assumptions about correspondence between networks should be tested. In the former case, for example, if the research question relates to the transfer of visual information between individuals in a network, then edges based on shared proximity are likely to be most informative (but see our further considerations below). But if the research question addresses the likelihood of ectoparasitic disease spread between individuals, then instances of physical interaction between individuals may be more appropriate. In the latter case, we would encourage descriptive studies to adopt richer analyses that encompass multiple methods of measuring associations, as do others ([Lehmann & Ross, 2011](#); [Madden et al., 2011](#); [Whitehead, 2008](#)). Furthermore, we would return again to the conclusion of our original study that any researchers using proximity as a proxy for interactions (and we appreciate this is often the only available source of data on dyadic associations) should be wary that proximity does not always equal interaction, and vice versa. For example, individuals are able to interact via olfaction, vocalizations and visual signals when not in close proximity, or may be in proximity but not interacting (we develop this further below). Consequently, the appropriateness of using proximity as a proxy for interactions will depend on the type of interaction identified as meaningful and important for the research question in the context of the biology of the study system.

The biology of a study species is likely to influence the appropriateness of different edge definitions for answering specific research questions. The definition of an edge should be dictated not solely by what is possible for a study species, but by what is appropriate for it with respect to the study question and the species' biology; one should not use instances of close proximity to

infer grooming when the research question is 'does social rank influence grooming equality?', for example, unless this link has been empirically demonstrated (preferably repeatedly) beforehand. Since, for some study systems, building the social network that is most appropriate for a given research question can be prohibited by logistical constraints on data collection, while other methods may be more practical, Farine's question remains: can proximity networks be a proxy for interaction networks? Before we expand on this in more detail, we would mention again that this question is distinct from the value of proximity measures to describe social structure/organization: we find proximity measures valuable for both this task and for hypothesis testing in networks (but see [Macdonald & Voelkl, 2015](#); [Whitehead & Dufault, 1999](#)). As we mention above, we are in agreement with Farine that the gold standard in network studies requires a multinet framework. In our original article ([Castles et al., 2014](#)), we were largely concerned with issues of comparability between studies that use different methods to define an association, and raised the issue of using proximity as a proxy for interactions in the discussion of our findings. Where we disagree with Farine is in his assertion that proximity edges can sometimes be used to infer interaction edges or vice versa without prior testing of this assumption. This does not preclude the use of proximity edges to determine, for example, individuals' preferred associates (for an example, see [Carter et al., 2009](#)).

Below, we consider under which circumstances we might reliably expect a correspondence between proximity and interaction networks in an effort to provide guidelines for researchers wishing to use proximity as a predictive surrogate for interaction (see also [Whitehead & Dufault, 1999](#)). This need not be limited to difficult-to-observe species, but could also apply to different methods of collecting data that involve remote rather than direct observation, such as the use of global positioning system collars to assign group membership by some measure of proximity. We also appreciate that understanding how and why different networks may or may not correspond or interrelate is an important research topic in its own right. However, we have not yet imagined any case in which one could assume a correspondence between networks without testing for it, although our thought experiment provoked some overlooked considerations in social network studies: (1) some interactions can occur between individuals of different subgroups, (2) proximity networks describe only opportunities for interaction and (3) individuals are likely to vary in both their gregariousness, i.e. their propensity to be in proximity to others, and their sociability, i.e. their propensity to take the opportunity to interact with others when in proximity to them. We use the baboon system as a worked example of our reasoning by way of explanation where necessary, and we assume for this exercise that the hypothetical proximity network that is putatively predictive of the interaction network is well sampled and representative of the 'true' proximity network.

Before we address these points in more detail, we should first take a brief digression to define the term 'group' here. Up to this point, we have used the term to mean a set of behaviourally connected individuals in which the majority of individuals are connected to most others; this is what [Whitehead \(2008\)](#) refers to as a 'community' and is the equivalent of a troop in baboons. From here, however, we use the term to refer to a 'subgroup', a subset of a group that is behaviourally connected (either by proximity or interaction) at a particular point in time ([Castles et al., 2014](#)), that is, the level of observation at which social network data are collected. To return to our first consideration then, it is important to address the assumption that researchers make about the proximity needed for interactions ([Whitehead & Dufault, 1999](#)). As we mention above, individuals are able to interact via olfaction, vocalizations and visual signals when they are not in close proximity, but this is rarely

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considered as we suspect that it is implied that the interactions are physical. For example, Farine considered only physical interaction between individuals in his empirical example. In most cases, but not all (consider, for example, olfactory signals provided via latrines or the scent marking of surfaces), we acknowledge that individuals will have to be within a particular proximity to interact using these other modalities that are of shorter duration. Our point is not that proximity is not important for interaction, but that the range over which visual, auditory and olfactory signals can be transmitted is often beyond the range that is used to define group membership by proximity (and conversely, physical interactions are often well inside the range considered for group membership by proximity). This is not a semantic point, but a conceptual one about how we define edges and thus groups by proximity, and how this will limit comparability of networks. To illustrate by an example, baboons can interact via visual signals (using 'come hither' faces and lip smacking) over tens of metres and via vocalizations over hundreds of metres; often these interaction distances are well beyond what we consider as group membership by our proximity rules. As such, individuals can readily and frequently interact between groups: conceptually, individuals could have an association index of zero but a nonzero interaction index. Of course, physical interaction requires group co-membership (however spatially defined) and here again the research question should drive the types of interactions that are reasonable to consider; we mean only to highlight an unconsidered assumption that may lead to a mismatch between edge definitions that may lower comparability between networks and studies.

Regarding the second consideration, association matrices represent only opportunities for interaction: they describe who can interact, but not who does interact. While this statement seems obvious, the use of proximity as a proxy of interaction is predicated on the implicit assumption that the relationship between proximity strength and interaction rate is probabilistic (and also assumes, as we do for the rest of this line of argument, that the interaction occurs over a short distance that necessarily places interacting individuals in the same group as defined by proximity; see our point above). This raises a problem with zero edges in the association network. It is logical to assume that individuals who are never in close proximity will never interact: proximity edges valued zero must be coupled with interaction edges valued zero. However, following this logic, the presence of zero–zero proximity and interaction edges will 'tether' any linear model that investigates the correlation between these values to the origin (see Figure 1 in Farine, 2015); in fact, these models must logically pass through the origin. Combined with the impossibility of negative rates of association, the presence of zero–zero values should increase the probability of at least a weakly positive correlation between proximity and interaction edges as soon as there are any nonzero interaction edges, and tells us only that individuals interact with those with whom they have an opportunity to interact (and suggests that proximity edges valued zero should be removed for this kind of analysis as they bias the relationship towards the origin). The only logical argument that holds is that individuals that are never in proximity do not interact. However, we cannot make the assumption that proximity edge weights will provide (detailed) predictive data on differential rates of interactions between those individuals that are connected. Consider, for example, Figure 1 in Farine (2015): none of the dyads exhibiting an (above average) proximity edge weight of 0.5 were observed interacting over the 6-week study. Thus, proximity networks rather show who is connected and who is not, and therefore who can interact (at some unknown rate, which may include 0) and who cannot.

We feel that it is at this point that disagreements may arise about the usefulness of proximity as a proxy for interaction,

and raises our third consideration. We argue that assumptions regarding the patterns of interactions between connected individuals should not be made, since individuals can vary not just in their gregariousness (the propensity to be in proximity to others), but also their sociability (the propensity to interact with others to whom they are in proximity). Furthermore, these propensities need not be positively correlated, and may be influenced by a range of social factors. This may lead to relationships between proximity and interaction that deviate from a neutral probabilistic model (i.e. increasing probability of interaction with increasing time spent in proximity), and, depending on patterns of within- and between-individual variation in these two traits, may result in the correspondence between proximity and interaction differing for different dyads' edges: specifically, individuals exhibiting similar association edge weights, and so similar gregariousness, may have different interaction edge weights if they differ in their sociability. While this is similar to Farine's fourth point about calculating rates of interaction while controlling for time in proximity as opposed to calculating the proportion of an individual's interactions directed to other individuals, we mean to highlight here the individual variation that may make proximity edge weights a poor predictor of interaction probability.

For example, we consider a hypothetical population (Fig. 1) in which dyads interact on average on half the occasions that they occur in the same group as defined by proximity (we assume that the probability that dyads interact, or $P(\text{interact})$, is $0.5 \times P(\text{co-occur})$). The dashed line in the graph, therefore, describes the average relationship between shared proximity and interaction rate for this population. This relationship is likely to differ between species and may not necessarily be linear. In this hypothetical example, we have plotted three dyads, A, B and C, which co-occur with a probability of 0.5. Dyad B interacts at the average rate for the population (near 0.5) and sits close to the line. However, dyads A and C interact more and less than expected than the average for the population, respectively, and consequently sit in darker parts of the plot. All three dyads are equally gregarious (to be more

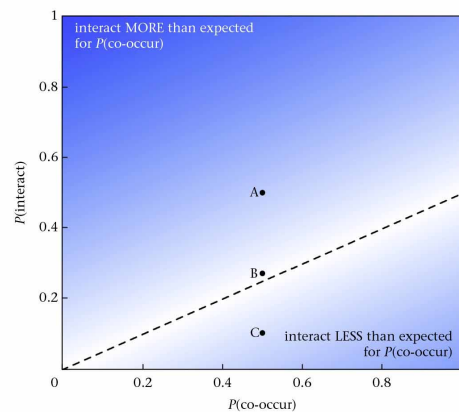


Figure 1. The relationship between the probability of interacting ($P(\text{interact})$) for a given probability that a dyad will co-occur in the same group ($P(\text{co-occur})$). The dashed line represents the average interaction rate for the population. The blue shading represents whether individuals are more or less likely to interact than expected for the average of the population, with lighter (white) shading showing that dyads interact at the average rate. Three hypothetical dyads (A, B and C) are shown (see text for details).

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accurate, the result of the combination of the individuals' gregariousness in the dyads makes them equally gregarious); however, dyads A and C are more and less sociable than expected for their gregariousness, respectively. If researchers are not interested in this variation but are simply interested in determining those individuals who are likely to interact, then using proximity networks as a proxy for interaction probability (which requires individuals to be in close proximity) might be reasonable. However, if researchers are interested in this variation then information on who can and cannot interact clearly does not provide detailed insight into social interactions between individuals, since a priori assumptions cannot be made about the relationship between time in proximity and interaction rates. In this case we feel that researchers should (in order of decreasing preference): (1) collect and use data on individual interactions; (2) test this assumption in their study system, perhaps on a smaller subset of the network with more intensely collected data, before proceeding with the use of proximity data; and (3) use proximity as a proxy for interaction (probability) with caution, understanding that this assumption may not necessarily hold.

Next, we address two other conceptual issues raised by Farine. We first consider the potential confusion that is introduced in social network analyses by making a distinction between fission–fusion societies and stable social groups. There is an argument that a particular edge definition will be more informative for species of a particular social organization (Farine, 2015). As we mention above, we made no judgement on the value of proximity and interaction edges as being more or less accurate representations of the 'real' social network in our original paper (Castles et al., 2014). We suggest only that the different methods provide a different aspect of an individual's social environment, both of which we believe are important and both of which should be collected and compared when possible. Furthermore, we are certainly in agreement that a species' biology should determine the rules used to define edges in networks for a particular method. However, we think it misleading to make assumptions about how informative a particular method is for species of particular social organizations for two reasons. First, it is impossible to categorize all species into particular social organizations, let alone categorize unequivocal types of social organization. Second, there is substantial variation within categories of social organization such as those suggested by Farine. As this variation is continuous, categorization is arbitrary and generalizations at the level of social organization are impractical.

Using the category of fission–fusion species as an example, there is variation among species in the extent of fluidity of individuals among groups, prohibiting the assumption that group co-membership is more informative than interaction in all fission–fusion species. Group membership in fission–fusion species can be highly fluid, where individuals in a local population form one community of connected individuals, such as in guppies, *Poecilia reticulata* (Croft, Krause, & James, 2004). It can also be arranged in a segregated community structure, where association between individuals from the same community is common but association between individuals from different communities is rare, such as in chimpanzees, *Pan troglodytes* (Symington, 1990) and eastern grey kangaroos, *Macropus giganteus* (Best, Seddon, Dwyer, & Goldizen, 2013). It can also be based around multilevel societies, in which there are tiers of closely connected individuals nested within 'higher' levels of clustered lower tiers, such as in African elephants, *Loxodonta africana* (Wittemyer, Douglas-Hamilton, & Getz, 2005) and hamadryas baboons, *Papio hamadryas* (Kummer, 1984). We note that these descriptions of the fission–fusion social organizations of these species were made using proximity (group co-occurrence) methods, demonstrating the usefulness of the proximity method for describing differences in

social organization. However, the assumption that group co-membership in chimpanzees is more informative than grooming equality should, returning to our earlier point, depend on the question that the research is trying to inform, not on the fact that they have a fission–fusion social organization. While this particular example may be hyperbolic, we mean only to highlight that a priori assumptions about the meaningfulness of one method for all species of a particular social organization is misguided, based in part on the complications associated with categorizing species and variation within categories. We would go so far as to argue that valuing one method above another is equally detrimental to social network studies and should be avoided, not least because we as human researchers are unaware of which distances or timings of co-occurrence, and proportions, counts or durations of interactions that we measure are actually meaningful to the species we study. Furthermore, both proximity and interaction measures are likely to be important and informative for particular biological processes, and we would prefer to see researchers moving towards more holistic frameworks in social network studies that use competing networks to test a priori hypotheses about the importance of social networks for animals.

Finally, three interrelated questions resulting from our consideration of these methodological issues remain to be discussed: what makes a network, how should sample sizes be considered in social network studies and at which level should data be pooled? These questions relate to Farine's idea of social scale and are generally beyond the scope of this reply to address in detail (being relevant research questions in their own right in many systems). One small consideration of note, however, relates to our point regarding the importance of research questions in determining edge definitions. We defined community above as a set of behaviourally connected individuals in which the majority of individuals are connected to most others. In baboons, a community (troop) is easy to define because connections between troops are so rare (Cowlshaw, 1995) and connections within troops are common (Castles et al., 2014). For species with higher fission–fusion organization, where communities are more transient and home ranges can overlap substantially (e.g. eastern grey kangaroos: Best et al., 2013), identifying communities and community membership is less straightforward, and may influence the results of social network analyses. Once community structure has been identified, we must ask which individuals should be included in the 'social network' for a given study. Should all individuals in the local population be included, even if the majority never have a connection to others (see our point above about zero-weighted edges)? Or should the communities be considered separately, even if there are some (sometimes many) between-community connections? While at the node level larger communities will result in larger sample sizes, a limit to the generalizability of network studies' results is not how large the communities are but how many communities are assessed for a particular research question (Croft, James, & Krause, 2008). For example, if a researcher is interested in the transfer of information among individuals, the relevant unit of analysis is not the number of individuals in the community but the number of communities in which the results can be replicated; the size of the community is irrelevant (unless one is interested in the transfer of information in communities of different sizes, of course). In our baboon system, in most cases we would rarely pool in a common network all of the individuals from both of the communities we study because of the zero-weighted edges that would be generated, but after this stage we may pool individuals (and control statistically for troop membership), as ever, depending on the research question (as we did in Castles et al., 2014). However, we have no prescriptive advice for this problem in other systems with more between-community connections; once again, we merely intend to highlight an issue

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that is infrequently considered in social network studies which requires the careful attention of researchers.

In conclusion, we reiterate that we do not argue that proximity data cannot or should not be used in social network studies, nor that proximity data are not informative, and we appreciate that in many systems proximity is the only readily available measure of association between individuals. We only caution against assuming that proximity is necessarily a proxy for interactions, and encourage researchers to test this assumption should it be used. We also advocate that the research question and study species' biology should drive the definition of edges (and nodes) in networks as well as the social scales at which these are measured.

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Phenotypic assortment in wild primate networks: implications for the dissemination of information

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1. Summary

Individuals' access to social information can depend on their social network. Homophily—a preference to associate with similar phenotypes—may cause assortment within social networks that could preclude information transfer from individuals who generate information to those who would benefit from acquiring it. Thus, understanding phenotypic assortment may lead to a greater understanding of the factors that could limit the transfer of information between individuals. We tested whether there was assortment in wild baboon (*Papio ursinus*) networks, using data collected from two troops over 6 years for six phenotypic traits—boldness, age, dominance rank, sex and the propensity to generate/exploit information—using two methods for defining a connection between individuals—time spent in proximity and grooming. Our analysis indicated that assortment was more common in grooming than proximity networks. In general, there was homophily for boldness, age, rank and the propensity to both generate and exploit information, but heterophily for sex. However, there was considerable variability both between troops and years. The patterns of homophily we observed for these phenotypes may impede information transfer between them. However, the inconsistency in the strength of assortment between troops and years suggests that the limitations to information flow may be quite variable.

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2. Introduction

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Individuals can acquire information either personally, by interacting with their environment directly, or socially, by attending to the behaviour of others [1]. For group-living animals, social information provides an alternative to gathering costly personal information [2], potentially facilitating decisions about foraging, movement, mate choice and predation [3,4]. Social information allows the rapid dissemination of novel information among group members and has thus also been widely implicated in the formation of traditions and cultures within species [5,6].

An individual's phenotype is likely to influence its propensity to either 'generate' social information—through personal information acquisition—or 'exploit' it—from information 'generators'. In the first case, for instance, certain phenotypes are more likely to solve cognitive tasks or discover novel foods than others. Sex, age, previous experience [7] and personality [8,9] can affect an individual's propensity to solve tasks. In the second case, personality phenotypes can affect the acquisition (and use) of social information. Shy geese (*Branta leucopsis*) [10] and baboons (*Papio ursinus*) [11] are more likely to use social information than their bolder conspecifics while foraging. Thus, the diffusion of novel information through a group may not show a uniform pattern of transmission, but rather a more heterogeneous pattern in which some individuals are generating information while others are exploiting it, either directly from generators or secondarily from other exploiters.

The dissemination of information through a group, however, is also predicted to differ with the social network—the patterning of social relationships—that characterizes that group [12,13]: individuals are predicted to be more likely to acquire social information from others with whom they associate more frequently [12]. Assortment by phenotype has often been observed in animal social networks [14–16]. A preference to associate with similar phenotypes, termed positive assortment or 'homophily', is thought to be adaptive by potentially facilitating cooperation among individuals [14,15,17]. However, homophily, combined with phenotype-specific information generating, may preclude some individuals from obtaining social information. This is because the individuals with phenotypes that generate information may be more likely to associate with others of similar phenotype and not with those who might rely more heavily on social information. On the other hand, negative assortment ('heterophily') may facilitate the transfer of information between information generators and exploiters. Thus, the propagation of information through a social network should be limited or enhanced by positive or negative assortment of information-generating phenotypes, respectively.

Researchers have tested whether information will transfer between individuals who are in close proximity and have assumed that measures of proximity reflect opportunities for information transmission between individuals (e.g. [18–20]). However, we still know very little about which behavioural measures of association best indicate information transmission opportunities, nor whether the type of behavioural measure matters for the complexity of information that has to be transferred. Indeed, animal social networks can be described using several different measures of association [21], and these are not always comparable [22,23]. This has important implications for understanding information flow in a network. For instance, individuals may be more attentive towards, and thus more likely to acquire or use information from, those with whom they have strong interactive bonds rather than those with whom they simply share space [12]. This supposition is supported by Boogert *et al.* [24], who found that starlings (*Sturnus vulgaris*) preferentially learnt novel foraging techniques from others with whom they perched, rather than from individuals with whom they foraged in close proximity. Importantly, these may not necessarily be the same individuals in both networks [22,23,25]. Thus, to understand the potential for information dissemination through social networks, there is a need to consider more than one method of measuring associations between individuals in those networks.

In this study, we investigated whether social networks of wild baboons were assorted by phenotype to explicitly address for the first time to our knowledge the potential for the dissemination of social information. We chose to study chacma baboons for several reasons. First, chacma baboons generate and exploit information according to phenotype: juveniles and bolder baboons are more likely to solve novel foraging tasks, thus generating novel information [9], while higher ranked, shyer individuals are more likely to acquire social information when foraging with unreliable cues [11]. Second, baboons show highly differentiated, non-random social relationships [22,23] and all individuals within a baboon troop are identifiable and travel together as a group, alleviating the issues of missing individuals that occurs in most other social network studies [21]. Third, baboons learn socially about novel foods from others [9,26], and it is reasonable to predict that individuals will learn from others with whom they are affiliated [12]. Finally, we have a uniquely rich dataset describing the social networks and phenotypes of over 100 baboons in two troops over a 6 year period. We quantified social networks using two

measures of behavioural association between individuals to ask whether baboon troops were assorted by individual phenotype. We considered four phenotypic traits that may influence the propensity to generate/exploit social information, namely sex, dominance rank, age and boldness. We also assigned individuals two further traits that directly estimated an individual's propensity to generate and exploit social information, respectively, on the basis of combinations of these four basic traits. To our knowledge, this is the first study to explore assortativity with such broad scope; the majority of studies describing social network characteristics occur either over one study period [16], in one study group [14,15], or use one method of determining a connection [14,16], limiting the generalizability of their findings for understanding the fine structure of animal social networks and the potential for the diffusion of social information. Within our broader question, and because of the scope of our data and analyses, we were able to further describe whether the patterns we observed could be generalized: (i) between the observation groups, (ii) between the measures of behavioural association, and (iii) among the years of observation.

3. Material and methods

3.1. Study site and species

We studied chacma baboons over 6 years, from May to November 2009, May to October 2010, June to September 2011, August to October 2012, August to October 2013 and May to July 2014 at Tsaobis Leopard Park, Namibia (15°45' E, 22°23' S). Two troops of baboons (J-troop and L-troop, study individuals present: $n_{2009} = J = 35, L = 24; n_{2010} = 32, 23; n_{2011} = 27, 23; n_{2012} = 31, 22; n_{2013} = 46, 49; n_{2014} = 44, 48$) have been habituated to the presence of observers at close range and are individually recognizable. We collected data annually from adult, sub-adult and juvenile baboons over the 2009–2014 period. Age (in years) was estimated from a combination of known birth dates and dental patterns of tooth eruption and wear [27]. Unmarked immigrant males' ages were estimated at 9 years old when they appeared in the study troops, as this is the age most males were observed to transfer from our study groups. Individual ranks were assessed through dominance interactions that were recorded during focal observations and ad libitum using MATMAN v. 1.1.4 (Noldus Information Technology 2003). Dominance hierarchies in both troops were strongly linear in all years (Landau's corrected linearity index: $h' > 0.6, p < 0.05$ in both troops in all years). Dominance rank was expressed relatively (which controls for group size), calculated from absolute ranks for each baboon using the formula $1 - [(1 - r)/(1 - n)]$, where r is the individual's absolute rank and n is the group size of the individual. Individual rank values therefore range from 0 (lowest rank) to 1 (highest rank) in each group year.

Boldness was measured in 2009, 2010, 2011, 2013 and 2014 by scoring responses to a novel food (for further details, see [28,29]). In all cases, individuals were presented with a stimulus when they were alone and moving between food patches. The stimuli were presented on the edges of game trails and paths regularly used by the baboons. All experiments were filmed to facilitate data extraction (Panasonic SDR-SW20, Kadoma Osaka, Japan; see movie files in [29]). Stimuli for the boldness tests consisted of novel food items which included hard-boiled eggs with the shell on or removed, or a small egg-shaped bread roll, all of which were dyed red or green (Moir's food dye), in 2009; semi-dried eighths of apple or pear, dyed red, in 2010; and eighths of an orange or equivalent-sized pieces of butternut squash in 2011; 3×2 cm pieces of carrot or gamsquash in 2013; and 2×3 cm pieces of potato or sweet potato dyed blue in 2014. Any naive individual that saw another individual interacting with a novel food was presented with a different novel food when they were tested. As an indication of an individual's willingness to interact with novelty and thus its boldness, we recorded the amount of time spent inspecting the food item (s) between approaching the food item and the end of the test, which was determined to be when the baboon either left or ate the item. If an individual did not inspect the novel food they scored 0, while inspection time for those individuals who inspected the food had a cut-off value of 120 s. In total, 58, 54, 50, 95 and 92 baboons received novel food presentations in 2009, 2010, 2011, 2013 and 2014, respectively (median number of presentations per individual = 2.0; range = 1–5 presentations). The substantial increase in sample size from 2013 onwards reflects the inclusion of a new generation of juvenile animals. Owing to funding limitations, boldness tests were not completed in 2012.

Previous research in this population indicates that the probability of generating or exploiting social information is not necessarily related to single traits but a combination of traits [11,29]. In light of this, we also categorized individuals according to: (i) their propensity to generate information, if they were bolder than average (median) for a given year's boldness scores for the troop and juvenile (younger

than 5 years for females, 8 for males) for that year [9]; and (ii) their propensity to exploit information, if they were shyer than average (median) *and* higher ranking than average (relative rank greater than 0.5) for that year [11]. We have analysed these separately (as information generator/not and information exploiter/not), as some individuals do not necessarily fall into an information generator/exploiter phenotype; for example, low ranking but bold adults are neither an information generator nor exploiter by our previous findings. Furthermore, in J troop in 2011, there were no individuals categorized as information exploiters because all higher ranking individuals inspected the novel food for longer than the median inspection time. In 2012, we could not estimate individuals' likely propensities to generate or exploit information as we did not measure boldness. While this is a crude categorization, it could still usefully illuminate patterns of assortment in likely information generators and exploiters that are potentially missed by analysing the constituent phenotypes (boldness, age and rank) separately.

3.2. Behavioural data collection

Observers followed the baboon troops from dawn until dusk during the periods of study. The behaviour of individual baboons was recorded using continuous focal sampling for periods of 15–60 min during the full-day troop follows. Focal observations that lasted under 15 min were discarded. Individuals were sampled in a semi-random manner such that the cumulative focal observation time for each individual was even in each of four time periods over each day (06.00–09.00, 09.00–12.00, 12.00–15.00 and 15.00–18.00). If an individual disappeared from the troop for greater than half the field season (either owing to emigration or death; $n_{2009} = 3$, $n_{2010} = 3$, $n_{2011} = 1$, $n_{2012} = 2$, $n_{2013} = 1$ and $n_{2014} = 0$), the individual was removed from the analyses for that year. Between 2009 and 2012, we avoided sampling females while they were in oestrus due to known changes in their social interactions with other troop members at this time [30,31]. They were, however, recorded when they were in close proximity to or observed grooming with other individuals under observation. Because of time and funding constraints in 2013 and 2014, we included oestrus females as focal individuals and collected the network data slightly differently (see below). Thus, only data from 2009 to 2012 are directly comparable among years; however, we have also presented the 2013 and 2014 data for within-year comparisons between the troops.

We recorded data using two methods to define an association. First, as information could transfer between individuals who are in close proximity (e.g. [20]), we continuously recorded the nearest neighbour [32] within 5 m of the focal individual during focal observations. If the focal baboon had no neighbour within 5 m, it was recorded as 'alone'. Assuming that an individual is more likely to acquire information from another the more time they spend together, we calculated the proportion of each individual's total observation time that it spent in close proximity to every other individual in the group. In 2013, owing to a change in protocol that made continuous recording of the nearest neighbour inaccurate, we instead recorded the nearest neighbour every 2 min during focal follows. Thus, in 2013, we calculated the proportion of each individual's total nearest neighbour scans that it spent in close proximity to every other individual in the group. In 2014, due to funding limitations that limited the numbers of observers in the field, the nearest neighbour data were recorded as scans independently of focal follows. In these scans, we searched for and quantified the nearest neighbour (within 5 m) of 'focal' individuals from a randomized list of study individuals within each troop. Because the baboon troops can spread over 1 km² while foraging (A. J. Carter 2009–2014, personal observations) and finding particular individuals can be time consuming, the observer (M.T.T.) searched for one of the first five individuals on the randomized list of baboons to optimize the number of independent nearest neighbour dyads that could be sampled each day. If a focal baboon had already been recorded in an already-sampled subgroup (i.e. subgroup membership had not changed between scans), that individual was not sampled for an hour to ensure that the sampled subgroups constituted independent data. We calculated the total number of times each individual was observed as the nearest neighbour of every other individual in the group.

Second, as information may preferentially be acquired by individuals who have strong social bonds [12], we recorded the time each focal individual spent grooming every other individual in the group. Grooming is an easily defined and observable social interaction and is also a standard measure of affiliative associations in primates. We calculated the proportion of each individual's total grooming time that it spent grooming every other individual in the group. Although grooming associations are not strictly independent from nearest neighbour associations (the nearest neighbour of a grooming baboon is usually the grooming recipient), we have previously found that networks created using these different association measures were generally not correlated [23]. We chose to normalize grooming for each individual instead of calculating the proportion of focal observation time dedicated to grooming

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Table 1. Assortativity (\pm s.e.) for social networks based on nearest neighbour proximity (nn) and grooming (groom) assortations for four phenotypic traits over the years 2009–2014 for two troops of baboons (J, L). (n.a. refers to phenotypes which were not measured in that particular year. Dashes (—) refer to phenotypes that did not occur in a particular year. Statistically significant assortments is indicated in *italics*.)

year	troop	network	boldness		relative rank		age (years)		sex		propensity to generate information		propensity to exploit information	
			assortativity index	assortativity index	assortativity index	assortativity index	assortativity index	assortativity index	assortativity index	assortativity index	assortativity index	assortativity index	assortativity index	
2009	J	nn	-0.024 ± 0.035	0.130 ± 0.044	0.143 ± 0.062	0.076 ± 0.045	0.104 ± 0.046	0.004 ± 0.053						
2009	L	nn	0.074 ± 0.053	0.282 ± 0.048	0.069 ± 0.060	0.072 ± 0.056	0.099 ± 0.061	0.040 ± 0.061						
2010	J	nn	0.022 ± 0.069	0.107 ± 0.061	0.038 ± 0.108	0.032 ± 0.055	0.065 ± 0.060	0.023 ± 0.068						
2010	L	nn	0.110 ± 0.107	0.248 ± 0.087	-0.058 ± 0.099	-0.007 ± 0.065	0.064 ± 0.050	0.154 ± 0.148						
2011	J	nn	0.028 ± 0.054	0.103 ± 0.054	0.070 ± 0.070	-0.025 ± 0.059	0.075 ± 0.054	—						
2011	L	nn	0.004 ± 0.070	0.016 ± 0.057	-0.027 ± 0.065	-0.161 ± 0.050	-0.060 ± 0.031	0.060 ± 0.104						
2012	J	nn	n.a.	-0.052 ± 0.060	0.043 ± 0.057	-0.095 ± 0.051	n.a.	n.a.						
2012	L	nn	n.a.	0.015 ± 0.069	0.008 ± 0.056	-0.277 ± 0.044	n.a.	n.a.						
2013	J	nn	0.055 ± 0.024	0.256 ± 0.025	0.068 ± 0.030	0.049 ± 0.029	0.107 ± 0.029	0.075 ± 0.028						
2013	L	nn	0.078 ± 0.052	0.151 ± 0.035	0.058 ± 0.030	0.073 ± 0.039	0.176 ± 0.031	0.010 ± 0.056						
2014	J	nn	0.116 ± 0.027	0.065 ± 0.037	0.176 ± 0.032	-0.025 ± 0.029	0.158 ± 0.027	0.077 ± 0.025						
2014	L	nn	0.094 ± 0.026	0.026 ± 0.033	0.213 ± 0.016	-0.125 ± 0.024	0.134 ± 0.021	0.006 ± 0.036						
2009	J	groom	0.216 ± 0.018	0.188 ± 0.037	0.176 ± 0.056	0.263 ± 0.048	0.220 ± 0.051	0.073 ± 0.051						
2009	L	groom	-0.050 ± 0.081	0.560 ± 0.053	0.113 ± 0.108	-0.019 ± 0.060	0.120 ± 0.067	-0.036 ± 0.093						

(Continued)

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Table 1. (Continued.)

year	troop	network	boldness	relative rank	age (years)	sex	propensity to generate information	propensity to exploit information
			assortativity index	assortativity index	assortativity index	assortativity index	assortativity index	assortativity index
2010	J	groom	-0.023 ± 0.076	-0.039 ± 0.008	0.132 ± 0.083	-0.131 ± 0.022	-0.156 ± 0.034	0.256 ± 0.003
2010	L	groom	0.230 ± 0.105	0.313 ± 0.053	-0.156 ± 0.070	-0.132 ± 0.054	-0.067 ± 0.005	0.240 ± 0.127
2011	J	groom	0.115 ± 0.015	-0.143 ± 0.017	0.023 ± 0.003	-0.158 ± 0.033	0.139 ± 0.009	—
2011	L	groom	-0.231 ± 0.023	0.120 ± 0.026	-0.010 ± 0.046	-0.052 ± 0.038	-0.053 ± 0.036	-0.094 ± 0.004
2012	J	groom	n.a.	0.095 ± 0.019	0.162 ± 0.024	-0.066 ± 0.036	n.a.	n.a.
2012	L	groom	n.a.	0.082 ± 0.131	0.107 ± 0.056	-0.332 ± 0.044	n.a.	n.a.
2013	J	groom	0.067 ± 0.003	0.044 ± 0.020	-0.196 ± 0.003	-0.154 ± 0.017	0.200 ± 0.028	0.055 ± 0.009
2013	L	groom	-0.076 ± <0.001	0.359 ± <0.001	-0.094 ± <0.001	-0.288 ± >0.001	0.169 ± >0.001	0.142 ± 0.000
2014	J	groom	-0.012 ± 0.033	-0.069 ± 0.060	0.076 ± 0.032	-0.277 ± 0.027	0.021 ± 0.032	0.031 ± 0.048
2014	L	groom	0.165 ± 0.041	-0.016 ± 0.021	0.129 ± 0.025	-0.474 ± 0.022	0.118 ± 0.024	-0.021 ± 0.022

each individual, as we felt that it better reflected particular *individuals'* strategic investment in their relationships with others. Owing to funding limitations in 2014, grooming data were collected ad libitum as events when observers moved through the troops. For each event, we recorded the identities and direction of the grooming dyads. To avoid pseudoreplication, and because we could not know who initiated every grooming event, an independent grooming bout was recorded only when the partner identities of a grooming dyad changed, or grooming ceased and the dyad moved to a different location. As such, we did not record reversals of dyads within one grooming bout, i.e. we did not record a new grooming record when individual A was observed grooming individual B, and B then groomed A without moving to a new location.

3.3. Statistical analyses

We created association matrices that were both weighted, as the proportion of time spent in proximity and grooming could vary between 0 and 1, and directed, as in both cases the connection could not be mutually returned. This resulted in a total of 24 association matrices for the combinations of troops, years and association methods. We then tested whether each network was assorted by rank (ranging from 0 to 1), sex (male/female), boldness (the natural log of (the time spent inspecting the novel food + 1)), age (1–26 years), and propensity to generate information (high/low) and exploit information (high/low) using the *assortnet* package [33] in the statistical software R v. 3.0.3 [34]. Weighted assortativity calculates the degree to which associations occur between individuals of similar phenotypes and ranges from -1 , where individuals are always found with individuals of a different phenotype, to 1, where individuals are always found with individuals of the same phenotype [33]. In the case of sex and the propensity to generate/exploit information, we calculated discrete assortment, and in all other cases we calculated continuous assortment. Standard errors, calculated by jackknife simulation [33], that do not overlap 0 indicate significant assortativity in the network structure.

In our analysis, we assessed the effects of each phenotype independently rather than concurrently in a single test, because there is no statistical technique that will investigate the effects of multiple phenotypes on (weighted) network assortativity. However, one implication of this approach is that it may lead to spurious relationships if the phenotypes are intercorrelated. To assess whether this was the case, we created correlation matrices of the four uncombined phenotypes for the troops and years (see the electronic supplementary material, table 1). We focused on pairwise correlations approaching or exceeding $|r| > 0.70$ as a critical threshold beyond which collinearity may be a serious problem [35]. Of the possible 66 combinations of phenotypic correlations across troops and years, only 4 (6%) approached or exceeded this threshold. These reflected positive correlations between sex and rank (adult males are higher ranking than females) in both troops in 2011 and 2012 (when the proportion of adults in the sample was at its highest; the relationship between sex and rank is much weaker in juveniles). However, these correlations did not appear to lead to any spurious relationships in our analysis, as the observed patterns of assortment by sex and rank were in the opposite rather than the same direction (see below).

4. Results

In total, we created 24 social networks based on two methods of measuring a connection between individuals for the two troops in the six study years (figure 1). We then tested whether these networks were assorted by the four phenotypes (table 1 and figure 2). In the four years with comparably collected data (2009–2012), we found that grooming networks were almost twice as likely to be assorted as proximity networks (35 out of 41 versus 19 out of 41 networks, or 85% versus 46%, respectively) (table 1). Information generators were assorted in every grooming network (100%, or 6 out of 6 cases). Age, sex and rank all led to equally high levels of assortment in the grooming networks (88%, or 7 out of 8 networks, in each case), followed by boldness (67%, 4 out of 6) and the propensity to exploit information (1 out of 5, 20%). Phenotypic assortment in the proximity networks was not only lower but much more variable, being most common in relation to the propensity to generate and exploit information (100%, 6 out of 6; and 80%, 4 out of 5; respectively), followed by rank (63%, 5 out of 8), sex (50%, 4 out of 8), boldness (33%, 2 out of 6) and age (25%, 2 out of 8). Phenotypic assortment was also high for all traits in both network types in both 2013 (96%, 23 out of 24 cases) and 2014 (66%, 16 out of 24 cases).

In grooming networks, where phenotypic assortment occurred, the patterns were consistently positive for rank, age and boldness (71%, 5 out of 7; 86%, 6 out of 7; 75%, 3 out of 4), equal for the propensity to generate or exploit information (50%; 3 out of 6; 50%, 2 out of 4) but negative for sex (88%, 7 out of 8). Thus, animals of similar rank, age and boldness, but different sex, were more likely to be

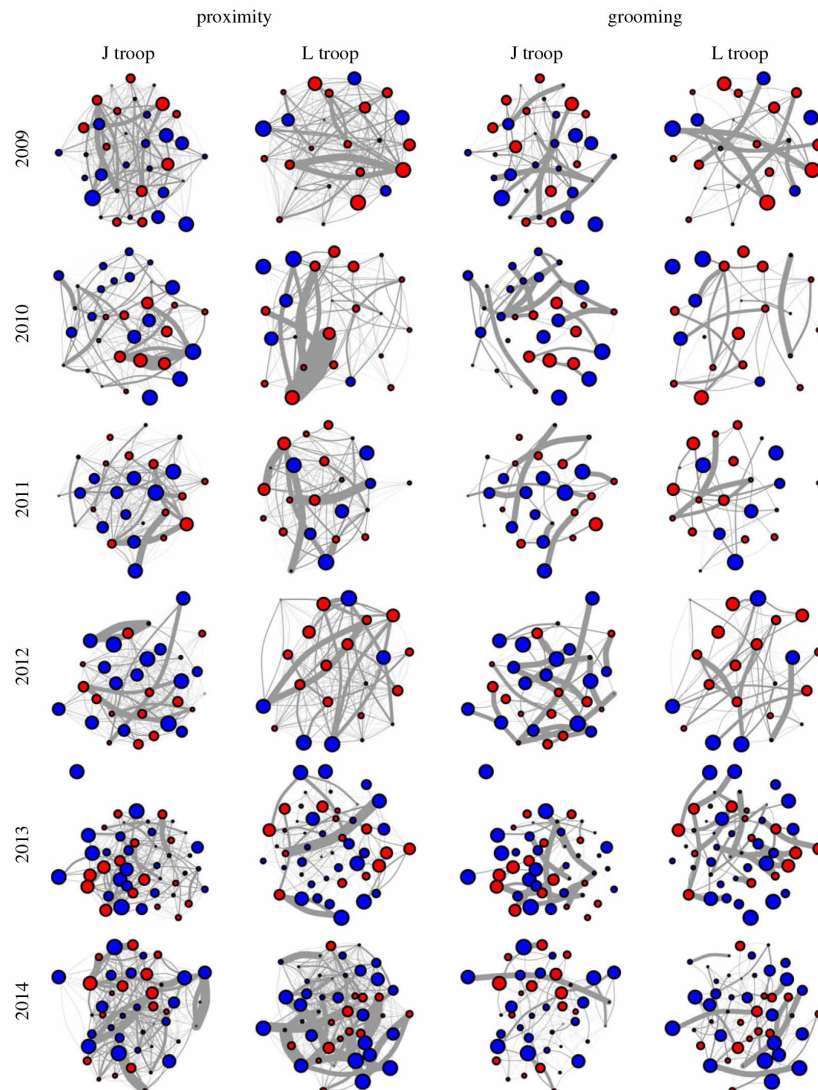
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Figure 1. Social networks based on the time spent in close proximity to (left) and grooming (right) other individuals, for two troops of baboons (J and L) over 6 years (2009–2014). Each node indicates an individual, and the lines connecting the nodes represent the connections between individuals. Node colour indicates sex (blue, male; red, female), while node size indicates rank (larger nodes designate higher ranks). Line thickness indicates the connection strength, with thicker lines designating stronger connections (i.e. a greater proportion of time spent in close proximity to or grooming). However, note that the line thickness is not comparable between proximity and grooming (we have increased line thickness in the proximity networks to make weaker connections more obvious). Node position is conserved within years for each troop.

associated when grooming; by contrast, no such associations were observed according to the propensity to generate/exploit information. Similar patterns were observed in the proximity networks in those cases where assortment occurred. Similar patterns were also observed in 2013 and 2014 in both network types, with the exception that those with a propensity to generate/exploit information were more likely to be positively assorted in both years and age-assortativity reversed in the 2013 grooming networks.

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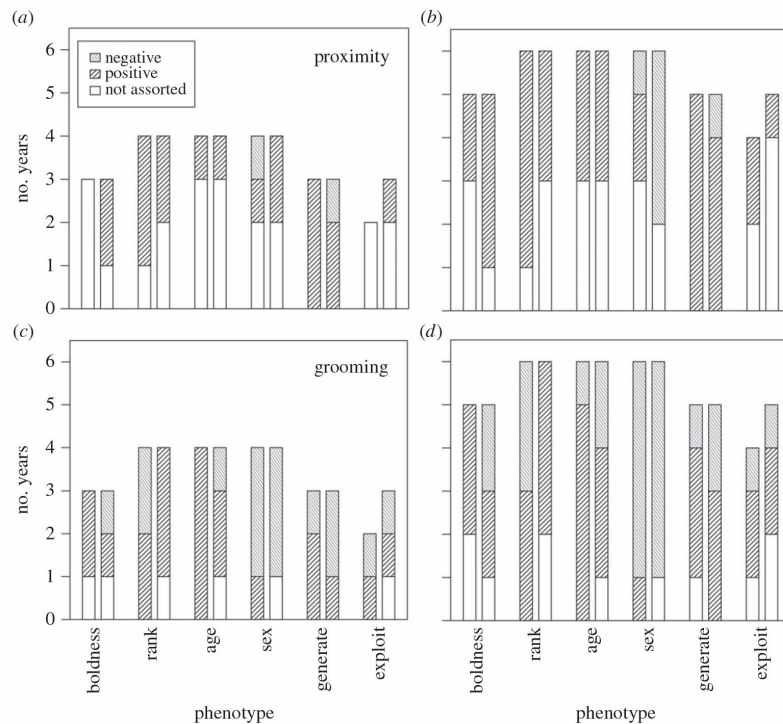
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Figure 2. Network assortment patterns for six phenotypes in two troops of baboons. Counts of the types of assortment over 4 years (*a,c*) and 6 years (*b,d*) are presented for proximity (*a,b*) and grooming (*c,d*) networks. Assortment type is indicated by shading (see legend). Each phenotype shows the assortment for J (left bars) and L (right bars) troops.

In general, the groups also showed similar patterns of phenotypic assortment (figure 2). Looking within years at each phenotype–network combination, when significant assortment was observed in one group it was also usually observed in the other. However, there were a substantial minority of instances (34%, 17 out of 50) where this was not the case. Similarly, where both groups showed significant assortment, the direction of assortment was usually the same, but there were a number of occasions when the direction differed (24%, 8 out of 33). These differences were most common for boldness (50%, 2 out of 4), followed by propensity to generate information (33%, 2 out of 6), rank (29%, 2 out of 7), sex (14%, 1 out of 7), age (13%, 1 out of 8) and propensity to exploit information (0%, 0 out of 2).

5. Discussion

We assessed, for the first time to our knowledge, broad-scale patterns of individual assortativity in animal social networks in relation to the potential generation and exploitation of social information. Using baboons as a model system, we tested whether individuals were assorted by six phenotypic traits which can influence an individual's mode of social information use: sex, rank, age, boldness and the propensity to generate (bolder juveniles) and exploit (higher ranking shy individuals) information phenotypes. We demonstrated that: (i) assortment was common in grooming networks, which overall showed homophily for rank, age, boldness and the propensity to generate and exploit information, but heterophily for sex; (ii) proximity networks were less frequently assorted, in approximately half of the cases, but similar and more consistent patterns of homophily and heterophily among years were observed where assortment did occur; and (iii) between the two troops, there were broadly similar patterns in the occurrence and direction of assortment, albeit with considerable variability. Our results have implications for understanding the transfer of information between individuals in social networks,

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and we discuss these implications below before considering the importance of broader investigations in animal social network studies.

As a rule, if only animals of a particular phenotype are information generators, then any degree of homophily in that phenotype is going to impede information transmission to other group members. We have previously reported that younger (juvenile) and bolder baboons are more likely to solve novel foraging tasks [9]. This suggests that these individuals have a propensity to generate information and may therefore often act as information generators in the troop (although all individuals have the potential to act as information generators at some point). If so, our finding that grooming networks typically showed homophily in both these phenotypes, and the combination of these phenotypes (propensity to generate information), indicates that the diffusion of information through baboon troops may be restricted by its social structure. It remains to be seen whether the lower instances of assortment in many proximity networks is sufficient to compensate for these effects, though—importantly for our hypothesis—the vast majority of proximity networks showed homophily for those with a propensity to generate information. Heterophily, which would actively promote information transmission, was only consistently found in one phenotype, namely sex, which was previously found to be unrelated to solving novel foraging tasks [9]. As we mention in the Introduction, naive individuals may acquire social information directly from information generators or secondarily from information exploiters. The limitations to information transmission due to homophily that we describe may apply only to those cases of direct transmission between information generators and exploiters; however, after an initial primary transfer between an information generator to an exploiter, homophily may then promote information transmission among secondary information exploiters.

We see our ‘information phenotype’ framework as an exciting future research direction. We encourage researchers that are interested in understanding information transmission processes to integrate individual differences in information phenotypes with the social environment. Our previous work investigating individual differences in information use [9,11] and that of others which investigate the consistency of foraging strategies that rely on the use of personal and social information [10,36] suggest that individuals may differ consistently in how they collect and process information. This will have implications for the transmission of information in groups (we develop this further below). However, the categorization of individuals according to their propensity to generate/exploit information, while usefully based on combinations of other phenotypes here, requires further exploration. While we are not suggesting that individuals will exclusively generate or exploit information, we predict that individuals will have a tendency to prefer one information acquisition strategy over the other. This preference may be based on their phenotype, as we have suggested, and/or their position in their social network and thus their opportunities to exploit information. Future research could also investigate whether individual differences in information plasticity (i.e. the flexibility with which individuals switch between generating and exploiting information) could also be predicted by an individuals’ phenotype [36]. For example, some individuals in our study could be categorized as neither high nor low propensity to generate/exploit information; it is possible that these individuals are more flexible in their use of information acquisition strategies.

Our goal in this study was to predict whether information transfer would be promoted or retarded by patterns in the fine structure of social networks, specifically through the assortment of phenotypes that may influence modes of information acquisition. However, one aspect of social information transfer that may limit our ability to predict its transmission through social networks involves the difference between social information acquisition and its use. We have shown evidence that some individuals may acquire social information but not use it ([9], see also [37]), which would limit how far information could diffuse through a network. It may be unreasonable to assume that an individual will always use the social information that it has acquired [37], but this possibility is rarely, if ever, considered in studies modelling social information diffusion (e.g. [38]). Individual differences in the use of acquired social information have two far-reaching implications for studies not only of social information diffusion but also for studies of social learning, and traditions and culture in animal societies. First, simulation studies of social information diffusion and social learning probably consistently overestimate the rates at which information can diffuse among individuals in a network. This is because simulations assume that information will always diffuse between naive and informed individuals even though informed individuals may not demonstrate their knowledge [9]. Such knowledgeable non-demonstrators should be considered functionally naive in simulations, as they cannot or will not demonstrate to naive individuals, even if they associate at high rates. Second, because social information will not transfer from informed but non-demonstrative individuals to truly naive individuals, the formation of traditions in animal societies may not necessarily be limited by individuals’ abilities to acquire a novel skill, but

by individual differences in the propensity to use that skill once it has been acquired. Simulations and descriptive studies like ours may be useful for exploring the opportunities for information transfer between individuals and the particular inter-individual routes this information might take. However, direct measurement of information flow is needed in different social networks through time in order to establish whether it actually occurs.

We considered two types of network for possible information transmission. These were based on grooming and proximity associations. Although we cannot currently say which is most important for information transmission, it seems likely that both will play a role. Assuming that information transmission requires close visual contact [9], spatial proximity will be important, though we emphasize that this will depend on the type and complexity of the information that is being generated. However, among their neighbours, individuals may be most attentive to those with whom they share strong social (grooming) bonds (cf. [12,24]). The finding that grooming networks showed stronger assortment than proximity networks suggests that assortment may largely reflect patterns of social affiliation, but that these assortment patterns are attenuated in proximity networks as the signal is diluted (or in some cases reversed) by the movements of animals which take them away from the immediate vicinity of preferred social partners. Previous research in baboons has shown that social bonds are often formed with animals of similar age and rank, at least among adult females, who form the stable core of the group (*Papio cynocephalus*: [39], *P. ursinus*: [40]). The findings of homophily in these assortment patterns are therefore expected. The finding of heterophily in the assortment patterns for sex is more surprising, as female baboons tend to prefer forming bonds with other females [41], but most likely reflects the combined effects of male–male avoidance and the prevalence of female–male grooming interactions during both oestrus (between sexual partners) [42] and lactation (between mothers and male ‘friends’ who protect their infants) [42].

No previous research has considered whether bolder/shyer baboons are more likely to associate with each other or not; our analysis is, to our knowledge, the first to suggest that this can happen, and although the pattern is variable, it is in line with previous findings in chimpanzees (*Pan troglodytes*) [15] and guppies (*Poecilia reticulata*) [14]. These previous studies have suggested that homophily for personality traits could promote cooperation among individuals. In guppies, for example, boldness is measured by a tendency to inspect a predator [14], and cooperative predator inspection occurs more frequently among affiliated individuals [17], thus homophily for boldness may facilitate cooperation among bolder associates. Why baboons should demonstrate homophily for boldness is unclear, unless boldness has a heritable component (e.g. [44]), and these patterns reflect family associations.

While the diffusion of information in baboon groups may often be limited by homophily, we also observed substantial variation in assortment both between troops and years (see also [23]). One possible methodological source of inter-annual variation within the 2009–2012 period is the diminishing proportion of juvenile animals sampled. Between 2009 and 2012, while the numbers and identities of individuals sampled in each troop remained relatively constant, the proportion of the troop that was sampled decreased as the numbers of infants and juveniles increased with the births that occurred after 2008 (the last occurrence of individual marking). In 2013 and 2014, the sample size of individuals increased again, as did the proportions of the members of study troops that were included in the networks, following troop capture and a new round of individual marking in 2012 for all those animals born since 2008 (figure 1). It is therefore possible that the similar patterns of assortment observed in 2009 and 2013 partially reflect the similar proportional sampling of the troops (all weaned baboons) in these 2 years. Nevertheless, inter-annual variation in the biological processes that we have discussed above and go on to describe below is also very likely to contribute to these patterns. This methodological complexity highlights two important considerations, both for our current study and more generally. First, the role of juveniles in contributing to the fine structure of a network may be overlooked, especially for long-lived, social mammals such as many primates and cetaceans, where relationships with and between juveniles are often ignored (e.g. [39,40]). In our study population, juveniles are particularly important in their role as information generators [9], and omitting them from social networks may generate different predictions and give different results from those networks in which they are included. Second, continual demographic changes in networks make direct comparisons between time periods difficult, especially in the wild where demographic changes cannot be controlled ([23], cf. [45]). Thus, researchers studying social networks in the wild will often have to make decisions about which individuals to include and how to follow them longitudinally—either: (i) the same core group of individuals is followed and their relationships with individuals that immigrate, emigrate, are born and die are largely ignored; or (ii) all individuals are included and confounds between demographic and temporal changes are accepted as a complication of longitudinal studies. We deal further with the issue of demographic changes below.

Changes in group demography, and the associated alterations in social networks, are also very likely to contribute to the variation in assortment between troops and among years [45–47]. For example, the immigration of several non-natal adult males in both troops between 2011 and 2014 may have contributed to the stronger patterns of negative assortment by sex in their proximity networks in those years. Furthermore, extreme inter-annual environmental variation at the study site (A. J. Carter 2009–2014, personal observation) may have caused changes in social structure, as has been found in other baboon populations in response to changes in season [48]. As mentioned earlier, male–female relationships will be affected by females’ reproductive states, and it is likely that stochastic variation in the proportion of females in any one state at any one time might affect the network structure and patterns of assortment within it. Furthermore, female–female relationships will be affected by female reproductive state in at least two ways: (i) mothers with infants attract more grooming than at times when they do not have an infant [49,50], and (ii) oestrus females are the targets of aggression from other females [30], which presumably will affect both proximity and grooming interactions among females. The finding of extreme inter-annual variation has two implications. First, while the transfer of information may be limited by the social network at some points in time, individuals are likely to have access to information generators at others. Thus, the flow of information may be promoted or limited by temporal variation in the patterning of relationships. Second, high temporal variability in networks makes it difficult to generalize about the flow of information in social networks from a single point in time; a full understanding of how information diffuses through social networks is likely to require assessments at multiple time periods or in multiple groups.

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Data accessibility. Networks and phenotype data are available on figshare. Figshare (<http://dx.doi.org/10.6084/m9.figshare.1239171>).

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Conflict of interests. We have no competing interests.

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Chapter 2 – Switching spatial scale reveals dominance-dependent social foraging tactics in a wild primate

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A.E.G.L. conceived the study, designed and implemented the data collection in the field, conducted analyses and wrote the manuscript. G.C. conceived the study, contributed to its design and implementation, and provided comments on drafts of the manuscript.

Chapter 3 – Information use and resource competition: an integrative framework

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A.E.G.L. conceived the study, designed and analysed the model, and wrote the manuscript. J.P.O., T.C., and J.M.R. provided conceptual input, assisted mathematically, and commented on drafts of the manuscript. G.C. conceived the study, contributed to its design, and provided comments on drafts of the manuscript.

Chapter 4 – Social constraints on social information use depend on resource distribution

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A.E.G.L. conceived the study, designed and implemented the experiment, conducted analyses and wrote the manuscript. A.B. contributed to the experimental design, implemented the experiment, and commented on drafts of the manuscript. J.M.R. commented on drafts of the manuscript. G.C. conceived the study, contributed to its design and implementation, and provided comments on drafts of the manuscript.

Chapter 5 – The eco-evolutionary dynamics of social dominance

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A.E.G.L. conceived the study, designed and analysed the model, and wrote the manuscript. G.C. conceived the study, contributed to its design, and provided comments on drafts of the manuscript. J.M.R. provided conceptual input and commented on drafts of the manuscript. T.C. conceived the study, contributed to its design, advised on integral projection modelling, and provided comments on drafts of the manuscript.

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