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Review

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

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

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

In this review, we argue that the elucidation of these mechanisms is a priority, in particular the mechanisms by which variation in social foraging behaviour drives individual-level time budget differences. There is a growing appreciation that to study group-level patterns of behaviour it is necessary to understand how these emerge from individual-level behaviours (Conradt & Roper 2000; King et al. 2008; Lihoreau et al. 2010; Petit & Bon 2010). A classic example of this is in social insects, where colony- (or group-) level phenomena such as social networks (Fewell 2003; Naug 2009) and collective foraging (Sumpter & Pratt 2003; Lihoreau et al. 2010) and decision making (Passino et al. 2008; Marshall & Franks 2009) are the product of the behaviours of each individual colony member. It follows, therefore, that to study group-level time

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budgets it is necessary to understand how each group member decides how to allocate its time. These individual-level decisions will be strongly influenced by social foraging success, and so individual-level time budgets clearly play a crucial mediating role between social foraging behaviour and group-level time budgets. To date, the determinants and consequences of individual time budgets have received relatively little attention, although individual-level differences in time budgets have been implicated in group-level cohesion and behavioural synchrony, which play an important role in the functioning of social groups and so the performance of the individuals within it (Conradt & Roper 2000; Ruckstuhl 2007; Main 2008; Sueur et al. 2011a). Furthermore, a greater understanding of individual-level time budgets will provide insight into group-level time budgets, which have themselves been implicated in constraining the group's size (Dunbar 1992; Korstjens et al. 2006; Pollard & Blumstein 2008) and, through the requirements of minimum group size for population viability, species' geographic ranges (Dunbar 1998; Lehmann et al. 2006, 2010; Korstjens et al. 2010).

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

INDIVIDUAL-LEVEL SOCIAL FORAGING BEHAVIOUR

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

Ecological Environment

A habitat's food distribution plays a key role in determining decisions made by foragers, such as which patch to exploit and when they leave a patch in search of another (Giraldeau & Caraco 2000; Nonacs 2001; Waite & Field 2007; Giraldeau & Dubois 2008; Hamilton 2010). Recent empirical studies of the influence of food distribution on social foraging have tended to be confined to group-foraging birds. They do, however, broadly support theoretical predictions that foragers should: (1) consider the underlying patch qualities and co-forager characteristics and distribute themselves across patches to maximize individual benefits (e.g. shorebirds, Folmer et al. 2010; the ideal-free distribution, Fretwell & Lucas 1969, reviewed in Waite & Field 2007; Hamilton 2010); and (2) leave patches earlier in higher quality habitats (e.g. common cranes, *Grus grus*, Alonso et al. 1995; red knots, *Calidris canutus*, van Gils et al. 2003; the marginal value theorem, Charnov 1976, reviewed in Nonacs 2001). The food distribution in a habitat can also influence the type of feeding competition experienced within social groups. Increased levels of feeding aggression, that is contest (or interference) competition rather than scramble (or depletion) competition, have been shown in habitats with increased patch quality (Wrangham 1980; Hamilton 2002; Stillman et al. 2002), defensibility (van Schaik 1989; Isbell 1991; Sterck et al. 1997) and clumping (i.e. resources concentrated in fewer patches; Vahl et al. 2005; Tanner et al. 2011; Tanner & Jackson 2012).

It has also become increasingly apparent that the information a forager possesses about its environment, and whether it collects this by directly searching the environment or by monitoring the behaviour of others, plays an important role in social foraging behaviour (Valone & Templeton 2002; Danchin et al. 2004; Dall et al. 2005). The availability of these two sources of information, and a forager's ability to monitor them both simultaneously, can be determined by a habitat's physical structure (Templeton & Giraldeau 1995; Coolen et al. 2001). For example, where habitat characteristics restrict visibility, and so the distance over which individuals can search for their own foraging opportunities, foragers may more readily exploit the food discoveries of others (capuchin monkeys, *Cebus apella*, Di Bitetti & Janson 2001; Ruxton et al. 2005; bison, *Bison bison*, Fortin & Fortin 2009). The importance of these two sources of information and whether they can be collected simultaneously is recognized by producer–scrounger (P–S) and information sharing (I-S) models of social foraging behaviour (Giraldeau & Beauchamp 1999; Giraldeau & Caraco 2000; Ruxton et al. 2005; Beauchamp 2008b). Both models describe how, in a group of foragers, an individual can either search for food itself or monitor others and exploit their discoveries. The models are differentiated by whether or not they treat these behaviours as compatible, as in I-S models, or incompatible (i.e. an individual must do one or the other, produce or scrounge, at any one time) as in P–S models. Empirically, P–S models appear to have received more direct support (spice finches, *Lonchura punctulata*, Mottley & Giraldeau 2000; zebra finches, *Taeniopygia guttata*, Mathot & Giraldeau 2010a), although searching and monitoring can be compatible under some circumstances (violating P–S assumptions). For instance, the ability of starlings, *Sturnus vulgaris*, to assess patch quality was enhanced when the environment allowed them to concurrently feed and monitor others more easily (Templeton & Giraldeau 1995). Similarly, food type can also affect foragers' abilities to collect information by determining whether they can handle a food item and simultaneously scan for other foraging opportunities (samango monkeys, *Cercopithecus mitis erythrarchus*, Cowlishaw et al. 2004), as well as directly influencing foraging success by determining the handling time required per food item (European blackbirds, *Turdus merula*, Cresswell et al. 2001; roe deer, *Capreolus capreolus*, Illius et al. 2002; grass-cutting ants, *Acromyrmex heyeri*, Bollazzi & Roces 2011) and its nutritional benefit (baboons, *Papio* spp., Whiten et al. 1991; spider monkeys, *Ateles chamek*, Felton et al. 2009).

Social foraging behaviour can also be influenced by a habitat's predation risk, with increased risk leading to greater individual vigilance requirements (Brown 1999) and foraging group sizes, resulting in increased feeding competition (Barton et al. 1996; Barton 2000). Furthermore, high predation risk can inhibit or reduce foragers' use of a habitat altogether. Studies on chacma baboons, *Papio ursinus*, bison, and vervet monkeys, *Cercopithecus aethiops*, have shown that groups will trade off habitat quality with predation risk, often resulting in them using habitats that are not the most resource rich (Cowlishaw 1997; Fortin & Fortin 2009; Willems & Hill 2009).

Individual Traits

The importance of individual characteristics such as age, sex and morphology is widely recognized by ecologists (Bolnick et al. 2003) and can have important implications for foraging behaviour where

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

Individual characteristics can also influence a forager's spatial position within a group, and so its foraging behaviour. In general, as an individual moves towards the centre and away from the leading edge of a foraging group they experience greater feeding competition but also reduced predation risk (Hirsch 2007; Morrell & Romey 2008). An individual's position on this competition-predation gradient tends to be determined by its competitive ability. In species such as ringtailed coatis, *Nasua nasua*, and forest buffalo, *Syncerus caffer nanus*, adult males tend to occupy central positions whereas juveniles tend to be on the periphery (Melletti et al. 2010; Hirsch 2011). However, in species with more complex intragroup social structures, competitive ability (and so spatial position) tends to be determined by factors such as rank (chacma baboons, *Papio ursinus*, Cowlishaw 1999; capuchin monkeys, Di Bitetti & Janson 2001; see 'Social Environment' below).

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

Individual variation in social foraging behaviour, particularly when linked to differences in individual energy requirements, are likely to result in differences in energy reserves, which in turn are predicted to feed back on social foraging tactics (Barta & Giraldeau 2000; Rands et al. 2003; Morrell & Romey 2008; Mayack & Naug 2011). Barta & Giraldeau's (2000) risk-sensitive producer–scrounger model predicts that individuals should scrounge (exploit others' food discoveries) more when they have lower energy reserves. This prediction has been empirically validated (house sparrows, *Passer domesticus*, Lendvai et al. 2004; zebra finches, Mathot & Giraldeau 2010b), but validation of other energetic models has proven more difficult because of the technical challenges associated with directly and noninvasively measuring energy reserves. New techniques, such as urinary C-peptide analysis (Higham et al. 2011), may allow empirical tests of such models in the future.

Social Environment

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

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

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

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

TIME BUDGETS

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

Individual-level Time Budgets

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

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

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

To our knowledge no study has yet investigated how time budgets vary between individuals with differing social networks and kinship bonds with other group members. Additionally, despite some indirect evidence (e.g. vervet monkeys, Isbell & Young 1993; chacma baboons, Barrett et al. 2006), we know of no study that has directly investigated how the reallocation of resting and/or social time to incorporate extra feeding requirements in poorer environments varies between individuals, and how this may lead to some individuals being time budget stressed with consequences for their health, condition and, ultimately, fitness. Furthermore, most studies of individual time budgets tend to consider how time is allocated to activities over fairly long periods (e.g. months). However, individuals can also alter when during the day they allocate time to different activities in response to changes in food availability and climate (McNamara et al. 1987; Bednekoff & Houston 1994; Owen-Smith 1998; du Toit & Yetman 2005; Brodin 2007; Shannon et al. 2008), and this may vary between individuals of differing rank (Ekman & Lilliendahl 1993; Brodin 2007). Therefore, the effects of age, sex and rank on time allocation decisions may potentially be manifested through differences in the timing of activities across the day rather than differences in the absolute time allocated to activities (e.g. subordinate individuals allocating more time to feeding later in the day; King & Cowlishaw 2009).

Group-level Time Budgets

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

Foraging-related travel requirements

At the group level, a great deal of research has focused on the causes and consequences of daily ranging distances, with obvious implications for how individuals allocate time to travel. One particular focus has been on how group size relates to travel distance. The ecological-constraints hypothesis proposes how social groups' travel requirements vary with group size and with the environment (Milton 1984; Janson 1988; Isbell 1991; Wrangham et al. 1993; Chapman et al. 1995; Chapman & Chapman 2000; Gillespie & Chapman 2001; Chapman & Pavelka 2005). It describes how either a reduction in habitat quality (Gillespie & Chapman 2001) or increase in group size (Chapman et al. 1995; Chapman & Chapman 2000; Chapman & Pavelka 2005) leads to increased intragroup scramble competition. This leads to a reduction in per capita resource availability, such that groups have to cover a greater area each day to meet their energy requirements, ultimately constraining any further increases in group size (Chapman et al. 1995; Gillespie & Chapman 2001). Correspondingly, reductions in food availability have been associated with increased day ranges in primates (Gillespie & Chapman 2001; Asensio et al. 2009; Mbora et al. 2009; Harris et al. 2010), carnivores (Wrangham et al. 1993) and elephants (Wittemyer et al. 2007). Where these increased ranging costs are sustained over longer timescales (e.g. months rather than days) this can lead to groups fissioning to offset these costs (Asensio et al. 2009). An alternative, and not mutually exclusive, response to increased intragroup scramble competition is for groups to spread out more, such that each individual has a larger search area (Altmann 1974; Janson 1988; Isbell 1991; Chapman & Chapman 2000). This second scenario has received much less attention, perhaps because the constraints on group spacing imposed by habitat visibility and predation risk make it a less common response than changing day range. Nevertheless, it has been demonstrated in primates (Henzi et al. 1997; Isbell et al. 1998; Cowlishaw 1999; Gillespie & Chapman 2001) and implicated in other species of mammal (Thouless 1990; Hirsch 2011) and bird (Moody et al. 1997).

It is not the case, however, that a group's travel costs always covary with resource availability. In some situations, group sizes and travel costs are constrained by other costs and benefits of grouping besides scramble competition. For instance, in their meta-analysis of primate and carnivore grouping patterns, Wrangham et al. (1993) suggested that those populations and species that have greater-than-expected group sizes were subject to higher predation risk. In this situation, predation risk keeps group sizes at the maximum allowable given local foraging conditions, meaning that the per capita food share, and so travel costs, remains constant across group sizes (Chapman & Chapman 2000). Social costs, such as aggression and infanticide, may also constrain group sizes in some situations, leading to smaller group sizes and lower travel costs (Treves & Chapman 1996; Steenbeek & van Schaik 2001; Chapman & Pavelka 2005; Snaith & Chapman 2007, 2008).

Reallocation of resting and social time

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

Time spent resting was often assumed to be 'free' and available for use in other activities if required (e.g. Altmann & Muruthi 1988; Dunbar 1992), despite the suggestion that it may be important in physiological processes such as digestion and thermoregulation (Herbers 1981). More recent studies have supported this suggestion, showing that groups spend more time resting when under

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greater heat stress (Stelzner 1988; Dunbar 1992; Di Fiore & Rodman 2001; Hill et al. 2004; Hill 2006; Korstjens et al. 2010) or when their diet contains less easily digestible food (Doran 1997; Korstjens & Dunbar 2007; Masi et al. 2009; Korstjens et al. 2010). Consequently, time allocated to resting is increasingly understood to include an 'enforced' component determined by the environment, either directly through thermoregulation requirements or indirectly through digestion requirements (Dunbar et al. 2009). The importance of this component has been highlighted by recent evidence in primates showing that enforced resting time predicts both biogeography (Korstjens et al. 2010) and group size (Pollard & Blumstein 2008).

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

LINKING SOCIAL FORAGING BEHAVIOUR TO TIME BUDGETS: INDIVIDUAL-BASED MODELLING APPROACHES

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

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

These consequences of variation in individual- and group-level time budgets highlight the need to understand better the mechanisms that drive this variation. Individual-based mechanistic modelling (or agent-based modelling) is likely to prove useful in building this understanding, as it is specifically designed to examine how higher-level phenomena emerge from individual-level processes (Grimm & Railsback 2005). A similar approach is advocated by Sueur et al. (2011a) for the study of group cohesion and decision making, and has been used to demonstrate how individual differences within groups influence collective decision making (Couzin et al. 2005, 2011; Conradt et al. 2009; Sueur et al. 2009, 2010a; Lihoreau et al. 2010) and patterns of group cohesion or fission (Conradt & Roper 2000; Ruckstuhl & Kokko 2002; Yearsley & Pérez-Barbería 2005; Sueur et al. 2010b). However, as this review has argued, gaining a greater understanding of how social individuals interact with their environment to produce emergent group-level phenomena requires explicit consideration of their foraging behaviour. Studies by Rands and colleagues provide a good example of how individual-based models can be used in this approach. They modelled social individuals using state-dependent foraging rules and demonstrated that varying food availability and distribution could lead to differences in individual energy reserves, movement patterns and group sizes (Rands et al. 2004). Furthermore, they highlighted the importance of considering individual differences (in dominance), as incorporating them in the model led to greater differences in individual energy reserves and movement (Rands et al. 2006). In a separate dynamic game model of a foraging pair, they also showed that, where a cost to solitary foraging existed, synchronized foraging spontaneously emerged with one individual consistently leading the other (Rands et al. 2003). Again they highlighted the importance of individual

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differences, showing that when these differences were incorporated in the model the patterns of leader and follower emergence became more complex and harder to predict (Rands et al. 2008). Recently, Rands (2011) further extended this model, showing that although the subordinate member of the pair experienced a foraging cost, this also had implications for the dominant animal, as the subordinate was likely to become the leader, deciding when the pair foraged.

Unfortunately, many of these individual-based modelling studies did not compare their model outputs to empirical data, and none of the exceptions among the aforementioned studies explicitly considered foraging behaviour (red deer, Conradt & Roper 2000; tonkean macaques, *Macaca tonkeana*, Sueur et al. 2009, 2010b; golden shiners, *Notemigonus crysoleucas*, Couzin et al. 2011). The value of doing so is demonstrated by numerous studies of shorebirds, in which analyses of individual foraging behaviour have been used to build individual-based models simulating this behaviour. These models have then accurately described the observed variation in individual foraging success, the interference competition they experience and their distribution across resources (Goss-Custard et al. 1995a, b; Stillman et al. 1997, 2000, 2002; Amano et al. 2006). The foraging successes these models predict have then been extended to accurately predict observed population sizes and levels of mortality (Pettifor et al. 2000; Stillman et al. 2000, 2003), and have been applied to predict the effect of anthropogenic environmental change in shorebird populations (Durell et al. 2005, 2006). However, despite these models sometimes predicting the time that individuals spend feeding (Stillman et al. 2000; Stillman 2008), they have not linked their individual-level predictions of foraging behaviour to time budgets (instead making assumptions about individual energy requirements to predict population parameters from individual foraging success, e.g. Goss-Custard et al. 1995b).

To our knowledge, Ramos-Fernández et al. have undertaken the only study that has developed an individual-based model of social foragers to explore emergent individual and group-level phenomena (Ramos-Fernández et al. 2006). They found that, despite the use of simple foraging rules, complex subgrouping patterns and social networks could emerge. When the model had intermediate food distribution values and foragers only had partial knowledge of their environment, these emergent patterns matched those observed in spider monkeys (*Ateles* spp.). However, this model did not incorporate individual differences in the foragers, which may well explain why some of the model outputs were a poor quantitative fit to the observed values. In fact, the authors deliberately kept the model simple, as a 'null' model. This model, and the models of shorebird foraging behaviour, may, therefore, provide a useful starting point for future research investigating the mechanisms linking individual-level social foraging behaviour with time budgets at the individual and group level. In this endeavour, the inclusion of individual differences, such as differences in energy requirements or rank-related competitiveness, would seem an obvious first step. Furthermore, there is growing evidence that social foragers can alter their decision making to suit the habitat they are in or social position they occupy (Devenport & Devenport 1994; Sargeant et al. 2006; Biernaskie et al. 2009; Marshall et al. 2012). Future modelling work might, therefore, also seek to include this flexibility in decision making and explore how such flexibility influences individuals' and groups' abilities to maintain sustainable time budgets across differing environments.

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

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