Individual variation in cooperative behaviour in meerkats

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Preface

This dissertation is my own work and contains nothing which is the outcome of work done in collaboration with others, except as specified in the text and acknowledgements. The total length of the text does not exceed 60,000 words, including the bibliography and appendices. No part of this dissertation has been submitted to any other university in application for a higher degree.

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Summary

Individual variation in cooperation is a striking yet poorly understood feature of many animal societies, particularly in cooperative breeders where individuals assist in the care of young that are not their own. While previous research on these systems has emphasised the plasticity of helping and how it varies with current environmental and social conditions, in this dissertation I examine how individual variation is constrained and influenced by trade-offs with other behaviours and experiences in early life. I demonstrate that variation in cooperative pup care (babysitting and provisioning) is consistent within individuals over time (Chapter 3). Provisioning is more consistent than babysitting, although the two behaviours are highly correlated within individuals. I then focus on the variation in helping that remains once current factors, such as condition, group size and food availability, are taken into account. In Chapter 4, I explore the possibility that variation in helping can be explained by personality, or consistency in behavioural traits such as exploration or risk-taking. I find little evidence for consistent individual differences in field measures of personality traits, however, with such behaviours instead being group-specific. Early social experiences are known to have important and lasting effects on later fitness and behaviour: in Chapter 5, I demonstrate that, in female meerkats only, growing up in a group with more helpers is correlated with reduced cooperation later in life. This result suggests the importance of future fitness in influencing current cooperative behaviour, as females raised in larger groups are more likely to attain dominance. Finally, I examine the extent to which vocal communication between carers and young is influenced by variation in contributions to cooperation. Females are more sensitive to increased begging rate (Chapter 6), which reflects general sex differences in cooperative behaviour. Carers modify their vocalizations but not their foraging behaviour in the presence of pups, and the way in which they vocalize during provisioning events suggests these calls serve to increase efficiency of prey transfer (Chapter 7).

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1 • INTRODUCTION

After decades of research into the evolution of cooperation, individual variation in cooperative behaviour remains a striking yet poorly understood feature of many animal societies. In this dissertation, I investigate the causes and consequences of individual variation in cooperative offspring care in wild meerkats and how it can inform our understanding of carer-offspring communication.

1.1 Individual variation in cooperation

Cooperation occurs when one individual's behaviour benefits another individual, and selection acts on the behaviour partly because of this benefit (West et al., 2007). Darwin (1859) identified cooperation in the form of sterile workers in social insects as representing 'one special difficulty' posed to his theory of evolution by natural selection (p. 236): why do individuals act to increase the fitness of others, at a cost to their own direct reproductive success? This question has continued to puzzle evolutionary ecologists in recent decades, and has spurred a multitude of theoretical and empirical studies (reviewed in Clutton-Brock, 2002, West et al., 2007). In particular, the study of cooperatively breeding societies, where individuals assist in the rearing of non-descendant young, has played a major role in our understanding of the evolution of cooperation (Cockburn, 1998, Koenig and Dickinson, 2004, Solomon and French, 1997). The two broad types of explanation for the evolution of such behaviour are that individuals accrue indirect or direct benefits from helping (reviewed in West et al., 2007). Indirect benefits are explained by inclusive fitness theory (Hamilton, 1964), whereby individuals increase their fitness by helping relatives. Direct benefits may include 'paying to stay' on a good territory (Kokko et al., 2002) and group augmentation (Clutton-Brock, 2002, Kokko et al., 2001). In addition, both the helper and recipient may receive immediate mutual benefits (reciprocity), although this idea is not well supported in studies of cooperative breeders (Clutton-Brock, 2002, West et al., 2007).

As well as asking why cooperative behaviour has evolved in general, researchers have been struck by the extent to which different members in a group vary in their contributions to cooperation. Initially, this variation was of interest as a counter-argument to early criticisms that helping behaviour may simply be an unselected by-product of

parental behaviour, and not necessarily adaptive (Jamieson, 1989). There is now a wealth of studies demonstrating that helping has benefits to helpers as well as offspring and that individuals mediate their helping effort according to the relative costs and benefits incurred (reviewed in Emlen et al., 1991, Heinsohn and Legge, 1999). Table 1.1 summarizes results from a non-comprehensive sample of studies on cooperatively breeding birds and mammals where researchers have used multivariate analyses or feeding experiments, or both, to investigate the effects of age, sex, breeding status, group size and food availability on individual contributions to cooperation. In general, patterns of variation in helping support the prediction that individuals mediate their behaviour according to the costs and benefits involved: younger individuals often help less, for example, as they are still investing in growth (e.g. Heinsohn and Cockburn, 1994), and sex differences in cooperative behaviour can be explained in terms of the relative fitness costs of helping (Clutton-Brock et al., 2002).

While many studies have investigated variation in helping, it is often not clear how much of the total variation remains unexplained once factors such as age, sex and relatedness have been taken into account. Quantifying the extent of this unexplained variation is difficult, however, as there is no simple way of calculating the R^2 value of a mixed model (Orelien and Edwards, 2008) and published studies often show means and standard errors of model predictions rather than the raw data (e.g. Gilchrist and Russell, 2007, Canestrari et al., 2007, Clutton-Brock et al., 2002). Nevertheless, the magnitude of such variation is evident from anecdotal reports. Hatchwell and Russell (1996) describe a long-tailed tit nest in which one helper fed sporadically and the other frequently; and around one fifth of noisy miners studied by Arnold et al. (2005) did not feed chicks at all. A more detailed description of unexplained variation is given by Hodge (2007), who describes 'super-helpers' in the banded mongoose, or individuals that, even within their sex and age class, help up to five times that of the average level of helping for that class.

Table 1.1 (opposite) Studies of variation in cooperative offspring care in eight bird and two mammal species. For ease of representation, complex interactions were excluded and group and age were categorised. 'Food' refers to experimental feeding of carers. 'Status' refers to whether an individual was dominant (dom) or subordinate (sub), except in species where there was no clear dominant individual, where it refers to known breeder (dom) or non-breeder (sub).

Behaviour	Factor	Effect	Species	Reference
Incubating/ babysitting	Relatedness	none	Meerkat	Clutton-Brock et al., 2000
	Age	young<old	Apostlebird	Woxvold et al., 2006
			Banded mongoose	Hodge, 2007
			Meerkat	Clutton-Brock et al., 2000, 2002
			White-winged chough	Heinsohn & Cockburn, 1994
		none	Acorn woodpecker	Mumme et al., 1990
	Food	fed>unfed	Meerkat	Clutton-Brock et al., 2000, 2002
	Group size	small>large	Apostlebird	Woxvold et al., 2006
			Banded mongoose	Hodge, 2007
			Meerkat	Clutton-Brock et al., 2000, 2002
			White-winged chough	Heinsohn & Cockburn, 1994
		none	Acorn woodpecker	Mumme et al., 1990
			Laughing kookaburra	Legge, 2000
	Sex	female<male	Banded mongoose	Hodge, 2007
			Laughing kookaburra	Legge, 2000
		female>male	Meerkat	Clutton-Brock et al., 2002
		none	Acorn woodpecker	Mumme et al., 1990
			Apostlebird	Woxvold et al., 2006
	Status	dom<sub	Banded mongoose	Hodge, 2007
			Meerkat	Clutton-Brock et al., 2004
		dom>sub	Acorn woodpecker	Mumme et al., 1990
			Laughing kookaburra	Legge, 2000
Provisioning	Relatedness	kin>non-kin	Seychelles warbler	Komdeur, 1994, Richardson et al., 2003
		none	Arabian babbler	Wright et al., 1999
			Laughing kookaburra	Legge, 2000
			Meerkat	Clutton-Brock et al., 2001
	Age	young<old	Apostlebird	Woxvold et al., 2006
			Banded mongoose	Hodge, 2007
			Meerkat	Clutton-Brock et al., 2001, 2002
		none	Acorn woodpecker	Mumme et al., 1990
			Carrion crow	Canestrari et al., 2005, 2007
			Seychelles warbler	Richardson et al., 2003
	Food	fed>unfed	Meerkat	Clutton-Brock et al., 2001, 2002
			White-winged chough	Cullen et al., 1996
			Banded mongoose	Hodge, 2007
	Group size	small>large	Apostlebird	Woxvold et al., 2006
			Laughing kookaburra	Legge, 2000
			Meerkat	Clutton-Brock et al., 2001, 2002
			Arabian babbler	Wright, 1998b
		none	Acorn woodpecker	Mumme et al., 1990
			Banded mongoose	Hodge, 2007
			Carrion crow	Canestrari et al., 2008, 2005
	Sex	female<male	Banded mongoose	Hodge, 2007
			Laughing kookaburra	Legge, 2000
			Long-tailed tit	MacColl & Hatchwell, 2003
		female>male	Acorn woodpecker	Mumme et al., 1990
			Meerkat	Clutton-Brock et al., 2001, 2002
	Status	dom<sub	Meerkat	Clutton-Brock et al., 2004
		dom>sub	Acorn woodpecker	Mumme et al., 1990
			Carrion crow	Canestrari et al., 2008, 2007
			Laughing kookaburra	Legge, 2000
			Long-tailed tit	MacColl & Hatchwell, 2003
		none	Banded mongoose	Hodge, 2007

One explanation for residual individual variation is that the costs and benefits have not been fully accounted for. An often overlooked cost of helping, for example, is that of future reproductive opportunities, given the trade-off between current helping and own future reproduction (Williams, 1966). Experiments on primitively eusocial societies of paper wasps and hover wasps have demonstrated that, when an individual's chance of inheriting the breeding position is increased, it decreases its cooperative behaviour (Cant and Field, 2001, Field et al., 2006). Even if it is not always possible to have complete information on all the costs and benefits explaining variation in behaviour, this does not mean that the unexplained variation should be discounted as random noise around an adaptive mean (Wilson, 1998). Instead, individual variation in itself can be adaptive, or the product of natural selection, in addition to forming part of the raw material on which selection acts (Wilson, 1998). For example, in bluegill sunfish, individual differences in foraging behaviour reflect adaptations to the local environment (Ehlinger and Wilson, 1988); and male marine isopods exhibiting different mating strategies have equivalent mating success (Shuster and Wade, 1991).

Before describing the intricacies of research into individual variation, it is informative first to give an overview of what is meant by the term 'individual variation'. Given that this is such a common phrase in studies of evolution and behaviour, it is surprising that a specific definition of the concept is not clear. In fact, individual variation in behaviour can be viewed from two standpoints. Most commonly, individual variation describes the differences among individuals within a species or within a population, disregarding factors such as sex and age driving such variation (Hayes and Jenkins, 1997, Wilson, 1998) (interpretation 1). Once these factors have been considered, the term individual variation may be used to describe the residual, unexplained variation (interpretation 2). Both interpretations may contribute to our understanding of the evolution of behaviour. Investigating the residual, unexplained variation (interpretation 2) is important in identifying the causes of variation in behaviour. For example, we may have ascertained that some cooperative behaviour is explained by sex and relatedness yet there is large variation that remains unexplained, which would then lead us to investigate whether any factors were overlooked in previous studies. However, as selection acts on variation at the

level of the individual – in contrast to the researcher using multivariate tools to partition the variation – considering individual variation without controlling for other factors (interpretation 1) is also important when investigating the adaptive consequences of behaviour.

In the next two sections, I describe the approaches used to study individual variation in this dissertation. I explain the way in which consistency of variation can be measured (interpretation 1) before going on to explore how the residual individual variation (interpretation 2) can be explained both by correlations with behaviour in other contexts and in terms of the effect of the early environment. Throughout, I emphasise the importance of these approaches for the study of cooperative breeding; but individual variation can have widespread ramifications for studies of evolutionary ecology in general.

1.2 Quantifying individual variation: plasticity and consistency

1.2.1 Consistency across time

Individual variation can be partitioned into variation among individuals (inter-individual variation) and variation within individuals (intra-individual variation). Comparing the extent to which behaviour varies within individuals to that prevailing among individuals will give an idea of the consistency of behaviour, an often overlooked aspect of behavioural studies. Traditionally, behavioural biologists have assumed that behaviour is highly plastic, and sensitive to current ecological or social conditions (Komers, 1997). For example, female peacock wrasses make flexible decisions about where to spawn depending on the environment (Luttbeg and Warner, 1999). There is increasing evidence, however, that behaviour may be constrained within individuals (Pigliucci, 2001), just as there are limits on other aspects of phenotypic plasticity (DeWitt et al., 1998). A recent meta-analysis by Bell et al. (2009), for example, describes studies on several taxa that have found limited plasticity in a range of behavioural traits, including anti-predator, mating and foraging behaviour.

The consistency of behaviour may be quantified by measuring repeatability, or the proportion of total phenotypic variation (among and within individuals) that is due to among-individual variation (Lessells and Boag, 1987, Boake, 1989). High repeatability indicates that within-individual variation is low relative to among-individual variation, meaning that individuals are consistent in a variable population. While repeatability has been widely used as a tool for measuring intra-observer reliability (Carrasco and Jover, 2003), there is now an increasing number of studies using similar approaches to quantify the repeatability of behaviour (Bell et al., 2009). Most research on this subject has been conducted on mate choice, as predictability of male mating traits is often a necessary prerequisite for reliable signalling of quality (Boake, 1989). In addition, there is evidence for the repeatability of behaviours such as exploration (e.g. Dingemanse et al., 2002) and parental care (e.g. Nakagawa et al., 2007). In a laboratory study on blue jays, which cooperate with conspecifics to attain a food reward, there was anecdotal evidence that individuals were different in their propensity to cooperate and consistent in these differences (Stephens et al., 2002). There has been, to my knowledge, no study directly measuring whether cooperative behaviour is repeatable.

Investigating the repeatability of cooperative behaviour may provide empirical support for theoretical models of the evolution of cooperation. McNamara et al. (2004) used a game theory approach to demonstrate how the evolution of cooperation can depend on the existence of variation in types of individuals in a group, which may arise as a result of genetic and environmental factors. Understanding the repeatability of cooperative behaviour may also be a step in understanding any underlying genetic factors driving variation in cooperation, as repeatability can give an upper estimate to heritability (Boake, 1989). To date, only one study has shown that cooperative behaviour has a heritable component (Charmantier et al., 2007). Finally, investigating the repeatability of cooperative behaviour will be of relevance to the burgeoning field of animal personality, which will be introduced in the following section.

1.2.2 Personality types and behavioural syndromes

There is mounting evidence that individual differences in behaviour may be both constrained over time and correlated across functionally unrelated contexts. For example, individuals more likely to take risks in the face of predation tend also to be more aggressive toward conspecifics (e.g. Bell, 2005, Boon et al., 2008, Garamszegi et al., 2009). Such suites of correlated traits are known as 'behavioural syndromes' (Sih et al., 2004a, Sih et al., 2004b), while behavioural traits that are consistent over time are known as 'personality traits' (Dall et al., 2004). There is considerable discussion over the precise definition of these terms, however, which are often used interchangeably along with 'coping style' and 'temperament' (Réale et al., 2007, Sih and Bell, 2008). Moreover, as is often the case in emergent disciplines, many studies fall into the trap of demonstrating behavioural syndromes as interesting in themselves, without any further adaptive explanation (e.g. Kortet and Hedrick, 2007, Kralj-Fiser et al., 2007, Svartberg et al., 2005). In the context of cooperative breeders, however, there are three non-mutually exclusive reasons for which one may predict behaviours to be consistent within individuals or correlated across contexts: mechanistic constraints, life-history trajectories and individual specialisation.

Mechanistic constraints may provide a simple explanation for both personality traits and behavioural syndromes, in which underlying differences in state can result in consistent differences between individuals (Dall et al., 2004) and several behaviours may be under the control of the same genetic or hormonal pathway (Sih et al., 2004a). Theoretical models have demonstrated how differences in state variables, such as body size or energy reserves, in tandem with behavioural experience, can result in consistent individual differences between foraging pairs (Rands et al., 2003). As state variables have been shown to have striking effects on variation in cooperative behaviour (see feeding experiments in table 1.1), initial stochastic differences in state may also influence consistent variation in cooperative behaviour. Endocrinological mechanisms are a likely mechanism for behavioural syndromes in cooperative breeders. Given that hormones have pleiotropic effects across multiple behaviours (e.g. testosterone influences male singing behaviour and parental care in dark-eyed juncos, Ketterson and Nolan, 1992),

common hormonal mechanisms may underpin behavioural syndromes. In cooperative breeders, there is evidence that variation in helping behaviour may be explained by hormonal differences between individuals (Clark and Galef, 2000, Carlson et al., 2006b, Carlson et al., 2006a). This leads to the question of why individual differences in the underlying mechanisms occur in the first instance.

Second, suites of correlated behaviours may evolve as a result of trade-offs between life-history traits (Wolf et al., 2007, Stamps, 2007, Biro and Stamps, 2008) and the consequent life-history strategies that individuals pursue. For example, in species with a growth-mortality trade-off, behaviours that both increase growth and influence mortality, such as risk-taking and aggression over food, would be both consistent within individuals and correlated across contexts (Stamps, 2007). In cooperative groups, individuals face trade-offs both across different fitness-related behaviours at a given time (Young et al., 2005), or across investment at different time-points (Cant and Field, 2001). These trade-offs may result in consistent patterns in contributions to care across time and correlations in behaviour across contexts. Few empirical studies have specifically investigated the role of life-history strategies in the evolution of behavioural syndromes (Réale et al., 2009), with only one investigation in a cooperative breeder (Bergmüller and Taborsky, 2007). In this study on cichlids, the positive correlation between exploration and aggression, both which were negatively correlated with territory maintenance, was suggestive of individuals either pursuing a strategy of dispersing or remaining on the territory to help.

Finally, investigating syndromes within cooperative behaviours may increase our understanding of variation in cooperative behaviour in terms of individual specialisation. As in the study of alternative mating strategies, an individual may behave in a particular way depending on the actions of other individuals in the population (Gross, 1996). In cooperative groups, individual variation in cooperation is likely to depend on the behaviour of other individuals in the group, which may result in specialisation into different helper roles. While specialisation into cooperative roles, or division of labour, has been studied extensively in insect societies (reviewed in Bourke and Franks, 1995), there is increasing interest in individual specialisation in cooperative vertebrate groups

(Réale and Dingemanse, in press). For example, in noisy miners, individuals who invest more in mobbing contribute less to cooperative provisioning of chicks (Arnold et al., 2005). Most studies investigating variation in helping effort focus on provisioning rate of young without considering other cooperative behaviours, however, which may lead to a misrepresentation of an individual's overall contributions to cooperation across a range of behaviours (Komdeur, 2007).

1.3 Environmental influences on development

Understanding individual variation in cooperative behaviour may require consideration of environmental conditions during development, as these can have important effects on an individual's behaviour and phenotype later in life (Stamps, 2003, West-Eberhard, 2003). There is growing appreciation that conditions experienced early in life can have important downstream consequences on fitness, condition and reproductive success (Lindstrom, 1999, Forchhammer et al., 2001, Lummaa, 2003, Gluckman et al., 2005, Albon et al., 1987). The early environment may influence later phenotype, either through imposing constraints on development or adaptively preparing young for their later environment (Monaghan, 2008). On the one hand, individuals reared under adverse nutritional conditions may suffer from reduced competitive ability later in life, even if they underwent compensatory growth (e.g. Royle et al., 2005). In contrast, individuals may exhibit adaptive plasticity in response to early conditions, particularly in circumstances where the environment experienced in early life is predictive of later conditions (West-Eberhard, 2003). Here, I discuss the influence of early conditions, both in terms of the physical and social environment experienced, using our understanding from studies on non-cooperative species to predict how we may expect them to influence cooperative behaviour in social animals.

An important component of the physical environment in early life is food availability. The 'silver spoon' effect, whereby individuals born under good conditions have greater reproductive success as adults (Grafen, 1988), has been demonstrated in a number of species (reviewed in Lindstrom, 1999). In cooperative breeders, there is evidence that offspring raised in larger groups, which in turn receive more food, have improved

survival and breeding success (e.g. Russell et al., 2007, Ridley and Raihani, 2007). While the influence of early condition on later adult quality has been studied extensively in the context of survival and reproductive success, less is known about the way in which early physical conditions influence later behaviour. In some cooperative species, the conditions in which individuals are born may influence their ability to develop foraging skills (Heinsohn, 1991), which, if translated into being better able to afford the costs of cooperation, would lead to the prediction that environmental experiences influence later cooperative behaviour. For example, in meerkats, individuals which are in better condition when young demonstrate higher foraging efficiency later in life than their lighter littermates (Thornton, 2008a).

As well as the physical environment acting through the effects of nutrition and condition, the early social environment, or the presence of conspecifics and associated interactions with them, may also have lasting effects on later behaviour. Social experience may influence behaviour in young such as aggression or anxiety (Maestripieri et al., 1991), which may have downstream consequences on fitness-related traits such as reproduction or dispersal (Cote and Clobert, 2007). Furthermore, several studies have demonstrated that the amount and quality of care received by young individuals can influence later parental behaviour (reviewed in Fleming et al., 2002, Champagne and Curley, 2005, Maestripieri, 2005b). Cross-fostering and neurological studies on laboratory rats have elucidated the physiological mechanisms through which this process operates (Champagne and Meaney, 2007). Similarities between maternal and offspring parenting style are not entirely genetic, but instead arise in the postnatal period when the experience of behaviours such as licking and grooming influences oxytocin receptor density, which has permanent effects on later parenting behaviour (e.g. Champagne and Meaney, 2007). In a similar way, care provided by helpers may influence the expression of cooperative behaviour of young later in life, although this possibility has yet to be explored. Indeed, given that multiple carers are present, the role of care received in determining an individual's later behaviour may be more marked in cooperative societies than species in which a breeding pair or single parent cares for young.

1.4 Carer-offspring communication in a cooperative species

A comprehensive investigation of individual variation in cooperative offspring care, particularly the provisioning of young, requires consideration of the way in which the presence of offspring influences the behavioural decisions of adults. In this dissertation, I explore two separate aspects of carer-offspring communication. First, carers may respond to signals of need from begging young in terms of how much food, if any, they provide to young and whether they change their foraging behaviour in order to find more food to feed to young. I then explore the vocalizations produced by carers themselves, and discuss possible ways in which carers modify their calls when dependent young are present in the group.

In many avian species with biparental care, parents increase their provisioning rate in response to elevated signals of hunger from dependent young (Wright and Leonard, 2002). Commonly, there are differences within a pair in provisioning rules, with the sex that invests most in rearing the current brood showing a stronger response to increased begging (Kolliker et al., 1998, Kilner, 2002, Quillfeldt et al., 2004). The provisioning rules of carers within cooperatively breeding groups have received considerably less attention (Hatchwell and Russell, 1996, McDonald et al., 2009). Given the striking variation in contributions to care within groups of cooperative breeders (table 1.1), different categories of carer are predicted to vary in the extent to which they respond to increased begging, in accordance with the relative fitness benefits of investment in young. Of the few studies to date which have investigated variation in responsiveness to begging in cooperative breeders, the patterns of provisioning are equivocal. In Arabian babblers and bell miners, helpers and parents follow similar provisioning rules (Wright, 1998, McDonald et al., 2009) and, in superb fairy-wrens, responsiveness to experimental increases in begging is the opposite of that predicted from natural levels of investment (MacGregor and Cockburn, 2002). The clearest evidence of carers adjusting their sensitivity to begging in relation to the fitness benefits of helping comes from a recent study on banded mongooses (Bell, 2008), in which carers in good condition are more responsive to increased begging.

As carers increase the amount of food donated to young on hearing begging calls (Wright and Leonard, 2002) while simultaneously striving to meet their own nutritional requirements, they may adjust their foraging behaviour to compensate for the increased demand to find prey. Very few studies have investigated the way in which adults change their foraging behaviour (as opposed to offspring provisioning rate *per se*), potentially owing to the difficulty of direct observations of foraging in the wild. Some researchers have overcome this difficulty (e.g. Gray and Hamer, 2001, Lewis et al., 2002), using remote logging equipment to provide data on the foraging behaviour of seabirds. These studies compared different types of individual within the provisioning period, however, and not how adults change their behaviour depending on the presence of young. Investigating the influence of young on foraging behaviour in cooperative breeders would further our understanding of the costs of cooperative behaviour (Heinsohn and Legge, 1999): if carers cannot increase the amount of prey items found, then feeding young comes at a higher cost as they are donating a larger, albeit variable, proportion of total prey items.

Finally, while most studies on adult-offspring communication focus on how adults respond to signals from hungry young, less attention has been paid to vocal signals given by adults. In many social species, foraging individuals give a range of vocalizations, to space foraging distance between group members (Radford, 2004b), to initiate movement to new foraging patches (Boinski and Campbell, 1995) or to recruit other individuals to a shareable food resource (Brown et al., 1991). As such, social context plays a role in the type and frequency of calls given. The presence of mobile, dependent young in the foraging group is likely to have an influence on the type of calls given by adults (Radford and Ridley, 2006). In particular, adults may give specific calls during feeding events (Leonard et al., 1997). The function of these calls, particularly in mobile begging systems in cooperatively breeding groups, remains poorly understood, although recent evidence in pied babblers suggests that they may serve a function in offspring mobility (Raihani and Ridley, 2007).

1.5 Cooperation and communication in meerkats

In this dissertation, I investigate the causes and consequences of individual variation in cooperative behaviour and the dynamics of carer-pup communication in meerkats. Meerkats are an ideal species in which to investigate variation in cooperative behaviour. They live in highly social groups of up to 50 individuals, with a dominant pair monopolising reproduction and helpers of both sexes assisting in rearing young (Clutton-Brock et al., 2001a). Cooperative pup care involves two stages: babysitting, when one or more individuals remain with the litter before the pups are old enough to keep up with the foraging group; and provisioning, when pups are present in the foraging group but have yet to reach nutritional independence (Doolan and Macdonald, 1999). Contributions to both babysitting and provisioning vary widely among individuals according to their sex, age, foraging efficiency and dominance status (table 1.1, Clutton-Brock et al., 2002, Clutton-Brock et al., 2001a, Clutton-Brock et al., 2000). While individual variation is often accounted for in statistical models using individual identity as a random term, the extent and consequences of unexplained individual variation have yet to be investigated. Moreover, while there is evidence that individual contributions to babysitting and provisioning are correlated (Clutton-Brock et al., 2003) and that variation in contributions to cooperation are influenced by contributions in the previous breeding attempt (Russell et al., 2003b), no studies have yet examined the extent to which helping is correlated with behaviour in other contexts or how experiences in early life affect later individual variation in cooperative behaviour.

When pups are present in the foraging group, they emit loud begging calls to which adults respond by bringing prey items (Manser and Avey, 2000). Given the high variation in contributions to care, it is likely that different categories of adults vary in their sensitivity to these begging calls. Adults produce a repertoire of vocalizations themselves when foraging, both when pups are present in the group and when absent (Manser, 1998), which raises the possibility that they modify their calls in the presence of dependent young, as in pied babblers (Radford and Ridley, 2006, Raihani and Ridley, 2007).

I conducted my research on a population of meerkats at an established study site in the southern African Kalahari desert, which offers a number of advantages. This population has been monitored for over ten years, and most individuals are habituated to the presence of human observers (<1 m) allowing detailed behavioural data to be recorded, both through observations and field experiments. As individuals start helping within the first year of life (Clutton-Brock et al., 2002), this enabled me to study cooperative behaviour in a sample of offspring over the course of development in the three year time-scale of my study. Moreover, changes in cooperative behaviour could be analysed using the long-term database, which contains records of cooperative behaviour by hundreds of individuals of known life-histories over the course of their life-time.

1.6 Thesis structure

In chapter 2, I give a general introduction to the study species and the specific population on which this study is based, describing the work to date on factors influencing variation in cooperative pup care. I then ask, in chapter 3, whether individual variation in cooperative behaviour is consistent within individuals over time, focusing on babysitting and provisioning. I compare the repeatability of each type of behaviour, and whether different categories of individual differ in their repeatability. In chapter 4, I examine the extent to which variation in contributions to pup care may be explained by trade-offs between cooperative behaviour and behaviour in non-cooperative contexts. To investigate the role of the early social environment in shaping later contributions to helping, I conduct analyses in chapter 5 to test for correlations between group size during early development and later contributions to care. In chapters 6 and 7, I explore the consequences of individual variation in helping for carer-pup communication. I describe results from a playback experiment to measure variation among sex and status classes in responsiveness to increased begging rate (chapter 6). In chapter 7, I investigate whether any increase in generosity is associated with a change in foraging strategy, and whether carers modify their own vocalizations during the period of provisioning young. In chapter 8, I provide a general discussion on approaches to understanding individual variation in cooperation, synthesizing the findings of this study and offering suggestions for future avenues of research.

2 • STUDY SITE AND GENERAL METHODS

2.1 STUDY SITE

This study was conducted at the Kuruman River Reserve, a 3,500 ha site of uncultivated former ranch land in the southern Kalahari Desert (26°58'S, 21°49'E), in the Northern Cape province of South Africa (figure 2.1). The reserve was established in 1993 by Professor Tim Clutton-Brock to study the causes and consequences of cooperative behaviour in meerkats (Clutton-Brock et al., 1998b, Clutton-Brock et al., 1999a). In addition to this long-term study, research is being conducted at this site on the behavioural ecology of pied babblers, slender mongooses, fork-tailed drongos, yellow-billed hornbills and crimson-breasted shrikes.
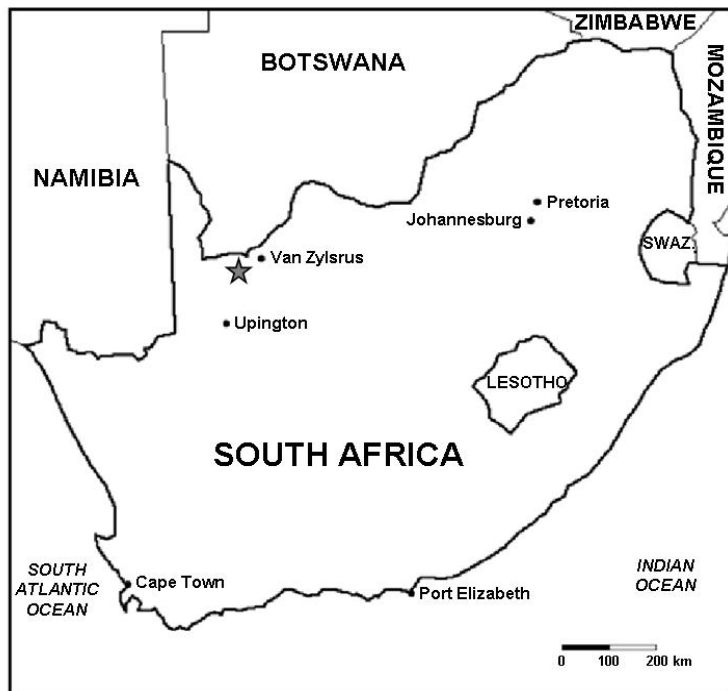
Figure 2.1 Location of the study site (star) within South Africa.

2.1.1 Habitat

The dry riverbed of the Kuruman River runs through the study site, beyond which the habitat comprises typical Kalahari thornveld, or broad open flat lands interspersed with sand dunes. The flat lands are vegetated primarily by perennial shrubs, annual grasses and scattered trees, while dune vegetation comprises perennial and annual grasses and perennial shrubs. Typical shrubs include drie doring ('three thorns') and raisin bush; and the most common trees are blackthorn, camelthorn and shepherd's trees. Particularly in

seasons of heavy rainfall, the annual Kalahari sourgrass, which can reach up to 120 cm in height, dominates certain areas of the landscape (figure 2.2).

Figure 2.2 The study site pictured during the dry part of the year (left) and when rainfall has resulted in growth of sourgrass (right).

2.1.2 Climate

The climate at the study site is typical of semi-arid desert, characterised by low and unpredictable annual rainfall and extreme temperature differences in the course of one day. There are two distinct seasons: a cold, dry winter during which temperatures often fall below freezing overnight (May to September) followed by a hot, wet summer when daytime temperatures can exceed 40°C and most of the rainfall occurs during occasional, heavy storms. Minimum and maximum temperatures were recorded daily with a minimum-maximum thermometer permanently suspended in the shade; and rainfall was measured using a standard rain gauge. Figure 2.3 illustrates the mean minimum and maximum temperature and monthly rainfall over the course of the study (from 1 January 1997 to 31 December 2008 inclusive).
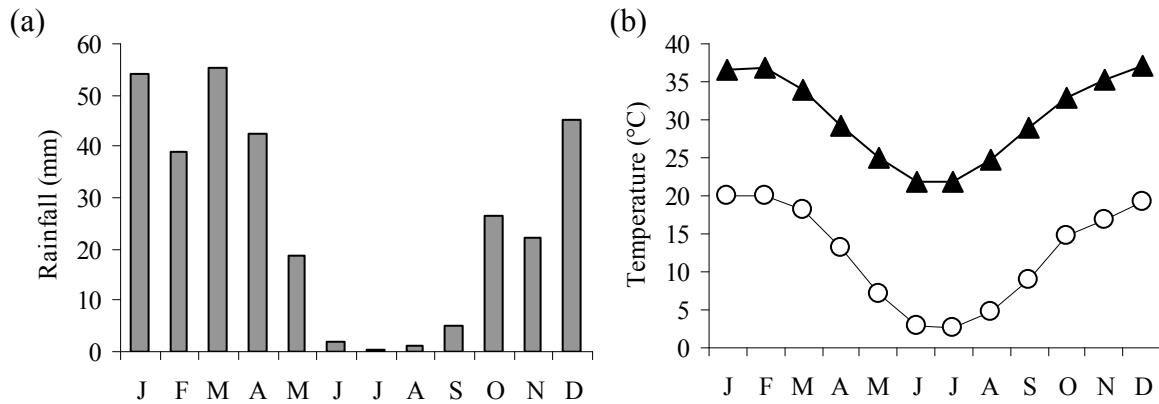
Figure 2.3 (a) Mean monthly rainfall; (b) Mean minimum temperature (open circles) and maximum temperature (filled triangles) over a 12 year period at the study site.

2.1.3 Fauna

The study site hosts a number of ungulates, including gemsbok, blue wildebeest, springbok and common eland, in addition to a wide variety of small mammals, reptiles, birds and insects. Present fauna include a number of aerial and terrestrial predators of meerkats. While all large terrestrial predators have been eliminated by ranchers over the course of the past century, smaller terrestrial predators remain, including caracals, African wild cats and Cape foxes. Aerial predators are often sighted, including martial eagles, tawny eagles, black-breasted snake eagles and steppe buzzards, all of which prey on adult meerkats. In addition, pups are vulnerable to predation by pale chanting goshawks, lanner falcons and gabar goshawks. Although there have been no observations of predation by snakes, several meerkat adults have died as a result of fatal bites from Cape cobras and puff adders, and it is likely that these species prey on pups.

2.2 STUDY SPECIES

Meerkats (*Suricata suricatta* Schreber 1776), also known as suricates, are small (<1 kg) carnivores belonging to the mongoose family (Herpestidae), which comprises 37 species in 18 genera and two subfamilies (Veron et al., 2004). Meerkats are obligate cooperative breeders, living in groups of up to 50 individuals (Clutton-Brock et al., 2008). Within the mongoose family, meerkats are one of the most highly gregarious species, with other well-studied social mongooses including the banded mongoose (Cant, 2003) and dwarf

mongoose (Creel and Waser, 1994). Meerkats are desert-adapted, with their distribution restricted to the semi-arid regions of south-western Africa (including southern Angola, Namibia, Botswana and South Africa). They are not threatened and their conservation status is categorised as 'least concern' by the International Union for Conservation of Nature (IUCN, 2008).

2.2.1 Daily activities and foraging

Meerkats are diurnal mongooses, getting up at dawn and spending up to an hour sunning at the burrow before commencing foraging. Meerkats are opportunistic generalists, with their diet largely comprising invertebrates, including beetle larvae, scorpions and millipedes, but they may also eat small reptiles, rodents and birds (Doolan and Macdonald, 1996, Brotherton et al., 2001). Individuals locate prey primarily using olfaction, digging up prey items from the sand using their foreclaws (figure 2.4). They forage in cohesive bands throughout the day, although in the hotter months of the year they cease foraging in the middle of the day to rest in the shade or underground. Groups return to the burrow at dusk, often engaging in social behaviour such as grooming and playing before going underground for the night (Kutsukake and Clutton-Brock, 2006b, Sharpe, 2005). They use a series of known sleeping burrows throughout their territory, which they occasionally share with Cape ground squirrels. Territories are defended from neighbouring groups through aggressive interactions and scent marking (Jordan et al., 2007).

Figure 2.4 Meerkat digging for prey in the sand.

2.2.2 Reproduction

Reproduction in meerkats is influenced by rainfall and the majority of litters are born between October and April (Clutton-Brock et al., 1999b). There is high reproductive skew in meerkat groups, with a dominant breeding pair monopolising around 80 percent of reproductive attempts (Griffin et al., 2003). Behavioural tactics are employed to achieve reproductive suppression in females, involving escalated aggression towards and temporary eviction of subordinate females when the dominant female is pregnant (Young et al., 2006, Kutsukake and Clutton-Brock, 2006a). While within-group reproduction in subordinate males may be limited by their high relatedness to resident females, they frequently leave the group on temporary prospecting forays to mate at neighbouring groups (Young et al., 2007). Individuals become sexually mature around 8–11 months of age and dispersal from the natal group is unlikely in individuals under a year old (Clutton-Brock et al., 2002). In females, permanent dispersal is uncommon and tends to follow expulsion from the group, whereas dispersal is more voluntary in males (Clutton-Brock et al., 1998a).

2.2.3 Cooperative behaviour

Group members of both sexes contribute to cooperative behaviours, which include burrow renovation and sentinel duty (Clutton-Brock et al., 2002). Perhaps the most striking form of helping, and the focus of this dissertation, is cooperative care of young. There are two main types of cooperative care: babysitting, where one or more helpers remain at the natal burrow to guard the pups while the rest of the group forages throughout the day (when pups are aged 0–20 days, approximately); and pup-feeding, where adults provision food items to pups when they are old enough to keep up with the foraging group but have yet to develop skills of independent foraging (aged 20–90 days, approximately) (Doolan and Macdonald, 1999). In addition, females in the group may allolactate, or provide milk to young even if they have not successfully bred themselves (Doolan and Macdonald, 1999).

Contributions to cooperative rearing of young have been the focus of much research on meerkats in the past ten years. Individual contributions to babysitting and provisioning

vary according to age, sex, weight, dominance status and group size, but not relatedness to young (see table 1 in Introduction, Clutton-Brock et al., 2002, Clutton-Brock et al., 1998b, Clutton-Brock et al., 2000, Clutton-Brock et al., 2001a, Clutton-Brock et al., 2004). In males, individuals with higher circulating levels of cortisol contribute more to provisioning (Carlson et al., 2006a) and decisions to babysit are preceded by elevated levels of prolactin (Carlson et al., 2006b). Costs of cooperative behaviour are minimised by individuals adjusting how much they help according to their contributions during the previous breeding attempt (Russell et al., 2003b). There is no evidence that individuals specialise in babysitting or provisioning: instead, these behaviours are positively correlated within subordinate females (Clutton-Brock et al., 2003). Finally, cooperative care has important fitness consequences for young. Individuals raised in groups with more helpers have higher weight gain and improved chances of survival until adulthood (Clutton-Brock et al., 2001b), and also higher reproductive success as adults (Russell et al., 2007).

2.2.4 Communication

Inter- and intragroup communication between group members is an important facet of social living, and meerkats use both olfactory and vocal signalling to this end. Scent-marking, both through anal-gland secretions and latrines, is common, particularly by dominant individuals and during periods of reproductive conflict (Jordan, 2007). Meerkats produce a range of vocalisations depending on context. When predators are detected, for example, individuals give alarm calls which encode information about both the urgency and type of predator seen (Manser, 2001). While foraging, adults emit a range of vocalizations with different purported functions, including close calls to maintain group cohesion and lead calls to coordinate group movement (Manser, 1998). Finally, like many altricial young, pups beg vocally to solicit being fed by adults (Manser and Avey, 2000) and give specific call types according to social context (Kunc et al., 2007), such as repeat calls to stimulate provisioning by adults and high-pitched calls to attract their attention during a feeding event.

2.3 STUDY POPULATION

This study was based on a combination of analyses of the long-term database (chapters 3 and 5) and my own behavioural observations and experiments (chapters 4, 6 and 7). A population of meerkats has been continually monitored since 1993 at the Kuruman River Reserve by a team of at least eight researchers at any given time. In total, behavioural and life-history data have been recorded on 1,856 individuals in 40 groups over this period (1993–2009). In the period of this study (2005–2008), I collected additional behavioural data on 11 groups, and the 17 litters born during this time. Research was carried out under permit from the Northern Cape Conservation Service, South Africa.

All individuals in the study population were habituated to close observation (<1 m), enabling the collection of detailed behavioural observations without any measurable effect of observer presence. Animals were identifiable through the unique code of their subcutaneous transponder chips, inserted soon after birth (Clutton-Brock et al., 2001a). Rapid identification of individuals during field observations was made possible through the application of unique dye-marks (adults) or hair cuts (pups). In general, one individual in each group was fitted with a radiocollar (figure 2.5), which enabled location of groups using a Telonics TR-4 receiver (Telonics Inc., Mesa, U.S.A.) and custom-made antenna (Africa Wildlife Tracking, Pretoria, South Africa). Details of the capturing, marking and tracking protocol are described by Jordan et al. (2007).

Figure 2.5 Meerkat group with radio-collared individual in the centre. Individual on the far left has a dye-mark visible on its shoulder.

2.4 DATA COLLECTION

2.4.1 Life history data

Reproduction. Groups were visited 3–4 times per week during the breeding season, hence the birth dates for most litters were known to an accuracy of three days. In addition, the dates that pups emerged from the sleeping burrow and started foraging with the group were recorded. After a litter had been born into a group, all females were checked for signs of lactation (prominent nipples and evidence of suckling or milk). During the period before pups started foraging with the group, all groups with pups were visited twice daily to record the identity of babysitters.

Age categorisation. Unless otherwise stated, age was categorised as follows: <90 d (pup), 90–180 d (juvenile), 180–360 d (sub-adult), 360–720 d (yearling) and >720 d (adult). 'Group size' was measured as the number of individuals >90 d of age in the group on a given day, as individuals younger than this age rarely contribute to cooperative activities (Clutton-Brock et al., 2002).

Dominance. The dominant male and female in the group were evident from their behavioural interactions with other same-sex group members, including aggression, marking and assertions of dominance. In this dissertation, I use the term 'subordinate' or 'helper' for all other individuals (>90 d old) in the group. When analyses include both dominant and subordinate individuals, the term 'carer' is used.

2.4.2 Behavioural observations

Typically, observers arrived at the group before the meerkats got up in the morning and followed them for 3–4 hours to collect data while they were foraging. In the afternoon, groups were located by radio-tracking and followed for at least another hour of foraging before they returned to the sleeping burrow. Most individuals (>90 %) were trained to be weighed on a top-pan scale balance to an accuracy of 1 g in return for a small reward of water or crumbs of hard-boiled egg (figure 2.6). Individuals were weighed before they commenced foraging in the morning ('morning weight'), at the end of the morning observation session ('lunch weight') and again in the evening prior to going below ground ('evening weight'). Morning weight gain was calculated as the difference from morning to lunch weight divided by the time spent foraging.

Figure 2.6 Meerkat being enticed onto the scales for a reward of water.

Behavioural data were collected through a combination of *ad libitum* data, focal observations and scan sampling (Altmann, 1974). *Ad libitum* and focal data were recorded on Psion LZ-64 handheld data loggers (Psion Teklogix Inc., Ontario, Canada). *Ad libitum* data were recorded whenever observers were at a group and no experiments were being conducted. In this dissertation, these data were mainly used to calculate provisioning rates. For any provisioning events in the group, the identity of the carer and pup, and also the size and type of prey item fed, were noted. Focal watches were conducted to measure the foraging behaviour and success of individuals over a period of 20 minutes. The ethogram in Appendix II gives details of all behaviours and prey size categorisations recorded during focal watches. Scan sampling was used to measure pup behaviour and interactions with carers at the burrow, largely because their behaviour did not change frequently enough to merit focal watches. Scan samples were either written down in notebooks or collected on a Zire 22 handheld computer (Palm Inc., U.S.A).

2.4.3 Experimental data
In addition to observational data, a variety of behavioural experiments were conducted, including playback experiments, presentations and feeding experiments. Full details of experimental protocols are given in the relevant chapters.

2.5 STATISTICAL ANALYSIS

Analyses were conducting using the free software package R for statistical computing (R Development Core Team). All tests were two-tailed. Parametric tests were conducted where possible. Where necessary, the data were transformed to achieve normality of error, using logarithmic, arcsine square-root or Box-Cox transformations as required (Crawley, 2002).

Most analyses in this dissertation required multivariate statistics on data with repeated measures of individuals and groups. To this end, I used linear mixed models (LMMs) and generalized linear mixed models (GLMMs), which allow both fixed and random terms to be fitted. LMMs were used when the response variable was continuous and normally distributed and the error structure was Gaussian, whereas GLMMs were used for non-normal data. If data were binary (1/0) or proportional, the error structure was binomial; if data were counts, the error structure was Poisson-distributed. Random terms account for non-independent data, such as two observations from the same individual, and may be nested or crossed according to the structure of the data: for example, individuals may be nested within groups, but if individuals change groups then the two random effects are crossed.

In general, model simplification was conducted following the stepwise approach described by Crawley (2002). A maximal model was fitted including all terms and interactions of biological interest, and the significance of terms was assessed using likelihood ratio tests which compared the deviance of models with and without the term of interest. Random terms were first inspected, and those which did not explain significant variance were excluded from the model. Fixed effects were then sequentially removed according to their level of significance until a minimal model was reached in which the removal of any terms significantly decreased the fit of the model. Terms which had been removed were then added back to the minimal model to confirm that they were not significant. Further details on statistical approaches particular to each chapter are described in the methods section for that chapter.

3 • IS INDIVIDUAL VARIATION IN COOPERATIVE BEHAVIOUR PLASTIC OR CONSISTENT?

3.1 NOTE

This chapter was prepared as a manuscript for submission to the *Journal of Evolutionary Biology*. I designed the study and wrote the paper, while Shinichi Nakagawa provided statistical advice and the R code to calculate measures of repeatability.

3.2 ABSTRACT

Recent models for the evolution of personality, using game theory and life-history theory, predict that individuals should differ consistently in their cooperative behaviour. However, the consistency of individual differences in cooperative behaviour has rarely been documented. In this study, we used a long-term dataset on wild meerkats to quantify the repeatability of two types of cooperative pup care, babysitting and provisioning, and examined how it varied across age, sex and status categories. Contributions to both babysitting and provisioning were significantly repeatable and positively correlated within individuals. Moreover, provisioning was more repeatable than babysitting and the repeatability of babysitting increased with age and was higher for subordinates than dominants. These results provide support for theoretical predictions that life-history trade-offs favour the evolution of consistent individual differences in cooperative behaviour, and raise questions about why some individuals consistently help more than others across a suite of cooperative behaviours.

3.3 INTRODUCTION

Individual variation in cooperation is a striking feature of many animal societies (Komdeur, 2006). In cooperative breeders, where individuals contribute to rearing non-descendant young, the causes and consequences of individual variation in helping have been widely documented (e.g. Woxvold et al., 2006, Gilchrist and Russell, 2007, Canestrari et al., 2005). Nevertheless, few studies have considered whether such variation is consistent within individuals over time, a characteristic that is receiving increasing attention in the burgeoning fields of phenotypic plasticity (Pigliucci, 2001, Nussey et al., 2007) and animal personality (Sih et al., 2004b, Dingemanse and Réale, 2005). Recent models using game theory invoke variation in behaviour as a prerequisite for cooperation to evolve (McNamara et al., 2004), and, pertinently, argue that social awareness, where

individuals monitor the cooperative behaviour of others, favours the evolution of stable individual differences in propensity to cooperate (McNamara et al., 2009). Alternatively, life-history trade-offs may result in the evolution of consistent individual differences in behaviour (Dall et al., 2004, Stamps, 2007, Wolf et al., 2007). In cooperative breeders, individuals commonly face a trade-off between remaining in their natal group to help and dispersing to breed (Emlen, 1982). Initial differences in body weight or growth may select for different behavioural types who pursue particular life-history trajectories (Biro and Stamps, 2008), and consequently mediate their cooperative behaviour according to their likely fate as a disperser or helper.

In spite of theoretical predictions that there should be high individual consistency in cooperation, which would require either high among-individual or low within-individual variation, no study has yet partitioned individual variation in cooperation in such a way. Instead, most empirical work on variation in cooperative behaviour has demonstrated the influence of current ecological and social factors, such as food availability or group size, on contributions to helping (e.g. Legge, 2000, Clutton-Brock et al., 2001a), often ignoring within-individual variation. While the influence of the social and physical environment on cooperative behaviour would suggest that helping is plastic, consistency and plasticity are not mutually exclusive characteristics, as individuals can vary in their helping from one breeding attempt to the next yet remain sufficiently different from other individuals in the population. A systematic study partitioning variation among and within individuals would elucidate the extent to which cooperative behaviour is plastic or consistent.

The most widely followed approach to quantifying consistency is to measure repeatability, which gives the proportion of total phenotypic variation that is due to variation among individuals (Lessells and Boag, 1987). Formally, repeatability (R) is defined as

$$R = \frac{s_a^2}{s_a^2 + s_w^2} \qquad \text{[Eq. 3.1]}$$

where s_a^2 is among-individual variation and s_w^2 is within-individual variation.

Most empirical work on the repeatability of behaviour has focused on male courtship displays or mating behaviour (e.g. Clark and Moore, 1995, Garamszegi et al., 2006) and female preference for these traits (e.g. Holveck and Riebel, 2007, Forstmeier and Birkhead, 2004). Traditionally, researchers conducted a one-way ANOVA to measure repeatability (e.g. Freeman-Gallant, 1998, Clark and Moore, 1995), which is a simple and effective technique but limited by its assumptions. Recent developments in statistical modelling have enabled measuring more accurate repeatability of traits that do not follow a normal distribution (Carrasco and Jover, 2005, Browne et al., 2005), while controlling for confounding factors, such as sex or age. As a consequence, one can compare repeatability estimates across categories of individuals within a population.

Indeed, one may expect variation in the degree of consistency for different types of individual within a cooperative group as a result of variation between types of individuals in the relative costs of helping (Heinsohn and Legge, 1999), and consequently the extent to which helping is constrained or sensitive to environmental conditions. Younger individuals, for example, may be less consistent as they are growing and hence more sensitive to food availability, with their behaviour yet to be canalised (Bell et al., 2009). If there are sex differences in the relative benefits of cooperative behaviour (Hodge, 2007), then males and females may exhibit different levels of consistency, with the sex that benefits less from helping being less repeatable. Finally, if breeders incur the costs of reproduction consistently across breeding attempts (Williams, 1966), they are likely to have higher repeatability than helpers who mediate their cooperative effort according to more variable environmental characteristics.

In addition to investigating consistency in behaviour over time, there is increasing interest in correlations between behaviours across different contexts, termed behavioural syndromes (Sih et al., 2004b, Réale et al., 2007, Dingemanse and Réale, 2005). Investigating behavioural syndromes in cooperative breeders may help explain individual variation in light of trade-offs between different types of cooperative behaviour and individual specialisation according to life-history strategies. Negative correlations would suggest that individuals specialise into particular roles, akin to division of labour in insect

societies (reviewed in Bourke and Franks, 1995). In contrast, positive correlations would indicate a helping syndrome, whereby individuals are either particularly helpful or selfish, and would in turn raise the question of why selfish, or less cooperative, individuals are tolerated. The only two studies to date investigating behavioural syndromes in cooperative breeders are suggestive of individual specialisation, or division of labour, with negative correlations between individual contributions to types of cooperative behaviour in noisy miners (Arnold et al., 2005) and cichlids (Bergmüller and Taborsky, 2007).

We investigated temporal and contextual consistency of cooperative behaviour in meerkats. Meerkats are obligately cooperative mongooses living in groups of up to 50 individuals, with a dominant pair monopolising access to reproduction and subordinates of both sexes assisting in rearing young (Clutton-Brock et al., 2001a). Adults provide two primary types of alloparental care: (1) babysitting, where one or more carers remain at the natal burrow to guard the pups while the rest of the group forages throughout the day (when pups are aged 0–20 days); and (2) provisioning, where adults provide pups with food items when they are old enough to join the foraging group but have yet to develop skills of independent foraging (aged 20–90 days) (Doolan and Macdonald, 1999). Certain categories of individuals contribute to cooperation more than others: dominant individuals tend to do the least helping (Clutton-Brock et al., 2004); females contribute more to both babysitting and provisioning than males (Clutton-Brock et al., 2002); and helping effort changes with age (Clutton-Brock et al., 2002). Furthermore, within females, babysitting is positively correlated with provisioning (Clutton-Brock et al., 2003). While there is evidence that individuals compensate for the cost of cooperative behaviour by changing their contribution depending on their effort in the previous breeding season (Russell et al., 2003b), no study has yet looked at the extent to which individuals are repeatable in cooperative behaviour over longer time-scales, nor whether the degree of repeatability varies according to age, sex or status.

In this study, we used a long-term database to investigate: first, whether contributions to babysitting and provisioning are repeatable over time; second, if repeatability varies

depending on the type of behaviour in question; third, whether repeatability changes with age, sex or status; and, fourth, if babysitting and provisioning are correlated, and how this correlation varies across age and sex-status categories.

3.4 METHODS

3.4.1 Measuring cooperative behaviour

To investigate patterns of repeatability in helping behaviour, we focused on cooperative pup care, which is primarily manifested in two behaviours in meerkats: babysitting and provisioning (Doolan and Macdonald, 1999, Clutton-Brock et al., 2001a). Analyses were based on per-litter measures of babysitting and provisioning collected between January 1998 and May 2008 from 646 individuals (2–19 measures per individual) rearing 200 litters in 18 groups. Age was classified into three categories: <1 y, 1–2 y and >2 y. This categorization was appropriate to the life-history of meerkats: as individuals reach sexual maturity at 7–11 months, those less than one year are still growing; between one and two years, adults tend to remain in their natal group to help and beyond two years, individuals are more likely to attempt to disperse permanently (Clutton-Brock et al., 2002), with few individuals surviving beyond four years of age.

Babysitting. Babysitting was measured as the number of half-days an individual remained to babysit a litter of pups in the period between the birth of a litter until the day pups started foraging with the group (around 25–30 days, Clutton-Brock et al., 2003). This was done on a half-day basis as individuals acting as babysitters often changed between morning and afternoon, particularly if the group returned to the burrow in the middle of the day. In the analysis, we controlled for variation in the total number of half-days an individual could have babysat (mean 42.5 half-days, range: 20–82), as not all groups were visited twice daily and the age at which pups start foraging with the group varied between 18 and 44 days (Clutton-Brock et al., 2008).

Provisioning. Provisioning was measured as the number of occasions an adult was observed to bring food to a begging pup during the peak period of provisioning (30–75 days, Brotherton et al., 2001, Young et al., 2005). In the analysis, we controlled for variation in observation time (mean 44.45 h, range: 11.57–105.80 h).

3.4.2 Statistical analysis

Statistical analysis was conducted using R 2.9.0 (R Development Core Team 2009). We calculated point estimates for repeatability of cooperative behaviour on the original scale by conducting a variance components analysis from a generalized linear mixed model (using the function glmmPQL in the library MASS, Venables and Ripley, 2002), with Poisson error family, as both babysitting and provisioning were count data (Carrasco and Jover, 2005). Overall repeatabilities for both babysitting and provisioning were calculated from models including dominance, sex and age category as fixed effects and controlling for total half-days (babysitting) and observation time (provisioning). As we were interested in comparing repeatability across different age and sex-status categories, we measured conditional repeatability by setting all other fixed effects at the mean and focusing only on the variable of interest (Carrasco and Jover, 2005). We calculated standard errors and 95 percent confidence intervals (CI) for repeatability using the Fisher's Z method (McGraw and Wong, 1996). Although the number of breeding attempts varied per individual, we were not concerned that this would affect repeatability as mixed models handle unbalanced designs (Gelman and Hill, 2007), and a recent meta-analysis demonstrated that repeatability does not vary with number of observations per individual (Bell et al., 2009).

We compared overall repeatabilities of babysitting and provisioning following the approach of Garamszegi (2006) and Nakagawa et al. (2007), conducting a linear mixed model with repeatability as the response term, behavioural type (babysitting or provisioning) as a fixed effect and age or sex-status category as a random grouping factor. Although these analyses produce p-values, we advocate the approach of comparing effect sizes and 95 percent confidence intervals rather than basing inferences on p-values (Nakagawa and Cuthill, 2007, Garamszegi, 2006, Nakagawa, 2004). Accordingly, we investigated differences between the seven different repeatability estimates for babysitting (which were more variable than those for provisioning, see below) by calculating pairwise differences of Z-transformed repeatability estimates and asking whether the confidence intervals overlapped with zero. Comparing effect sizes in such a way does not incur the issues of finding a significant difference by chance through

multiple statistical testing and hence we did not need to apply a Bonferroni correction (Garamszegi, 2006, Nakagawa, 2004).

To investigate the extent to which babysitting was correlated with provisioning, we divided the dataset according to the three age and four sex-status categories (subordinate female, subordinate male, dominant female and dominant male). For each subset, we calculated mean values of babysitting and provisioning for each individual, both Box-Cox transformed for normality, and conducted a Spearman's rank correlation test. To compare whether the strength of the correlation varied across different age or sex-status categories, we compared these seven different correlations by calculating pairwise *Z*-transformed differences and associated confidence intervals as described above.

3.5 RESULTS

In general, individuals were significantly repeatable in both babysitting and provisioning (babysitting, $R = 0.218$, 95% CI: 0.126 to 0.305, $p < 0.0001$; provisioning, $R = 0.513$, 95% CI: 0.473 to 0.551, $p < 0.0001$), with provisioning more repeatable than babysitting (LMM: $t_6 = 9.873$, $p = 0.0001$). Although the repeatability of provisioning was relatively invariant across different categories of age or status (table 3.1, figure 3.1b), there was more variation in babysitting (table 3.1, figure 3.1a). We compared differences in the point-estimates and standard errors for repeatability of babysitting (figure 3.2, table 3.1) and found that repeatability for individuals >2 y old was higher than for individuals <1 y and 1–2 y old, dominant individuals of both sexes had lower repeatabilities than subordinates and there were no differences between males and females in repeatability.

Babysitting and provisioning were positively correlated in general (Spearman's $r = 0.225$, 95% CI: 0.151 to 0.297, $p < 0.0001$), although the strength of the correlation varied when we considered subsets of the data separately (table 3.2). Nevertheless, when we compared differences in the point estimates for the correlations and their associated standard errors, there were no significant differences in the strength of the correlation across categories (difference in *Z*-transformed *r*: 0.052–0.226, lower 95% CI: -0.261 to -0.018, upper 95% CI: 0.177 to 0.690).
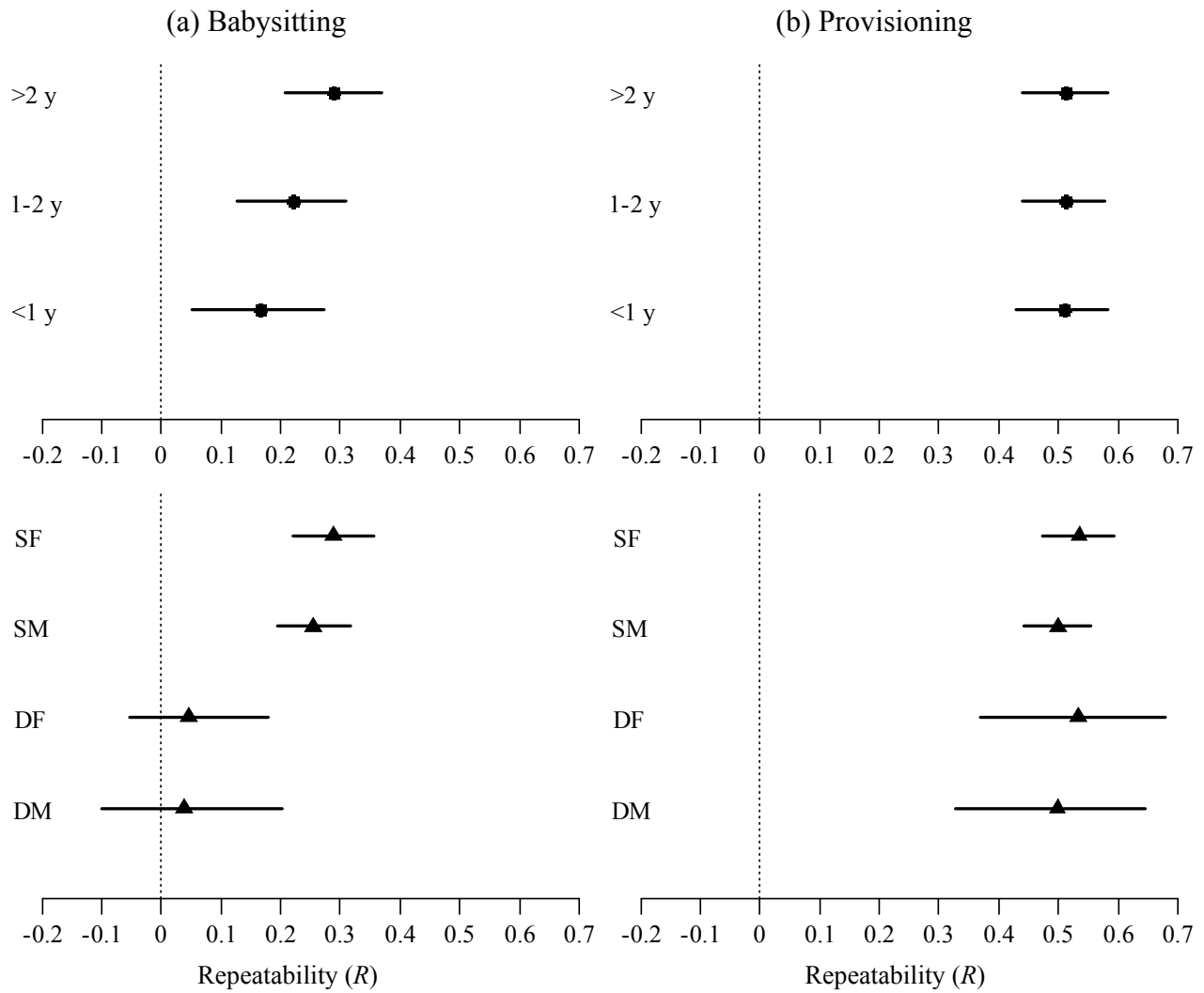
Figure 3.1 Repeatabilities and 95 percent confidence intervals for both (a) babysitting and (b) provisioning across all categories of individual. Those estimates whose confidence intervals do not cross the dotted line at 0 are significantly repeatable at the $\alpha = 0.05$ level.

	Babysitting			Provisioning		
	R (SE)	*p*	n(o), n(i)	*R* (SE)	*p*	n(o), n(i)
Age						
< 1 y	0.166 (0.056)	0.005	896, 562	0.510 (0.039)	<0.0001	896, 562
1-2 y	0.221 (0.047)	<0.0001	948, 521	0.513 (0.035)	<0.0001	948, 521
>2 y	0.288 (0.042)	<0.0001	738, 250	0.513 (0.036)	<0.0001	738, 250
Category						
SF	0.288 (0.035)	<0.0001	1013, 307	0.534 (0.030)	<0.0001	1015, 307
SM	0.255 (0.031)	<0.0001	1225, 331	0.499 (0.029)	<0.0001	1226, 331
DF	0.045 (0.058)	0.415	185, 34	0.533 (0.079)	<0.0001	183, 34
DM	0.039 (0.077)	0.613	159, 36	0.498 (0.081)	<0.0001	158, 36

Table 3.1 Repeatability estimates across categories for both babysitting and provisioning. Categories are abbreviated as follows: SF = subordinate female; SM = subordinate male; DF = dominant female; DM = dominant male. Shown are the repeatabilities and standard errors (see text for details), the associated *p*-value, and the number of observations, n(o), and individuals, n(i) used for the calculation of each estimate.

	r_S estimate (*CI*)	*t*	df	*p*
All	0.225 (0.151/0.297)	5.871	644	<0.0001
<1 y	0.241 (0.162/0.318)	5.882	560	<0.0001
1-2 y	0.294 (0.214/0.371)	7.012	518	<0.0001
>2 y	0.168 (0.045/0.286)	2.681	248	0.008
SF	0.190 (0.080/0.296)	3.381	305	0.001
SM	0.240 (0.135/0.339)	4.477	329	<0.0001
DF	0.084 (-0.261/0.411)	0.479	32	0.635
DM	0.301 (0.008/0.546)	2.069	43	0.045

Table 3.2 Results from Spearman's rank correlation tests, including r_S estimates and associated 95 percent confidence intervals, to investigate the association between babysitting and provisioning both in general and for the seven different subsets of data**.**
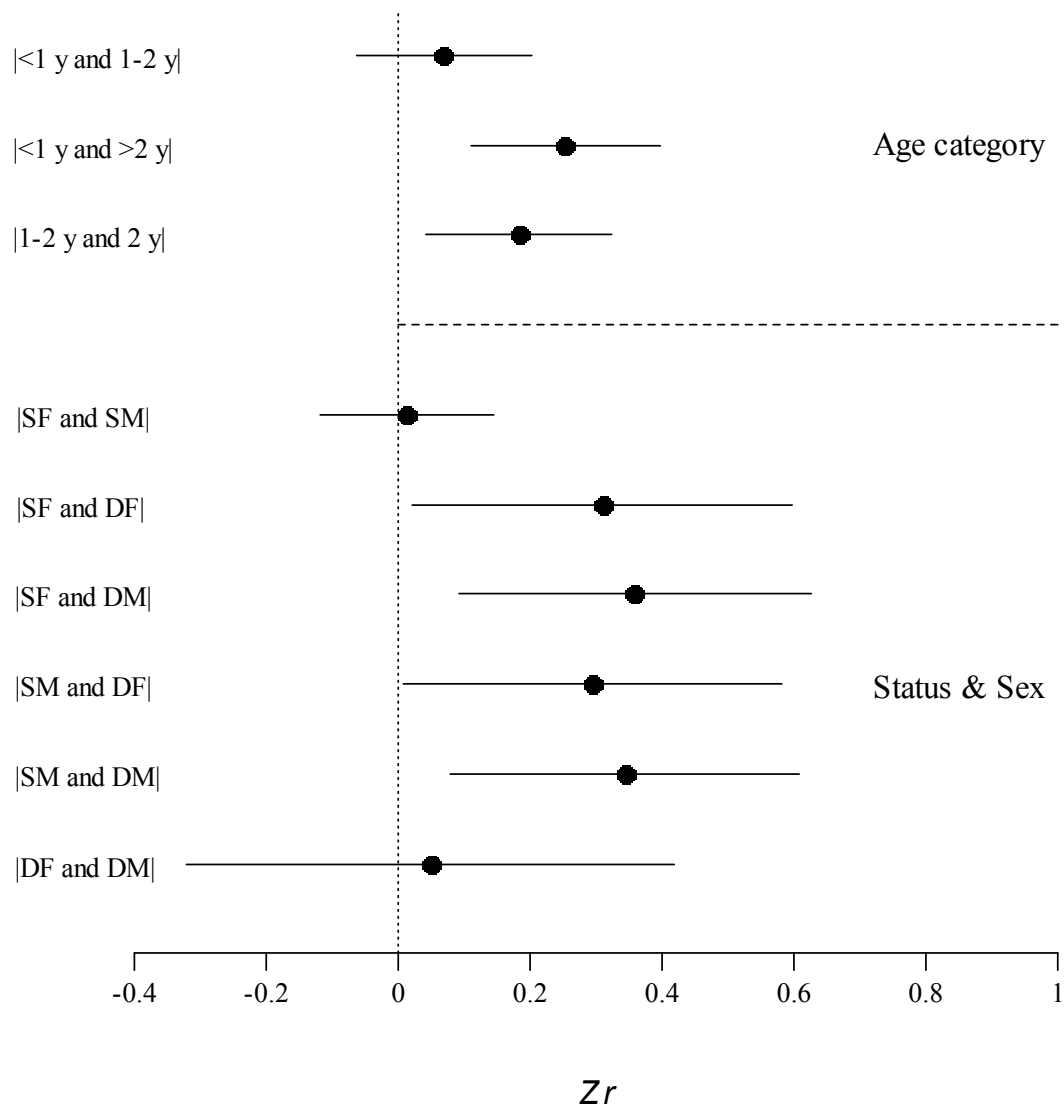
Figure 3.2 Differences in point-estimates of repeatabilities and 95 percent confidence intervals of the difference for seven categories of individual for babysitting only. Those differences whose 95 percent confidence interval does not cross the dotted line are significantly different at the α = 0.05 level.

3.6 DISCUSSION

Both babysitting and provisioning were significantly repeatable within individuals, with provisioning having higher repeatability. In light of a recent meta-analysis, which revealed that the mean repeatability of a range of behaviours across several taxa was 0.37 (Bell et al., 2009), our results indicate that meerkats are highly repeatable in feeding young ($R = 0.51$) and below average in repeatability of babysitting ($R = 0.22$). In addition to high among-individual variation in helping, therefore, individuals are relatively consistent in their helping over time. Although the consistency of cooperative behaviour is implicit from the inclusion of individual identity as a random term in mixed models (e.g. MacColl and Hatchwell, 2003b, Doutrelant and Covas, 2007), this is the first study to investigate directly the repeatability of cooperative behaviour in a wild mammal. Given that repeatability may, in some cases, indicate the upper limit of heritability (Boake, 1989, Hayes and Jenkins, 1997), a fruitful avenue for future research would be to investigate whether cooperative behaviour is heritable in this species, as has been shown in western bluebirds (Charmantier et al., 2007), and for provisioning effort of parents in cooperatively breeding long-tailed tits (MacColl and Hatchwell, 2003a).

Previous work on meerkats demonstrated that helping is condition-dependent, and individuals mediate the costs of helping by adjusting their contributions according to how much they helped in the previous breeding attempt (Russell et al., 2003b). Our analysis, based on a ten-year timescale (covering the lifespan of >95 percent of all individuals, Sharp and Clutton-Brock, 2010), shows that, despite short-term compensation, individuals remain consistently different from one another in their cooperative behaviour in the long term. These results lend support to recent theoretical models of cooperation, whereby variation in social awareness results in consistent individual differences in cooperative tendencies (McNamara et al., 2009). The role of social awareness in cooperative pup care in meerkats is unclear, however, as the situation is more complex than a repeated game between two matched players. Alternatively, consistency of cooperative behaviour supports the hypothesis that life-history strategies mediate individual differences in cooperation (Dall et al., 2004, Stamps, 2007, Wolf et al., 2007). Our results suggest that individuals follow set trajectories of cooperative behaviour,

which may arise as a result of initial individual differences in physiology or morphology, such as growth rates (Biro and Stamps, 2008).

Individuals were more repeatable in their provisioning than babysitting. As repeatability is a ratio (equation 3.1), differences in repeatability may arise because of variation in the numerator (among-individual variation) or denominator (total variation: within- and among-individual variation combined). Among-individual variation was higher for provisioning than babysitting, possibly because of the different time-scales on which decisions to babysit or feed pups were made. During the babysitting period, babysitters tended to remain with pups for at least half a day and often an entire day and hence babysitting was decided on a per-day basis (Clutton-Brock et al., 1998b). In contrast, during the provisioning period, all adults were exposed to the stimulus of vocal begging from pups (Doolan and Macdonald, 1999) and hence the decision of whether or not to feed pups was made every time a food item was found. Moreover, the high repeatability of provisioning indicates that most individuals were relatively invariant in this behaviour over their life-time and, consequently, it is not surprising that there was little variation across categories in repeatability estimates.

Repeatability of babysitting increased with age and was higher for subordinates than dominants. As helping may incur energy costs (Heinsohn and Legge, 1999), younger individuals may invest more in growth than in cooperative behaviour (Brotherton et al., 2001, Thornton, 2008c), which itself may be more sensitive to local conditions and consequently less repeatable. In addition, the role of life-history strategies could explain why repeatability increases with age, as trajectories may become increasingly fixed as individuals get older. In addition, we found dominant individuals to be consistently less cooperative in terms of babysitting than subordinates. This result was not an artefact of variation in sample size, as mixed models account for unbalanced data (Gelman and Hill, 2007). As discussed above, the difference between dominants and subordinates may be explained by the fact that repeatability is the ratio of among-individual variation compared to total phenotypic variation: if among-individual variation is low, as is the case for dominant individuals' babysitting, then repeatability in turn is low.

There was little evidence for sex differences in repeatability for either babysitting or provisioning. In their recent meta-analysis, Bell et al. (2009) found sex differences in repeatability of behaviour in general, with males more repeatable than females, although this was partly confounded by mate preference, which had low repeatability, being primarily measured in females. In the context of caring for offspring, males are more repeatable than females in their provisioning effort in house sparrows (Schwagmeyer and Mock, 2003, Nakagawa et al., 2007) and long-tailed tits (MacColl and Hatchwell, 2003a). Although provisioning behaviour is qualitatively similar when comparing biparental and alloparental systems (Emlen, 1997), we may not predict males to be more repeatable in meerkats for the same reasons as in biparental species, as provisioning effort is not known to function as a sexual signal in this species. However, we had predicted sex differences in repeatability, particularly as there are striking sex differences in cooperative behaviour in meerkats (Clutton-Brock et al., 2002). The absence of sex differences in repeatability serves as a reminder that, even if the mean levels of behaviour vary, the variability within individuals may not be different, and indicates that similar constraints act on males and females in determining the flexibility of their behaviour.

Finally, in line with a previous study (Clutton-Brock et al., 2003), we found that babysitting and provisioning were positively correlated within individuals, with the strength of the correlation relatively invariant across different categories, apart from a tendency to decrease with age. While there is increasing focus in studies of behavioural ecology on how behaviours are correlated across contexts, only two studies, to our knowledge, have considered behavioural syndromes in cooperative breeders (Arnold et al., 2005, Bergmüller and Taborsky, 2007). In contrast to these studies, we found positive associations across two types of helping behaviour. Demonstrating repeatability across time and correlations across contexts is suggestive of a helping syndrome, with different behavioural types for particularly cooperative or selfish individuals. Although we have focused on cooperative behaviours related to the care of young, future work will investigate correlations across other types of behaviour, including those in functionally different contexts, including exploration and aggression. The existence of different

helping types within a group sets the stage for further investigation of why certain individuals display particularly elevated cooperative behaviour and why less helpful individuals are tolerated.

To conclude, we have provided the first evidence that individual variation in cooperation is higher among individuals than within individuals, by considering two types of cooperative behaviour in a wild mammal. In spite of the fact that cooperative behaviour may be sensitive to current social and ecological conditions, such as group size or food availability (Clutton-Brock et al., 2001a, Legge, 2000), our results imply that individuals follow set trajectories in cooperative behaviour over time. Recent theory suggests that differences in underlying state variables, such as body size or growth rate, coupled with life-history trade-offs can result in the evolution of consistent individual differences (Dall et al., 2004, Stamps, 2007). In cooperative breeders, individuals may follow set life-history trajectories due to the trade-off between helping and breeding combined with intrinsic individual differences in body size. Further work investigating the repeatability of traits such as growth rate and foraging efficiency would help elucidate the mechanisms by which such trajectories are established.

4 • IS COOPERATIVE PUP CARE CORRELATED WITH BEHAVIOUR IN OTHER CONTEXTS?

4.1 ABSTRACT

Recent theory suggests that life-history trade-offs may result in the evolution of behavioural syndromes, or correlations across behaviours in different contexts. For example, foraging behaviour under risk of predation and aggression towards conspecifics are often correlated within individuals. In cooperatively breeding societies, the trade-off between helping and breeding may result in individuals pursuing different strategies with resulting correlations across behaviours. In this study, I investigated whether individual variation in cooperative pup care was correlated with variation in behaviour in other contexts. For example, individuals with a better chance of breeding may help less and take bigger risks to accrue resources necessary for reproduction. In addition, individuals may trade off investment in different cooperative activities against one another, resulting in individuals specializing in one particular cooperative behaviour. Using a combination of field experiments and behavioural observations, I measured whether individuals differed consistently in predator approach behaviour, exploration of a novel environment, foraging effort, vigilance, and propensity to be weighed by humans. Consistent individual differences were only evident in foraging, vigilance and propensity to be weighed. However, although there were weak positive correlations between provisioning rate and both vigilance and propensity to be weighed, there was little evidence that individual variation in contributions to care could be explained by behaviour in these contexts. I discuss methodological issues of measuring individual differences in social species in the wild and offer suggestions for other behavioural correlations that may be investigated.

4.2 INTRODUCTION

Individual variation in cooperative behaviour may be partly explained by considering variation in behaviour in other contexts. There is burgeoning interest in the extent to which behavioural traits are correlated across different contexts, or behavioural syndromes (Sih et al., 2004b, Sih and Bell, 2008). Recent theory suggests behavioural syndromes may arise as a result of life-history trade-offs (Biro and Stamps, 2008, Stamps, 2007, Wolf et al., 2007). In species with a growth-mortality trade-off, for example, behaviours that both increase growth and influence mortality, such as risk-

taking and aggression over food, would be both consistent within individuals and correlated across contexts (Stamps, 2007). A common life-history trade-off faced by individuals in cooperative groups is that between current investment in other individuals' young versus saving resources for own future reproduction (Cant and Field, 2001). In some species, individuals that are heavier when young may be more likely to breed later in life (e.g. Russell et al., 2007) and their resulting life-history strategy may be reflected in a suite of correlated behaviours. For example, heavier individuals may in turn be more aggressive, be more explorative, disperse earlier and contribute less to cooperative activities. Of the two studies to investigate behavioural syndromes in cooperatively breeding species to date (Arnold et al., 2005, Bergmüller and Taborsky, 2007), only the latter has discussed the role of life-history strategies. In cooperatively breeding cichlids, individuals that were more aggressive in defending the territory were also more exploratory in a novel environment (Bergmüller and Taborsky, 2007), suggesting that these individuals were following the life-history strategy of dispersing to breed independently compared to less aggressive and explorative individuals which remained as helpers on the natal territory.

Correlations between different cooperative behaviours may also help explain some individual variation in a given cooperative behaviour. Time or energy constraints may result in individuals which contribute more than average to one type of cooperative behaviour having lower contributions to another, particularly as cooperative behaviour can be costly (Heinsohn and Legge, 1999). As a consequence, individuals which seem less cooperative in any particular behaviour may not in fact be uncooperative in general, as not all forms of cooperation have been taken into consideration (Komdeur, 2007). Both Arnold et al. (2005) and Bergmüller and Taborsky (2007) found negative correlations between different types of cooperative behaviour across individuals. In noisy miners, individuals which mobbed predators more contributed less to chick provisioning (Arnold et al., 2005), and cichlids which defended the territory more spent less time maintaining it (Bergmüller and Taborsky, 2007). Although these studies both suggest that individuals have specialised into particular helper roles, akin to division of labour

(Bourke and Franks, 1995), repeated measures over multiple breeding attempts would be necessary to confirm that specialisation has indeed occurred.

Here, I investigated whether there were consistent individual differences in meerkats in several behavioural traits (mobbing a potential predator cue; exploration and activity in a novel environment; foraging and vigilance strategy; and response to human observers), whether there was a behavioural syndrome across these traits and the extent to which variation in any of these traits correlated with cooperative pup care (babysitting and provisioning, Doolan and Macdonald, 1999). Meerkats are highly cooperative mongooses living in groups of 3–50 individuals in arid regions of southern Africa, with a dominant pair monopolising reproduction and helpers of both sexes contributing to the care of young (Clutton-Brock et al., 2001a). Life-history parameters are likely to be important in determining individual differences in behaviour: body weight in early life predicts later breeding opportunities (Russell et al., 2007) and there is a trade-off between helping and breeding (Young et al., 2005). My first prediction was that individuals which were more likely to attain dominance would also exhibit reduced contributions to cooperation, higher exploratory behaviour and invest more in foraging time, given the importance of relative body size in competing for breeding opportunities, particularly in females (Clutton-Brock et al., 2006).

My second aim was to investigate whether cooperative pup care was negatively correlated with mobbing behaviour, as would be expected if individuals specialised in cooperative activities. A previous study on female meerkats found that individuals did not specialize in any single cooperative behaviour, and in fact that positive correlations were found across four types of cooperative behaviour (babysitting, provisioning, guarding and social digging, Clutton-Brock et al., 2003). More recently, Graw and Manser (2007) provided the first investigation of mobbing in meerkats, suggesting that it served as a multi-functional cooperative behaviour to deter predators and gather information about predator type. Here, I intended to build on these earlier studies by investigating whether, across males and females, mobbing was individually consistent

across repeated measures and, if so, whether individual contributions to mobbing were correlated with cooperative pup care.

4.3 METHODS

4.3.1 Boldness: investigation of secondary cue from a potential threat

Variation in propensity to investigate potentially threatening cues was measured through three presentation experiments: dog urine, bat-eared fox fur and a frozen mole snake. These cues mimicked natural predators of meerkats and have been previously shown to elicit a mobbing reaction, albeit at a lower level (Graw and Manser, 2007). The dog urine was sourced from the local veterinary surgeon and separated into 20 ml samples for each experiment. Samples were kept frozen and defrosted prior to being presented on a tray of sand collected locally to the area where meerkats were foraging. Both the bat-eared fox fur and mole snake were sourced from road kills. Bat-eared fox was used as the entire tail of an animal and presented inside a bolt-hole. The mole snake was kept frozen by being transported in a cooler box with ice and cleaned with ethanol in between presentations to minimise transmission of scent cues or pathogens between groups.

In total, I conducted 19 presentation experiments at seven groups (2–3 presentations per group, table 4.1). Each group was presented with at least two different stimuli, to measure repeatability of mobbing across trials (leaving at least 14 days between two presentations at the same group). I placed the cue near the centre of the group while playing a high-urgency recruitment call (Manser, 2001) to attract individuals to the location and ensure that all group members had the opportunity to respond to the stimulus. A second observer stood at least 2 m away to record the group's response on a Panasonic PV-GS300 video camera. During subsequent video analysis, I noted the identity of each individual approaching and leaving the cue for the duration of the experiment. Individuals younger than 90 d of age were excluded from the analysis, as young individuals tend not to participate actively in mobbing and instead follow adults (Graw and Manser, 2007). Mobbing time was calculated as the total duration an individual spent within 0.5 m of the

stimulus while displaying obvious mobbing postures (pilo erect, tail raised, growling vocalizations, Manser, 2001).

Group	Dog Urine	Fox Fur	Mole Snake
AZ	8	9	11
CD	13	10	10
D	No test	10	9
E	10	10	13
F	No test	10	8
L	12	13	13
W	11	11	9

Table 4.1 Number of individuals present in each group during presentation experiments to test boldness to inspect predator cues. Owing to limited sample availability, I did not use the dog urine sample on all seven groups.

4.3.2 Exploration: response to novel environment

I measured activity and response to a novel environment using a modified open-field test similar to Boon et al. (2007). Individuals were picked up gently by the base of their tail and placed in the centre of a novel box of dimensions 70 x 70 cm and their responses were recorded on video camera. As meerkats were occasionally handled by researchers, they were not distressed by this procedure. The sides of the box were made from chicken wire and 20 cm high, which was low enough so that they could jump out easily. The base of the box was made of hardboard material, with five equally spaced holes cut through it and marked with a grid of 10 x 10 cm lines on the surface to measure activity of individuals crossing each line (figure 4.1a). I also divided the box into nine different areas in order to measure the extent of exploration around the environment. If the individual did not jump out of the box of its own accord after 120 s, it was removed by the researcher. I analysed the videos to score the responses of individuals to being placed in the box, focusing in particular on the behaviours in table 4.2.
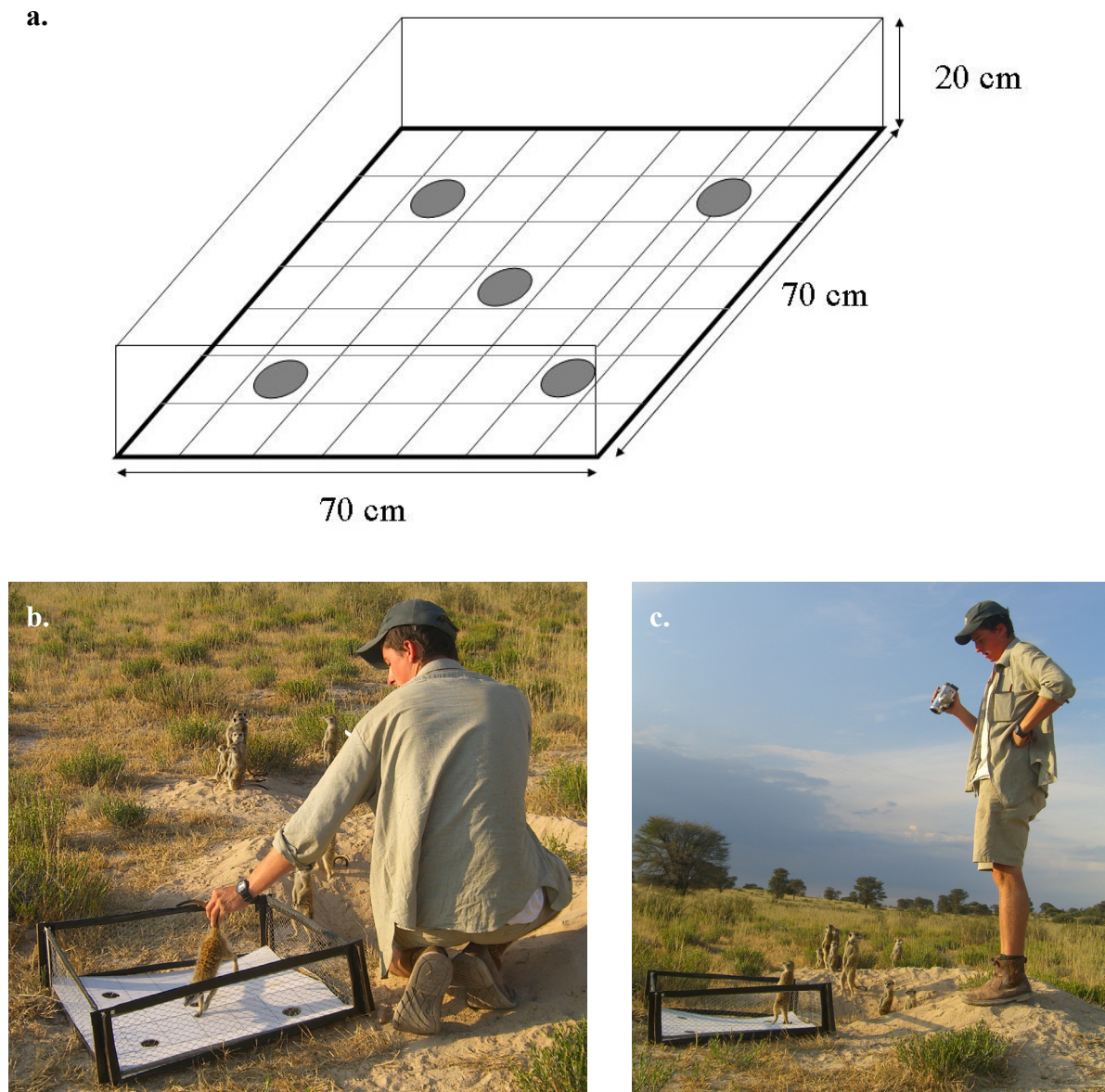
Figure 4.1 (a) Modified open field test to measure exploratory behaviour in meerkats. (b) and (c) Observer placing meerkat in centre of box and subsequently recording response on video camera.

Measure	Description
Duration	Time taken until individual jumped out (or removed) (0 – 120 s)
Area	Number of blocks in box the individuals moved into (1-9)
Activity rate	Number of 10 cm x 10 cm gridlines crossed per s in box
Moving	Proportion of time an individual walked around in the box
Exploring	Proportion of time an individual explored (sniffed or scratched the box)
Holes	Number of times an individual explored a blind-hole

Table 4.2 Ethogram of behaviours analysed in principal component analysis on individual responses to being placed in a novel environment.

4.3.3 Vigilance rate and foraging effort

Foraging behaviour was recorded through continuous focal watches, during which an observer followed an individual for 20 min, pausing the focal watch if more than half the group stopped foraging; or if the focal helper stopped foraging for more than 2 min (mean ± SE duration: 19.6 ± 0.1 min). Full details of all behaviours recorded during these focal watches are given in appendix II. Here, I focus on individual differences in vigilance rate, measured as the count of quadrupedal and bipedal vigilance bouts divided by focal duration; and foraging effort, measured as the proportion of time digging compared to total foraging (digging and searching) time. Analyses were based on 283 focal watches on 30 subordinate individuals, all >260 d old, from eight groups (15 females and 15 males; 2–18 focal watches per individual; 1–5 individuals per group). Focal watches were conducted when there were no dependent pups in the group.

4.3.4 Nervousness: propensity to be weighed

One of the central aims of the Kalahari Meerkat Project is to collect data on individual changes in weight (Kalahari Meerkat Project Protocol, unpublished). Meerkats are weighed by being trained to climb into a plastic box on electronic scales for a small reward of crumbs of hard-boiled egg or water and, more rarely, by being lifted by the base of the tail and placed in the box. There is commonly striking variation among individuals in their willingness to be weighed by human observers (personal observation).

I measured propensity to be weighed as whether or not an individual was weighed 100 percent of the time over the course of one month, on days when >80 percent of individuals in the group were weighed, to maximise the possibility that attempts had been made to weigh an individual and it had refused, rather than it not being weighed because of poor weather conditions. I used this binary measure instead of the proportion of days weighed because of the distribution of the data, as most individuals were weighed on most days. I excluded wild individuals which immigrated into the population and data on individuals less than 30 d of age, which were still in the process of developing a preference for the novel food type of hard-boiled egg (Thornton, 2008b). To avoid the possibility of individuals not being weighed owing to temporary absence from the group if they were babysitting or roving, or because of high aggression from pregnant dominant females targeted towards individuals approaching the scales, I used data from the non-breeding season (May to August) between 2005 and 2008 (inclusive). In total, I analysed 272 measures for 52 individuals from eight groups (2–10 measures per individual).

4.3.5 Statistical analysis

I used general and generalised linear mixed models to investigate individual consistency in the behaviours measured. Model simplification was conducted by comparing models with and without the fixed effect or interaction of interest, using a likelihood ratio test to determine whether including the additional term significantly improved the fit of the model (Crawley, 2002). In all models, I investigated whether the response variable in question was influenced by age category or sex. Age categorisation and additional fixed effects depended on the variable under consideration (see below).

Mobbing experiment. Models analyzing variation in mobbing duration also controlled for the additional fixed effects of stimulus type (dog urine, mole snake or fox fur), group size (number of individuals >90 days old in the group on day of observation) and dominance status. Age was divided into three categories: <1 y, 1–2 y and >2 y.

Novel environment test. I conducted a principle component analysis (PCA) to ascertain a composite score for individual responses, with the two most important principle components used in further analysis. Age was categorised around 180 d as follows: 'young' (mean = 91 d, range: 76–109 d) and 'old' (mean = 414 d, range: 292–832 d).

Foraging effort and vigilance rate. For both analyses, I controlled for potential influences of group size and whether the focal watch was conducted in the morning or afternoon. In addition, the following variables were used for specific analyses: time spent within 1 m of another adult and whether the focal watch was interrupted by a predator alarm (vigilance rate only); and total rainfall in 30 d prior to focal watch (foraging effort only). Age was categorised around 330 d as follows: 'young' (mean = 297 d, range: 263–323 d) and 'old' (mean = 443 d, range: 332–990 d).

Propensity to be weighed. Owing to the distribution of the data, age was categorised around 360 d as follows: 'young' (mean = 173 d, range: 93–336 d) and 'old' (mean = 559 d, range: 363–1052 d).

All analyses used datasets with at least two measures on each individual, for meaningful measures of consistency. I measured whether individuals were significantly repeatable by comparing models with and without individual identity as a random effect, including group as a random term if it explained significant variance in the data. I used the parametric bootstrap approach to test significance of random terms, as it gives a more accurate approximation of p-values than the likelihood ratio test (Faraway, 2006). This technique simulates a distribution of likelihood ratios 1,000 times, and compares the observed likelihood ratio with the simulated distribution to calculate a p-value.

If individual was a significant random term, I extracted the best linear unbiased predictor (BLUP), which gives a predicted value for each individual, independent of the fixed effect terms in the model and standardised to a mean of zero (Kruuk, 2004): for example, if age was a significant fixed effect, a positive BLUP value for an individual would indicate that it exhibited a higher level of the behavioural trait compared to that predicted for its age. I investigated correlations between individual BLUPS among different traits; and with BLUPS for babysitting and pup-feeding, both of which are highly repeatable within individuals (chapter 3). Because multiple comparisons were made, the threshold p-value was adjusted using the sequential Bonferroni method (Rice, 1989). As this approach can be over-conservative, however, I also tested whether the number of statistically significant results were more than expected by chance alone, using the

Bernouilli process (Moran, 2003), as described for a similar type of analysis in Dingemanse et al. (2007).

4.4 RESULTS

4.4.1 Boldness: investigation of secondary cue from a potential threat

In response to experimental presentations of secondary cues, there was considerable individual variation in duration of mobbing behaviour (range: 0–469 s). Mobbing duration varied according to stimulus type (LMM: $\chi^2 = 8.90$, $p = 0.01$, figure 4.2a) and was higher both for younger individuals (LMM: $\chi^2 = 20.8$, $p < 0.0001$, figure 4.2a) and in smaller groups (LMM: $\chi^2 = 9.45$, $p = 0.002$, figure 4.2b). There were no differences between the sexes (LMM: $\chi^2 = 1.11$, $p = 0.29$) or across dominance status (LMM: $\chi^2 = 1.19$, $p = 0.28$). Visual inspection of the data indicates a possible interaction between age and stimulus type (figure 4.2a), but statistical power was too low to include interactions in the model. Individuals were not consistent in their response over repeated measures (LRT $\chi^2 = 0.12$, $p = 0.31$), although there was high repeatability within groups (LRT $\chi^2 = 48.3$, $p < 0.0001$). In other words, repeated measures from the same group were more similar to one another than to measures from other groups.

4.4.2 Exploration: response to novel environment

Results from the principal components analysis are summarised in table 4.3. The first two components, PC1 and PC2, explained 76 percent of the variance in the data in total and were used in subsequent analysis. PC1 gave a score for exploratory behaviour and PC2 was negatively correlated with activity, hence the inverse of PC2 (-PC2) was used for subsequent analysis. PC1 (exploration) was higher for younger individuals (LMM: $\chi^2 = 5.77$, $p = 0.016$) and reduced with increasing trials (LMM: $\chi^2 = 9.53$, $p = 0.002$, figure 4.3). -PC2 (activity) was higher for younger individuals (LMM: $\chi^2 = 11.7$, $p = 0.0006$, figure 4.4a), and for males (LMM: $\chi^2 = 6.74$, $p = 0.009$, figure 4.4b), and there was a tendency for -PC2 to decrease with increasing trials (LMM: $\chi^2 = 3.08$, $p = 0.079$). Individuals were not significantly consistent over repeated trials in either PC1 (LRT $\chi^2 < 0.0001$, $p = 0.38$) or -PC2 (LRT $\chi^2 < 0.0001$, $p = 0.86$), although there was significant

repeatability at the group level for both PC1 (LRT $\chi^2 = 3.75$, $p = 0.008$) and PC2 (LRT $\chi^2 = 3.21$, $p = 0.012$).

4.4.3 Vigilance rate and foraging effort

Vigilance rate. Controlling for the significant effects of focal duration (GLMM: $\chi^2 = 13.9$, $p = 0.0002$), and whether or not there was a predator alarm (GLMM: $\chi^2 = 4.09$, $p = 0.043$), there was significant individual repeatability in vigilance rate across focals (LRT $\chi^2 = 34.9$, $p < 0.0001$), although groups were not significantly repeatable (LRT $\chi^2 = 0.84$, $p = 0.121$).

Foraging effort. Controlling for the significant effects of rainfall 30 d prior to the focal watch (GLMM: $\chi^2 = 9.22$, $p = 0.002$, figure 4.5a) and the interaction between age and group size (GLMM: $\chi^2 = 5.54$, $p = 0.019$, figure 4.5b), there was significant individual repeatability in foraging effort across focal watches (LRT $\chi^2 = 10.9$, $p < 0.0001$), but not for groups (LRT $\chi^2 = 0.31$, $p = 0.186$).

4.4.4 Nervousness: propensity to be weighed

Individuals under one year of age were more likely to be weighed 100 percent of the time than older individuals (GLMM: $\chi^2 = 6.88$, $p = 0.009$). In addition, there was significant repeatability at the individual (LRT $\chi^2 = 16.0$, $p < 0.0001$) but not at the group level (LRT $\chi^2 = 0.4$, $p = 0.13$).

4.4.5 Correlations across different types of behaviour

Results from the Spearman's rank correlation tests between all the pairs of individually repeatable behaviours are given in table 4.4. After sequential Bonferroni correction, only those correlations between foraging effort and propensity to be weighed and between babysitting and provisioning remained significant. Individuals which contributed more to babysitting were also more generous provisioners, and those which had higher foraging effort were less likely to be weighed. Six of the ten pairs tested were significant (figure 4.6), which is higher than expected by chance (Moran, 2003).
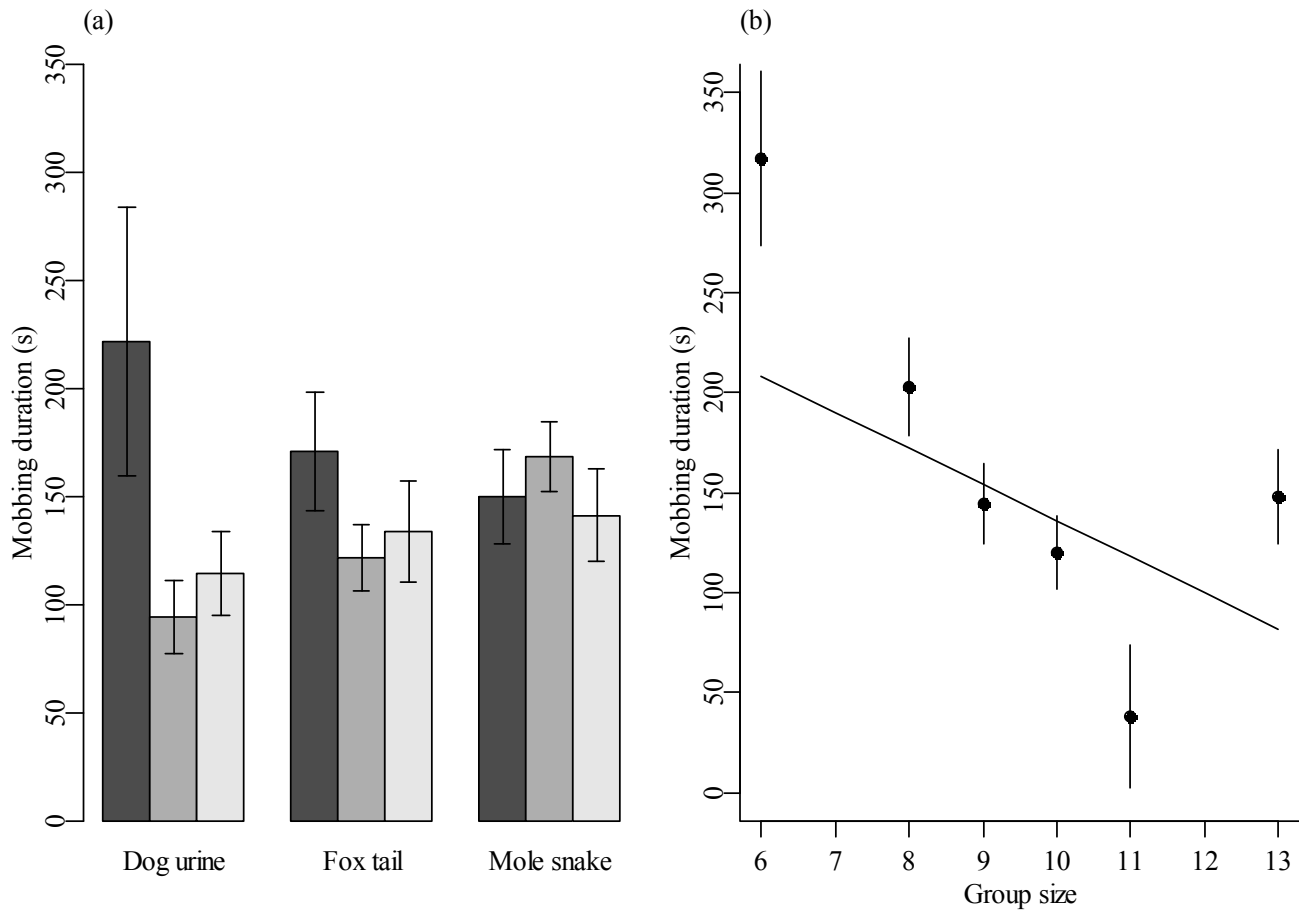
Figure 4.2 (a) Mean ± SE mobbing duration for different age catgories (dark: <1 y, grey: 1–2 y and pale: >2 y). There was a stronger mobbing response for the mole snake and fox tail than the dog urine, and mobbing responses declined with age. (b) Effect of group size on mobbing duration: individuals mobbed for less time in larger groups. Shown are the predicted effect from the GLMM (line) and the points of raw data controlling for other effects in the model (points).

	PC1	PC2	PC3	PC4	PC5	PC6
Duration in box	**0.480**	0.051	-0.528	0.641	-0.114	-0.254
Frequency investigated holes	**0.460**	-0.371	0.112	0.108	0.509	0.607
Proportion time moving	**-0.429**	**-0.427**	0.073	0.327	0.549	-0.469
Proportion time exploring	**0.422**	-0.188	0.750	0.125	-0.291	-0.352
Activity rate	-0.369	**-0.520**	-0.024	0.348	-0.571	0.382
Proportion of area explored	0.245	**-0.609**	-0.376	-0.577	-0.127	-0.280

Importance of components

	PC1	PC2	PC3	PC4	PC5	PC6
Standard deviation	1.713	1.285	0.808	0.544	0.525	0.434
Proportion of variance	0.489	0.275	0.109	0.049	0.046	0.031
Cumulative proportion	0.489	0.764	0.873	0.923	0.969	1.000

Table 4.3 Results from principle component analysis on response to being placed in a novel environment. PC1 was most strongly correlated with exploratory behaviour; and PC2 most strongly correlated (inversely) with activity.
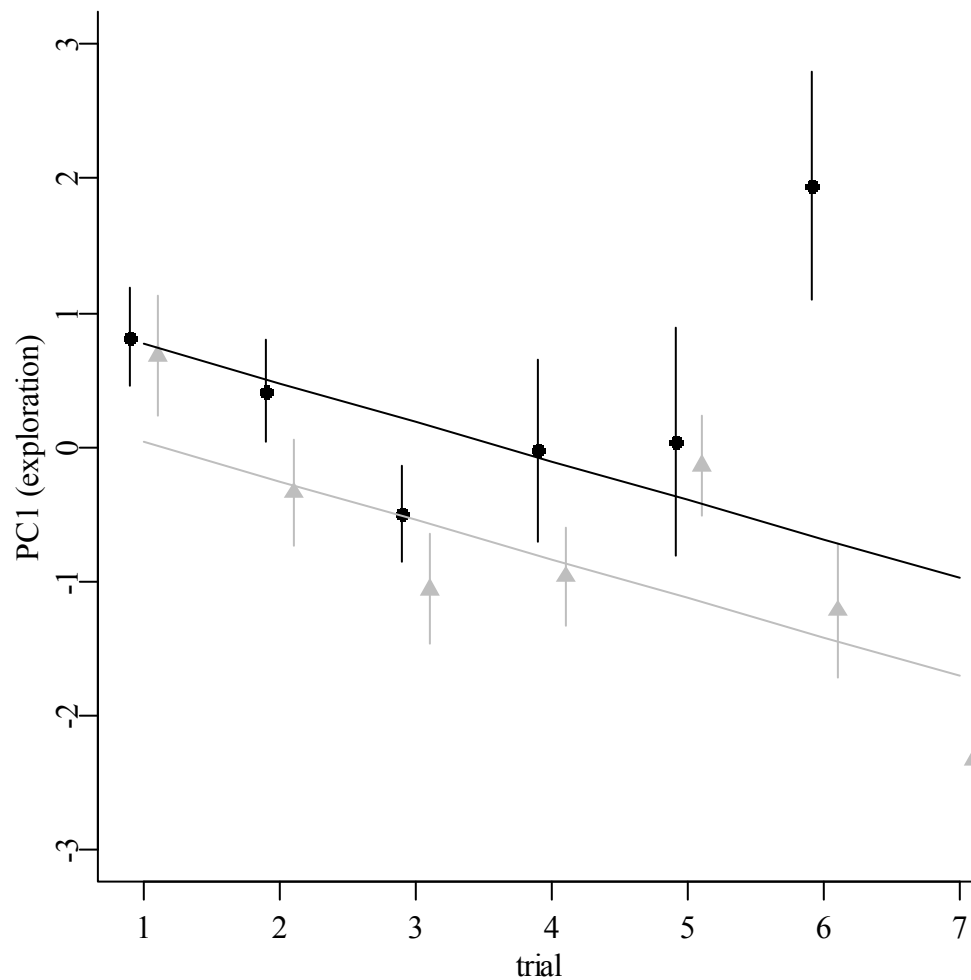
Figure 4.3 Mean ± SE exploration score (PC1) across increasing trials for young (black circle) and old (grey triangle) individuals. Lines denote the predicted effect from the GLMM. In general, younger individuals had higher PC1 than older individuals, and PC1 decreased over increasing trials. The highest maximum trial for young individuals was 6.
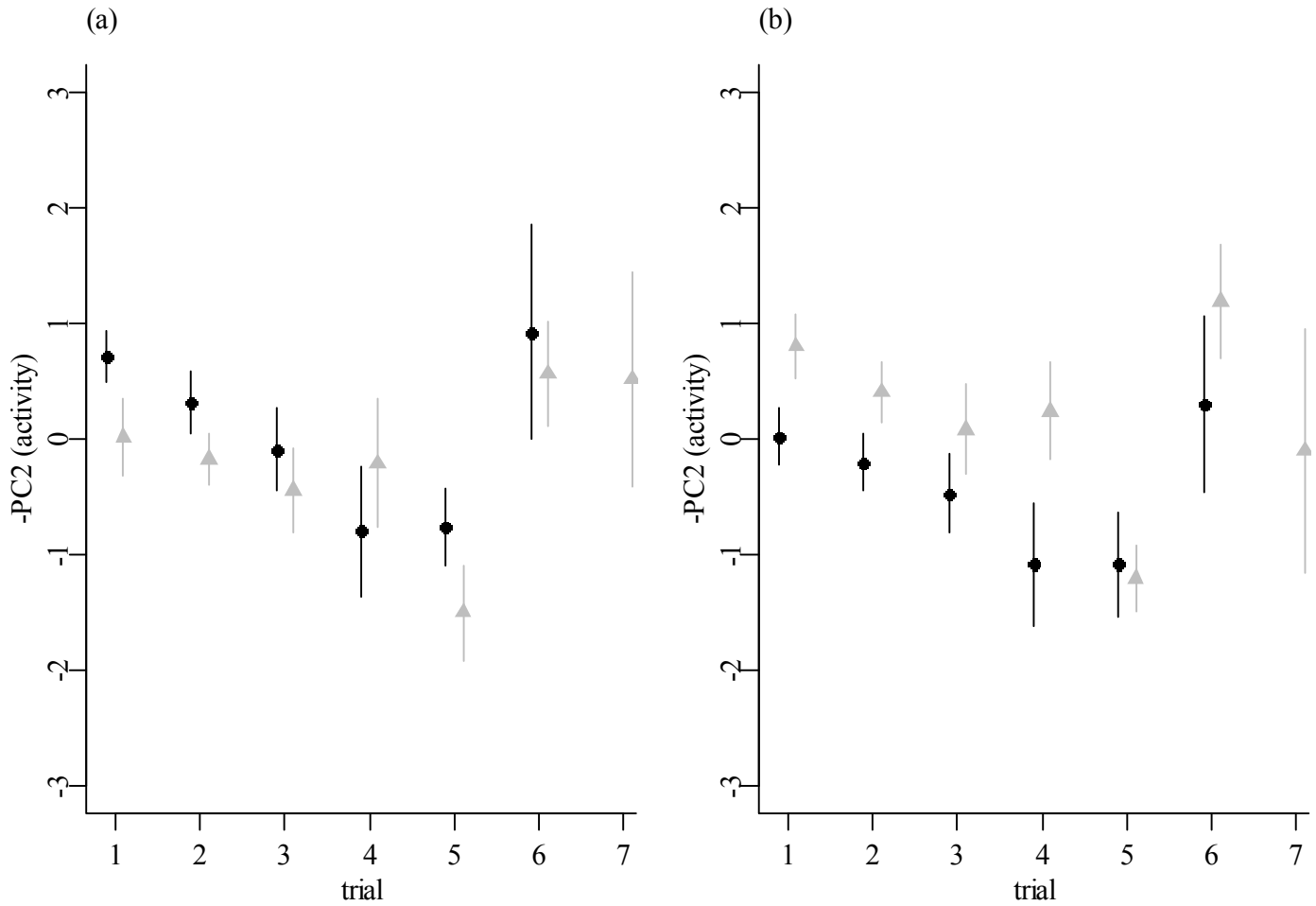
Figure 4.4 Mean ± SE activity score (-PC2) over increasing trials for (a) young (black circles) and old (grey triangles) individuals; and (b) for females (black circles) and males (grey triangles). Younger individuals and males had higher activity scores than older individuals and females, respectively. As the effect of trial was not statistically significant, predicted lines are not shown.

Figure 4.5 Mean ± SE Box-cox transformed relative time digging (to searching): (a) individuals spent less time digging when there had been more rainfall in the previous 30 d and (b) younger individuals (black circles) spent less time digging in larger groups; whereas older individuals (grey triangles) did not change their foraging strategy with group size.

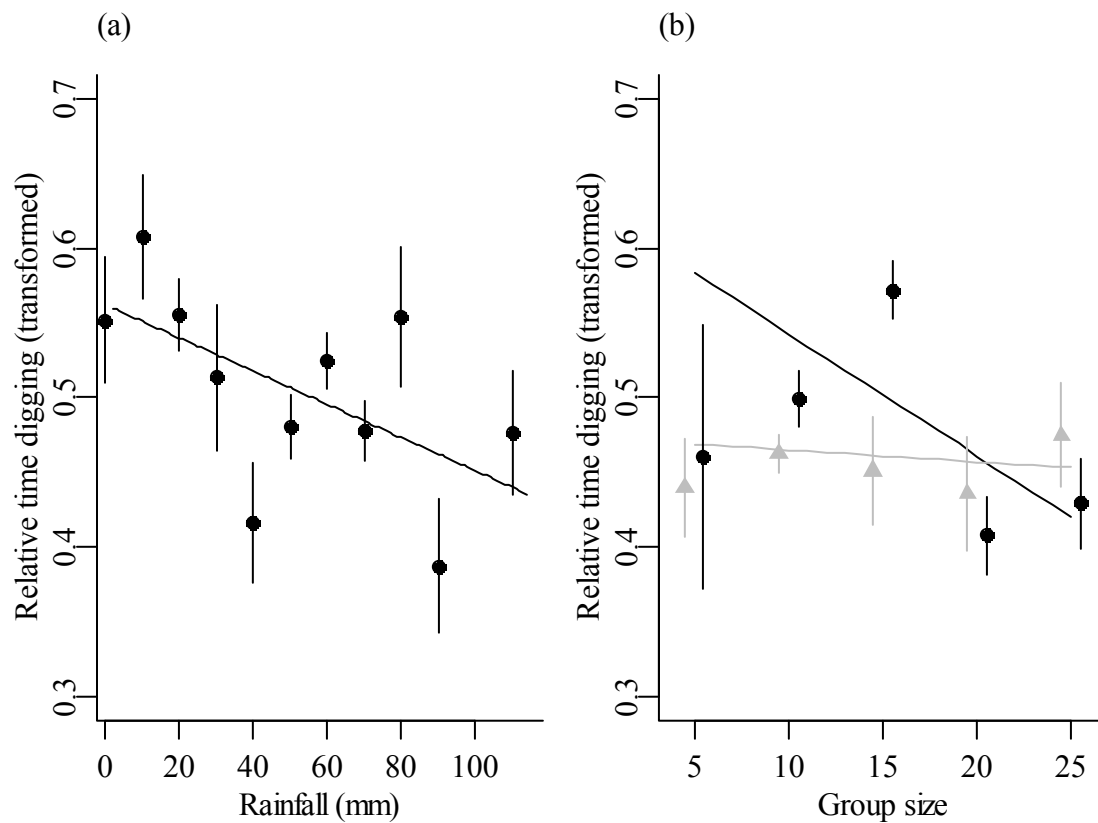| Behaviour pairs	r (95% CI)	t_{19}	p
Vigilance-foraging	-0.56 (-0.80,-0.17)	-2.96	**0.008**
Vigilance-weighability	0.52 (0.12,0.78)	2.69	**0.015**
Vigilance-babysitting	0.17 (-0.28,0.56)	0.74	0.466
Vigilance-provisioning	0.52 (0.12,0.78)	2.69	**0.015**
Foraging-weighability	-0.69 (-0.86,-0.36)	-4.13	**0.001***
Foraging-babysitting	-0.25 (-0.62,0.20)	-1.13	0.272
Foraging-provisioning	-0.33 (-0.67,0.12)	-1.52	0.144
Weighability-babysitting	0.43 (0.00,0.73)	2.09	0.050
Weighability-provisioning	0.48 (0.06,0.75)	2.37	**0.029**
Babysitting-provisioning	0.63 (0.28,0.84)	3.57	**0.002***
Number of significant tests			6 of 10
p§			< 0.0001

Table 4.4 Correlations between pairs of individually consistent behavioural traits. *P*-values in bold indicate correlations significant at α = 0.05, with an asterisk denoting those which remain significant after sequential Bonferroni adjustment. *§ p* value indicates probability of finding a significant result in 6 out of 10 tests by chance (Moran, 2003).
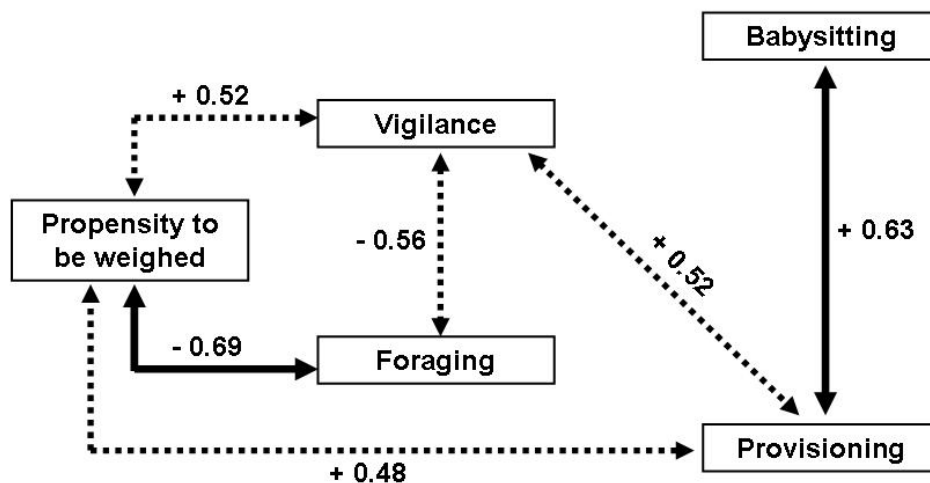

Figure 4.6. Diagram of correlations between different behavioural traits significant at the α = 0.05 level. Solid lines indicate correlations that remained significant after Bonferroni correction. Numbers indicate the direction and value of Spearman's *r*. For statistical details, see table 4.4.

4.5 DISCUSSION

While there were no consistent individual differences in mobbing behaviour or response to a novel environment, individuals were consistent in their foraging strategy and vigilance rate, as well as their propensity to be weighed by human observers. Six of the 10 pairs of individually consistent behavioural traits were correlated, which is higher than that expected by chance, yet there was no evidence that individual variation in cooperative pup care was related to individual variation in the non-helping contexts tested here. Below, I discuss these results in the light of the predictions presented in the introduction in addition to a more general discussion about investigating behavioural syndromes in social animals in the wild.

I did not find support for the first prediction that correlations between cooperation and risk-taking behaviour may occur as a result of underlying life-history strategies. Of the behaviours that were individually consistent (foraging effort, vigilance rate and propensity to be weighed), there were no significant correlations with cooperative behaviour after correction for multiple comparisons. It is possible that the behaviours measured were not the best suited to test this prediction. In meerkats, where aggressive competition for the breeding position is important, particularly in females (Clutton-Brock et al., 2006), a more likely suite of traits related to reduced cooperation may include aggression and growth, particularly for individuals closer to inheriting the breeding position, such as those which are older relative to their same-sex competitors (Hodge et al., 2008). Perhaps a more appropriate way to investigate life-history strategies and behavioural syndromes, therefore, would be to identify whether there are consistent individual differences in aggression and how these relate to dispersal, dominance and reproductive success (e,g. Boon et al., 2007, Dingemanse and Goede, 2004).

Provisioning rate was higher for those individuals that were easier to weigh and for individuals that were more vigilant, although these were not significant after correction for multiple comparisons. These correlations may be better understood by considering the way in which foraging effort, vigilance and propensity to be weighed correlated with one another. Vigilance rate and foraging effort were negatively correlated within individuals,

which is unsurprising given the common trade-off between vigilance and foraging (Lima and Dill, 1990). Less easy to interpret is the way in which propensity to be weighed related to vigilance rate and foraging strategy. Propensity to be weighed may not be the best measure for nervousness toward humans. Previous studies on wild collared flycatchers (Garamszegi et al., 2009) and bighorn sheep (Réale et al., 2009) have demonstrated individual differences in propensity to be trapped which are associated with personality traits in other contexts. Measuring propensity to be weighed in meerkats may not be analogous to these studies, however, as individuals are habituated to the presence of humans and therefore may not consider their presence as a threat. A better measure of nervousness toward humans would be to investigate individual differences in habituation in wild individuals.

My second prediction was that individuals would specialise in one particular behaviour owing to temporal or nutritional constraints limiting their investment across multiple types of cooperative behaviour. In line with the earlier findings of Clutton-Brock et al. (2003), my observations also demonstrated that meerkats did not specialize in pup care behaviours. In fact, individuals that were better babysitters (controlling for sex, age and dominance status) also contributed more to provisioning (as in chapter 3). I could not test whether individual contributions to cooperative pup care were correlated with mobbing, however, as individuals were not consistently different in mobbing behaviour. This result was unlikely to be an artefact of using low-threat predator cues (which would explain why younger individuals investigated them more, Graw and Manser, 2007), as there was no individual repeatability in mobbing of live snakes (B. Graw, unpublished data). For a thorough understanding of trade-offs across cooperative behaviours, it would be interesting to extend this type of analysis to include social digging and raised guarding (Clutton-Brock et al., 2002), in addition to cooperative pup care as examined here and previously (Clutton-Brock et al., 2003).

Measuring individual traits of social animals in the wild may be complicated by the presence of other group members. In terms of both mobbing and responses to a novel environment, there was high group consistency although individual consistency was low.

A number of studies have found that personality measures can be influenced by context (Dingemanse and Goede, 2004, Frost et al., 2007), in particular by the presence of conspecifics (Magnhagen, 2007, van Oers et al., 2005). The social environment is likely to be particularly important in cooperatively breeding species which live in highly complex social groups. A recent study by Magnhagen and Bunnefeld (2009) found that individual differences were higher when individuals were tested alone than when in a group. It would have been difficult to conduct a similar comparison in meerkats, however, as individuals become highly distressed if separated from the group (personal observation). Moreover, as they live in large groups of up to 50 individuals (Clutton-Brock et al., 2005), personality measures taken in isolation may not have much ecological relevance.

I found that exploration of a novel environment declined with increasing trials. Further work, requiring a larger sample size than that presented here, could investigate whether individuals differed in their habituation over trials. While most personality research has focused on differences in mean-level behaviour of individuals, there is increasing interest in variation in behavioural responses across an environmental gradient (Dingemanse et al., in press, Réale and Dingemanse, in press), akin to reaction norms in the study of phenotypic plasticity (Nussey et al., 2007). Martin and Réale (2008) recently provided the first direct examination of individual differences in habituation during a novel environment test. Variation among individuals in their change of response over trials could be indicative of specialists and generalists within populations (Wilson and Yoshimura, 1994), with some individuals being consistent whereas others more plastic in their response.

To my knowledge, only one other study has investigated behavioural syndromes across contexts in cooperative breeders (Bergmüller and Taborsky, 2007), based on a laboratory study on cichlids. Here, I present one of the first attempts at explaining individual variation in cooperative behaviour in relation to behaviour in other contexts in a wild, social mammal. Although the absence of strong correlations means that cooperative

behaviour and risk-taking behaviour do not seem to be correlated, the approach presented here may be applied to other types of behaviour

5 • HOW EARLY EXPERIENCES OF CARE INFLUENCE LATER HELPING BEHAVIOUR

5.1 ABSTRACT

Studies on systems with biparental care have shown that experiences of care early in life can have lasting effects on later parental behaviour. Here, I ask whether the amount of cooperative care an individual experiences early in life could influence its helping behaviour later on. First, I observed a sample of individuals from early development until maturity, in order to quantify the amount of tactile care received and elucidate whether early experiences of care directly correlate with later helping behaviour. Second, using a larger sample from the long-term study, I investigated whether indirect measures of early tactile care and direct measures of food received influenced later helping behaviour. The number of helpers present when an individual was born influenced the helping behaviour of males and females differently. Males born into big groups demonstrated slightly higher levels of helping than those born into small groups. In contrast, females born into larger groups had lower contributions to helping when adults. This may be explained by considering sex differences in the distribution of breeding success, as female meerkats compete more aggressively for reproductive opportunities. This study demonstrates the importance of considering early experiences in explaining individual variation in cooperative behaviour, a factor which has, until recently, been largely overlooked in studies of animal societies.

5.2 INTRODUCTION

Individual variation in cooperative behaviour may be partly explained by considering environmental conditions experienced in early life. There is increasing appreciation that both the physical environment and social experiences during development can have profound and lasting effects later in life (West-Eberhard, 2003). Conditions experienced during development can influence later fitness in a variety of ways (Lindstrom, 1999), for example, by affecting metabolic rate (Verhulst et al., 2006), competitive ability (Royle et al., 2005) or disease susceptibility (Gluckman and Hanson, 2004). There has been relatively little investigation of the effect of early care on later behaviour in cooperative breeders. In pied babblers, offspring which receive a longer period of post-fledging care are more likely to disperse as adults (Ridley and Raihani, 2007). No study has yet

explicitly tested the extent to which early experiences of care influence later contributions to caring behaviour in cooperative breeders.

One important measure of the early environment is food availability to young, which, in cooperative breeders, may depend on the number of helpers present (Emlen, 1991). Indeed, numerous studies have demonstrated the importance of helpers on juvenile survival and development (e.g. Russell et al., 2003a, Doerr and Doerr, 2007, Ridley, 2007, Hatchwell et al., 2004). More recently, there has been some evidence that helpers have an influence beyond the juvenile stage, with individuals who have received more care showing increased breeding success as adults (Russell et al., 2007, Hodge, 2005). It is not clear, however, how early experiences of care influence future helping behaviour and the associated fitness benefits to the helping individual. One may predict early conditions to influence later helping through effects on the relative costs and benefits on helping behaviour. Offspring born into bigger groups and who receive more food, for example, may acquire foraging skills more rapidly (Thornton, 2008a) and consequently increase their later cooperative behaviour, which is often influenced by foraging efficiency (Clutton-Brock et al., 2001a).

Just as the physical environment acts on behaviour through the effects of nutrition and condition, so may the early social environment have lasting effects on later behaviour, independently of nutritional effects. There is extensive evidence that experience of social contact in the postnatal period influences later social behaviour, potentially through organisational effects on the nervous system (reviewed in Cushing and Kramer, 2005). For example, young rhesus macaques born to abusive mothers are more likely to become abusive mothers themselves (Maestripieri, 2005a). Indeed, in our own species, it has long been acknowledged that social deprivation during childhood can have permanent psychological effects (Bowlby, 1969). The influence of maternal care on later behaviour has been most extensively studied in laboratory rodents (e.g. Fleming et al., 2002, Champagne and Meaney, 2007). In particular, tactile care (such as licking or grooming) can influence neural development (reviewed in Champagne and Curley, 2005), for example by influencing the density of receptors for oxytocin (Meaney, 2001). These

studies rely on cross-fostering experiments to elucidate whether such effects are caused by early social experiences rather than genetic similarities between offspring and their mothers, as parenting behaviour has also been shown to be heritable (MacColl and Hatchwell, 2003a). No study has yet to investigate whether early social experiences of young individuals in cooperative societies, where non-breeding helpers as well as parents provide care, have similar effects on later cooperative behaviour. Given that oxytocin influences social behaviour (Keverne and Curley, 2004), for example, it is possible that increased tactile care from helpers may increase the density of oxytocin receptors and hence expression of later cooperative behaviour.

Here, I investigated the effect of care experienced during development on later helping behaviour in wild meerkats, an ideal species for such an investigation as offspring receive variable amounts of care and adults show high variation in their contributions to cooperation (Clutton-Brock et al., 2000, Clutton-Brock et al., 2001a). The care received by pups occurs at two stages. First, pups remain at the natal burrow with one or more babysitters until they are old enough to forage with the group at one month of age (Russell et al., 2002). During this period, pups suckle their mothers or other females (allolactators), and are groomed and huddled by babysitters of both sexes (Doolan and Macdonald, 1999). The second stage of care starts once pups begin foraging with the group and are provisioned by helpers with solid prey items until they can forage independently at around 90 days of age (Brotherton et al., 2001).

To investigate the influence of early experiences on later cooperative behaviour, I focused on contributions to babysitting. I chose this behaviour from a range of cooperative activities exhibited by meerkats (Clutton-Brock et al., 2003) as it is comparable to the measures of maternal behaviour, such as huddling, measured in analogous studies in rats and primates. When babysitters remain at the burrow, they spend a large proportion of time in direct contact with pups, huddling and grooming them (S. English, unpublished data). Furthermore, as babysitters often forgo up to an entire day of foraging to guard the pups, it is a highly costly activity (Clutton-Brock et al., 2000). In addition, although some variation in contributions to babysitting can be explained by sex,

age, group size, weight and short-term changes in levels of prolactin (Clutton-Brock et al., 2000, Carlson et al., 2006b), there is still considerable variation unexplained. Early levels of care are likely to play an important role: a recent study has demonstrated that individuals born in good condition have increased foraging efficiency as adults (Thornton, 2008a).

I first quantified early care through direct observations of tactile care (huddling and grooming) while pups were being babysat. By following the development of these pups into adulthood, I investigated whether there was a relationship between tactile care experienced when young and later babysitting behaviour. Owing to the small sample size, as direct measures of tactile care were available only for a subset of individuals, I calculated a proxy for tactile care that would be available in the long-term database. I found that pups received more tactile care when more than one babysitter remained with the litter, which was in turn more likely in bigger groups. Consequently, I considered the following characteristics of an adult's early rearing environment on its contributions to babysitting: size of the group in which it was reared, whether allolactators were present, the proportion of days more than one babysitter remained with the litter (as a correlate of tactile care) and weight at independence (which relates to food received when young, Russell et al., 2002). I used multivariate statistical analysis to control for sex, age, weight and current group size. I predicted that individuals who received more care early in life, both in terms of tactile care and food provided, would demonstrate increased cooperative behaviour, specifically babysitting, at adulthood.

5.3 METHODS

5.3.1 Behavioural observations

Scan data

Between April 2006 and March 2008, I conducted scan observations of 18 litters (median litter size: 4, range: 2-5) in 11 groups early in their development while they were being babysat (aged 14–30 d), recording every four minutes whether any pup in the litter was receiving tactile care or not. Scan observations were not possible prior to 14 d as pups

remained below ground for the first two weeks of life (Doolan and Macdonald, 1999). Tactile care was defined as a pup being groomed or huddled (held in close contact by a babysitter). I also recorded suckling but, as this was confounded by food intake, I excluded suckling scans from the final analysis. Suckling was less frequent than huddling or grooming and the results were the same whether or not it was included as a measure of tactile care. I calculated the proportion of scans that any pup in the litter was receiving tactile care. Data were analysed per litter as pups often received care together and analyses on an individual basis yielded similar results.

Babysitting records

I used measures of babysitting from the long-term database both as an indirect measure of the amount of care received by young (see below) and to quantify the expression of cooperative behaviour later in life. Detailed records of babysitting have been collected on this population between December 1996 and March 2008. From the birth of a litter until the day pups started foraging with the group (around 25–30 d), groups were visited both in the morning and afternoon to ascertain the identity of all babysitters. This was done twice daily because individuals acting as babysitters often changed between morning and afternoon, particularly if the group returned to the burrow in the middle of the day. For each pup whose tactile care I measured, either directly or from the long-term database, I calculated their adult babysitting effort, as the proportion of half-days it remained to babysit out of the total number of half-days it could have babysat (when any adult in the group babysat the pups).

5.3.2 Statistical analysis

All statistical analysis was conducted using R 2.9.0 (R Development Core Team 2009). I conducted generalised linear models (GLM) and generalised linear mixed models (GLMM) with random terms to account for repeated measures (for example of litters or groups) using the lmer function (lme4 library in R, Bates et al., 2008). Random terms were only included if they accounted for significant variance in the data (Crawley, 2002). Maximal models were fitted with all fixed effects (and their interactions) of interest, and subsequent model simplification was done by removing model terms and comparing

models using likelihood ratio tests (Crawley 2002). The minimal model contained only those terms whose removal from the model significantly decreased the explanatory power of the model.

1. Factors affecting amount of tactile care received

I conducted a preliminary analysis on a subset of closely observed litters (18 litters in 11 groups) to investigate what characteristics of a group influenced the amount of tactile care received. Analyses were conducted on a per-litter basis as pups often received care simultaneously, and analyses on a per-pup basis yielded similar results. I investigated factors affecting the proportion of scans during which a litter received tactile care by using a GLMM with binomial error structure and logit-link function, fitting the fixed effects of pup age, number of babysitters present (babysitter number) and number of allolactating females in the group (lactator number), with litter as a random term (the variance attributed to group was not significant). Lactation in females was determined by examining their teats for signs of milk production (Scantlebury et al., 2002). As there were rarely more than three babysitters or more than two lactators present, these data were categorised as 1, 2, 3 or more than 3 (babysitter number) and 1, 2 or more than 2 (lactator number).

This first analysis revealed that pups received more care when there were more babysitters present (see below). Further analysis showed that the significant difference existed only when comparing the first category (one babysitter) and all others (more than one babysitter). Consequently, I investigated whether bigger groups were more likely to leave more than one babysitter with the pups. I used a larger dataset for this analysis, as detailed records of babysitters have been collected for over ten years. First, I conducted a GLMM with binomial error structure to investigate the effect of group size on whether one or many babysitters remained with the pups, including litter as a random term (the variance attributed to group was not significant). Group size was defined as the number of individuals over three months of age, as younger individuals younger rarely contribute to helping (Clutton-Brock et al., 2002). This analysis was conducted on babysitting records for 238 litters in 24 groups (n = 9,533 observations, 9–70 observations per litter).

2. Direct relationship between early tactile care and later babysitting effort

Of the 66 pups on which I had direct measures of tactile care received at the burrow, 40 survived to helping age (>3 months) with a litter present in the group (2-6 litters per individual). Consequently, I investigated whether there was a direct relationship between early tactile care received by these individuals and their later contributions to babysitting, controlling for any effects of group size, age and age-corrected weight, which have been previously shown to influence babysitting (Clutton-Brock et al., 2000). Age-corrected weight was measured as the ratio of an individual's actual weight to its expected weight for its age, with values more than 1 indicating heavier individuals and values less than 1 indicating lighter individuals. To calculate expected weight, I estimated the asymptotic exponential relationship between weight and age from a regression of weight against age for 1,258 individuals (using the nlme procedure in R to account for repeated measures, Crawley, 2002). I included these terms in a GLMM with binomial errors on proportion of half-sessions an individual was observed to babysit given the total number of half-sessions it could have babysat, including the additional fixed effect of proportion of scans the individual was observed to receive tactile care when young (arcsine-square-root transformed).

3. Effect of early experience on later contributions to babysitting

Owing to the small sample size of individuals with direct measures of care, I also investigated whether babysitting in later life was influenced by characteristics of the early rearing environment as recorded in the long-term dataset (which did not include direct measures of tactile care). I used a GLMM with binomial error structure to analyse the babysitting effort (proportion of half-days babysat) of 347 subordinate adults (more than one year of age) in 19 groups on 218 litters. Having accounted for factors known to affect babysitting effort (Clutton-Brock et al., 2000), that is, sex, log-transformed age (in days), age-corrected weight and current group size as well as any significant interactions, I considered the extent to which variation in babysitting could be explained by early group size (the number of adults present in the group when the babysitter itself was being babysat as a pup), weight at independence (between 85–95 d, once an individual is able

to forage for itself), total rainfall when young (for one month prior to birth as well as when babysat), whether more than one female lactated in the group and the proportion of days that more than one babysitter remained with the pups (as a proxy for tactile care), as well as how these effects differed according to sex of the individual. I included the random terms of current litter and babysitter identity (the variance attributed to group and babysitter litter was not significant).

5.4 RESULTS

5.4.1 Factors affecting amount of tactile care received

On the subset of closely observed litters (n = 18 litters), both pup age and babysitter number had an effect on tactile care received (grooming and huddling), with further analysis revealing that the significant effect was only between one or more than one babysitter (GLMM, pup age: χ^2 = 14.8, p < 0.001, babysitter number: χ^2 = 12.0, p = 0.007). Pups received less care as they grew older and more care if more than one babysitter remained with the pups (figure 5.1). No other terms were significant in the model. Using a larger sample from the long-term dataset of babysitting records (n = 238 litters), I found that group size had a significant and positive effect on whether or not more than one babysitter remained with the pups (GLMM: χ^2 = 84.7, d.f. = 1, p < 0.001, figure 5.2).

5.4.2 Direct relationship between early tactile care and later babysitting effort

Controlling for the significant effects of current group size and log-transformed age, I found that individuals that I had closely observed who received more tactile care when young contributed lower levels of babysitting as adults (table 5.1, figure 5.3). Owing to the small size of the dataset, some factors known to influence babysitting in adults (such as sex and age-corrected weight) were not significant in this model. In addition, there was no significant interaction between any of the fixed effects and sex.

5.4.3 Effect of early experience on later contributions to babysitting

For the large dataset drawn from the long-term data, an individual's current contributions to babysitting were influenced by its sex, age-corrected weight, age and current group size (table 5.2), as has been shown in previous studies (Clutton-Brock et al., 2000, Clutton-Brock et al., 2003). Controlling for these effects, an individual's babysitting effort was influenced by the number of helpers in the group during development (table 5.2), although there was no effect of other aspects of the rearing environment, including weight at independence, rainfall, the presence of allolactators or the proportion of days the litter had more than one babysitter. The effect of early group size depended on an individual's sex. In males, there was a weak but positive effect of early group size on later babysitting effort. On the other hand, females brought up in larger groups reduced their babysitting effort as adults (figure 5.4).

Fixed effect	Effect ± SE	LRT-χ^2	*p*-value
Age (log-transformed)	0.82 ± 0.23	8.44	0.003
Group size	-0.11 ± 0.03	11.8	<0.001
Tactile care (asin-sqrt transformed)	-1.21 ± 0.60	3.88	0.049

Table 5.1. Results from a GLMM investigating the influence of tactile care on later babysitting effort, controlling for the effects of log-transformed age and group size. The effect±SE for each significant factor is given from the minimal model, with the associated χ^2 and *p*-values from a likelihood ratio test of the model excluding that term, and the minimal model.

Fixed effect	Effect ± SE	LRT-χ^2	*p*-value
Sex (M)	3.58 ± 0.76	--	--
Age (log transformed)	0.55 ± 0.09	--	--
Age-corrected weight	-0.42 ± 0.41	--	--
Current group size	-0.05 ± 0.01	--	--
Early group size	-0.02 ± 0.01	--	--
Sex (M) * Age (log transformed)	-0.40 ± 0.11	12.5	<0.001
Sex (M) * Current group size	-0.03 ± 0.01	30.6	<0.001
Sex (M) * Age-corrected weight	-1.06 ± 0.51	4.25	0.039
Sex (M) * Early group size	**0.02 ± 0.01**	**5.58**	**0.018**
Weight at independence	*NS*	*0.11*	*0.736*
Days individual had >1 babysitter	*NS*	*0.16*	*0.691*
Presence of allolactators	*NS*	*0.23*	*0.629*
Rainfall when young	*NS*	*0.02*	*0.893*

Table 5.2. Results from a GLMM investigating the influence of early social experiences on later babysitting effort, controlling for current factors that influence babysitting. Significant early factors are in bold and those factors that were not significant are italicised. The effect±SE for each significant factor is given from the minimal model, with the associated χ^2 and *p*-values from a likelihood ratio test of the model excluding that term, and the minimal model. The latter could be calculated for interactions only, as all terms were bound in interactions.

(a)
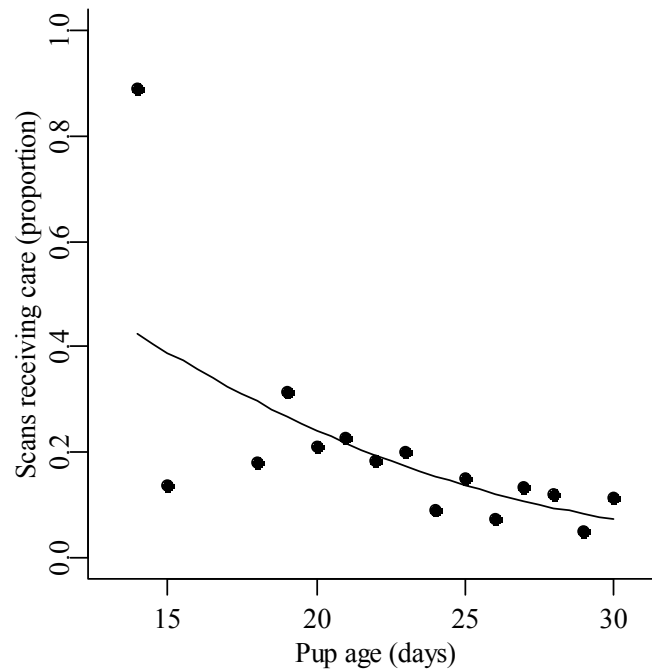
(b)
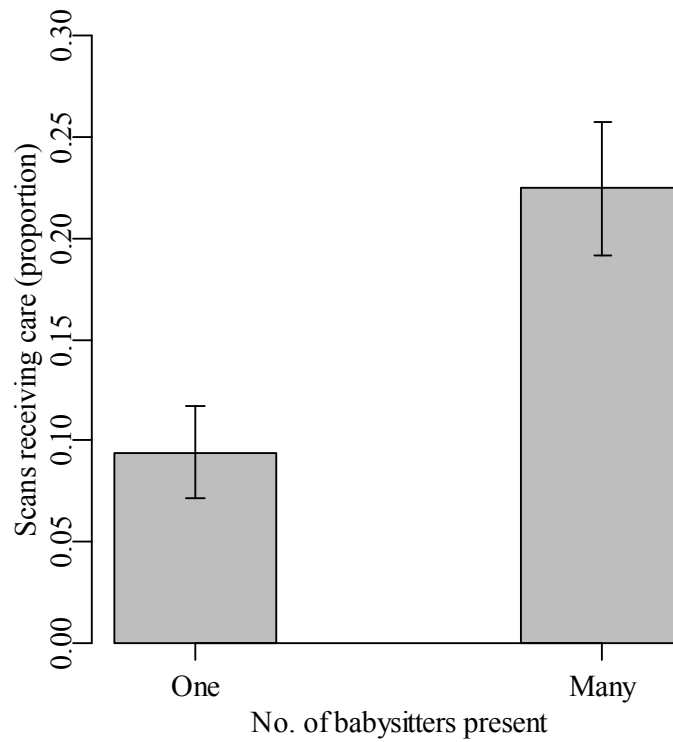
Figure 5.1. Pups in a litter received more tactile care when (a) they were younger and (b) more than one babysitter remained with the pups. Although the first point appears to be an outlier, the effect of age remained significant if values < 20 d were excluded.
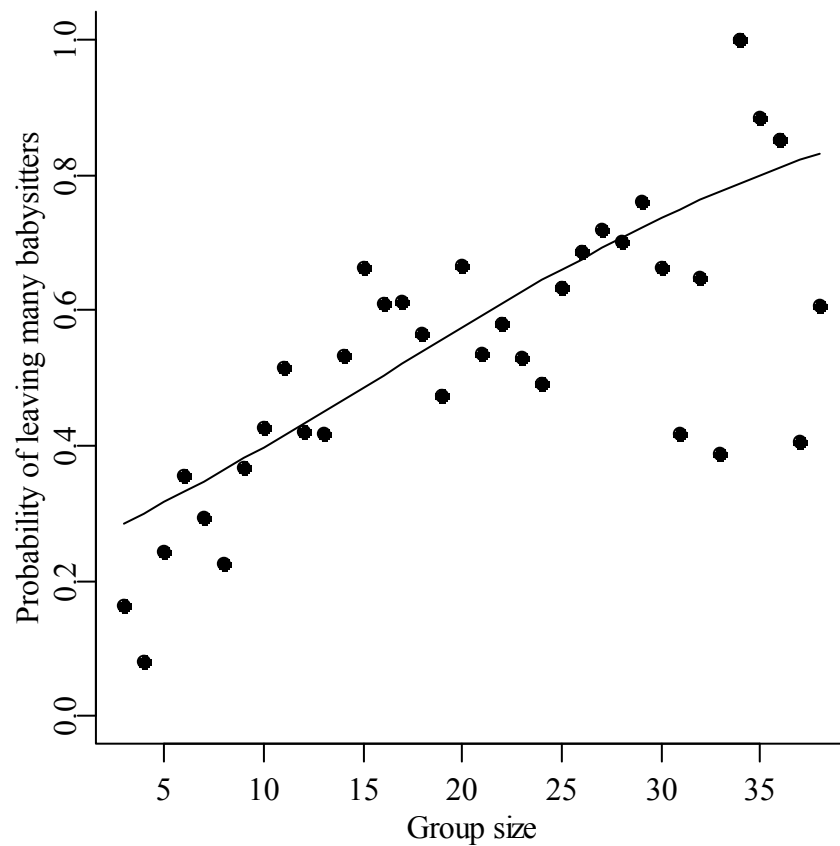
Figure 5.2 Probability of leaving more than one babysitter increased with increasing group size. Points give mean values for each category of group size controlling for repeated measures in the model, as well as the predicted line from the GLMM based on data from 9,533 observations from 238 litters.
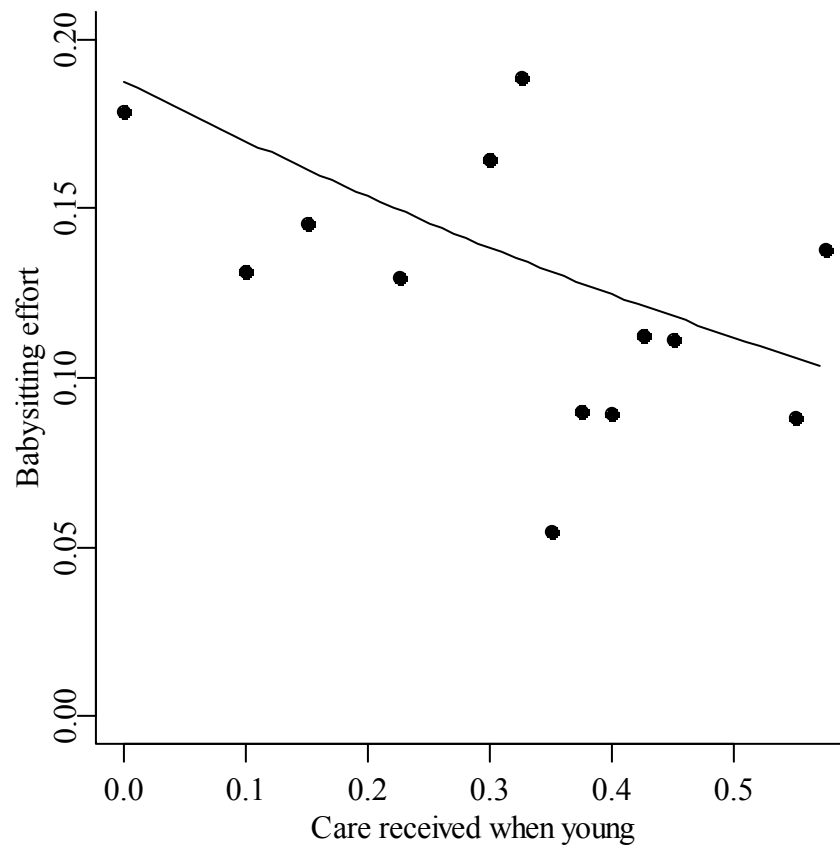
Figure 5.3. Individuals who received more care (arcsine-square-root transformed proportion) when young were less likely to babysit when older. Line is the prediction from a GLMM controlling for current group size and age, and repeated measures of litter and babysitter identity. Points give mean values for each category of care received when young of the raw data controlling for other terms in the model.
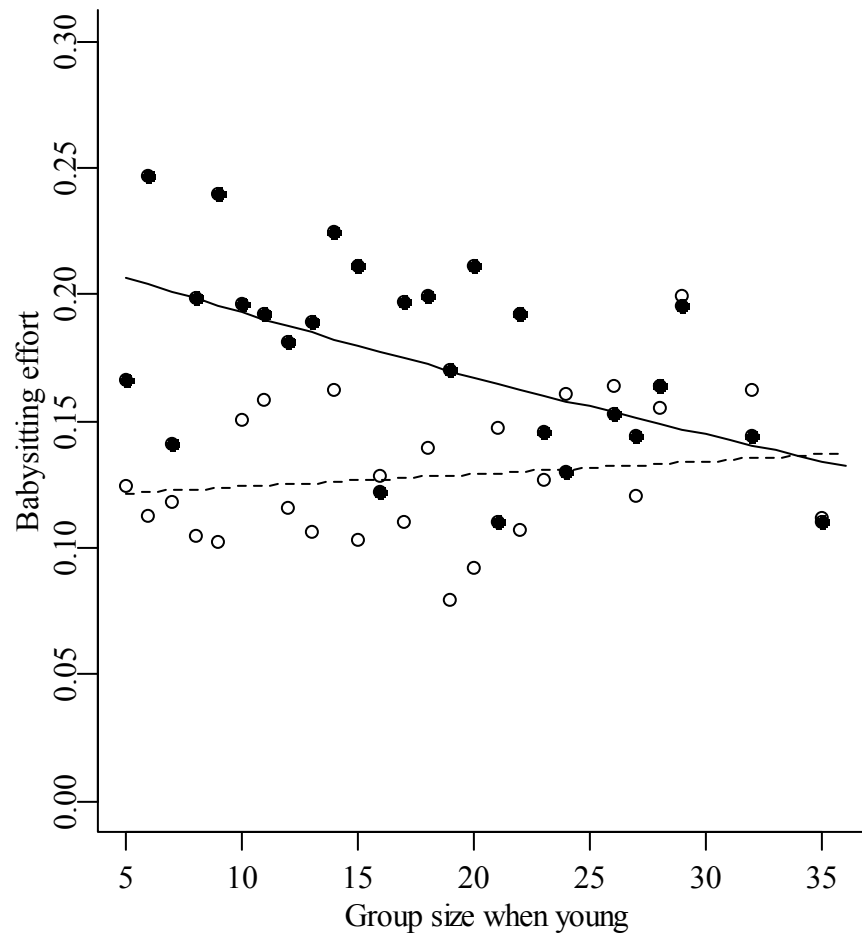
Figure 5.4. Effect of early helper number on current babysitting effort. Lines are predictions from a GLMM controlling for the effects of sex, log-transformed age, current group size and age-corrected weight for males (dotted line) and females (solid line). Points give mean values for each category of early group size of the raw data controlling for all other effects for males (open points) and females (solid points).

5.5 DISCUSSION

Individual variation in helping behaviour may be partly explained by differences in early experiences of care. Pups received more tactile care when there were more babysitters present, which was in turn more likely in larger groups. When I considered the influence of early conditions on later cooperative behaviour, I found a negative relationship between tactile care experienced when young and later babysitting, based on an analysis of a subset of individuals for which these fine-scale measures were available. Extending this analysis using indirect measures on the long-term dataset, I found that, after controlling for the effects of sex, age, current group size, weight and foraging efficiency, the amount of care experienced when young influenced later cooperative behaviour for females but not males. This study adds to the growing body of evidence that conditions experienced during development can have lasting effects in later life, but the way in which these mechanisms act in a cooperative system may be complex.

The effect of helper number on tactile care received may describe a previously unconsidered mechanism by which helpers benefit offspring in cooperative breeders. While a number of studies have described the effect of helpers on offspring fitness (e.g. Russell et al., 2003a, Canestrari et al., 2008), there is still considerable debate over how to measure the benefits of helpers (Cockburn et al., 2008). Increased tactile care can play an important role in terms of improved neural development and later stress response behaviour (Champagne and Curley, 2005). Consequently, a previously overlooked benefit of increased helper number may be that additional helpers provide more tactile stimulation to pups during their sensitive period of development, which in turn could have long-term consequences. Indeed, in this study I found that early helper number influenced later contributions to babysitting. Helper number influenced whether one or more babysitters remained with the pups, which in turn was correlated to tactile care received by pups. As the effect of helper number on later babysitting remained when controlling for any influence of early or current weight, this suggests that helpers have an influence that extends beyond simply providing food.

The direction in which early care influenced later cooperative behaviour was, however, surprising. Individuals who received more tactile care when young exhibited reduced cooperative behaviour as adults. These results contrasted those from studies on which I had based my predictions: in both rhesus macaques and laboratory rodents, there is a positive relationship between an individual's maternal behaviour and the maternal behaviour of her young (Fairbanks, 1996, Fleming et al., 2002). As my analysis is based on a small sample size, the results presented here should be interpreted with caution. In general, inferences made from correlational studies should be treated with care (as discussed in Cockburn et al., 2008), particularly in cases where confounding factors may not have been correctly identified. However, my confidence in the relationship between early care and later helping increased when analysis on the extended dataset demonstrated that early helper number, a proxy for tactile care, was negatively correlated with helping behaviour in females.

In contrast to the extensive research effort into understanding the mechanisms by which early maternal care influences the development and expression of maternal behaviour (Champagne and Curley, 2005), we have very little understanding of similar mechanisms in cooperatively breeding mammals, partly due to the ethical concerns of conducting such research in the wild. For example, measuring oxytocin receptor density would require decapitating individuals to dissect their brains (e.g. Champagne and Meaney, 2007) and cross-fostering experiments are likely to result in unfamiliar offspring being deserted. Mechanisms in parental care systems are complex, involving neuroendocrine changes and epigenetic effects on DNA methylation (Champagne and Curley, 2005, Weaver et al., 2004). Consequently, it is difficult to extend predictions based on these studies to more complex systems such as cooperative breeders, further complicated by the fact that, in cooperative systems, carers are often not parents and hence hormones underlying expression of cooperative behaviour may be different (e.g. Schoech et al., 1996). There is large scope for further work on this topic, and collaboration between neuroendocrinologists and behavioural ecologists would prove fruitful in increasing our understanding of the role of social experiences in the development of cooperative behaviour.

The number of helpers during the babysitting period was correlated with the later helping behaviour of males and females differently. Although I found no direct effect of weight at independence, the presence of allolactators or the proportion of days many babysitters remained with the litter; all of these aspects of the early rearing environment were correlated with group size when young (results not shown). Consequently, helper number can be considered as an overarching measure of the amount of care received when young, and, as such, it is intriguing that helper number has a differential influence on the sexes. While early helper number had a weak positive effect on later helping in males, it had a more striking and negative effect on later helping in females. Sex differences in the effect of early conditions on later fitness traits have been demonstrated in a number of species, including tawny owls (Appleby et al., 1997), red deer (Kruuk et al., 1999) and water pythons (Madsen and Shine, 2000). More pertinently, the influence of maternal care on later behaviour had an effect in females but not males in laboratory mice (Curley et al., 2008).

In meerkats, sex differences are evident across the spectrum of their behaviours, from the development of cooperative behaviour (Clutton-Brock et al., 2002) to responsiveness to begging (English et al., 2008). The differential effect of early helper number on later babysitting may be understood in light of sex differences in variation in reproductive success, with only a small fraction of females succeeding in breeding, whereas males have more equal opportunities to breed. Consequently, female meerkats are the more competitive sex (Clutton-Brock et al., 2006), with size being especially important for females in terms of gaining the reproductive position. In addition, early helper number is an important predictor of future reproductive success (Russell et al., 2007). Taken together, these results suggest that females who are born into larger groups are more likely to breed later on. While I have focused on the influence of early conditions on contributions to helping, an individual's behaviour may also be affected by future life-history decisions (Cant and Field, 2005). As females born into larger groups are more likely to become the primary breeder in the group, it is possible that they reduce their contributions to helping to maintain good condition so that they can outcompete their

rivals. Further analysis could build on these results, by investigating whether females who are more likely to inherit the breeding position exhibit compensatory reductions in cooperative behaviour, as has been seen in some primitively eusocial insect societies (Cant and Field, 2001, Field et al., 2006).

This study provides the first direct investigation of the role of early social experience in influencing later cooperative behaviour in a natural population. I have demonstrated here that it is possible to measure long-term consequences of early experiences of tactile care in natural populations where experiments may not be feasible or ethical. As I found that litter-of-origin did not explain significant variance in contributions to babysitting, it is unlikely that genetic effects confounded my results. By comparing results from these studies in tandem with tightly controlled experiments in the laboratory, we could achieve a more comprehensive understanding of the importance of early conditions for determining cooperative behaviour in adulthood. Extending these studies to other cooperative systems could further our appreciation of variation in cooperative behaviour in social groups.

6 • SEX DIFFERENCES IN RESPONSIVENESS TO BEGGING

6.1 NOTE

This chapter was published as English, S., H. P. Kunc, J. R. Madden and T. H. Clutton-Brock. (2008). Sex differences in responsiveness to begging in a cooperative mammal. *Biology Letters* **4**, 334-337. Hanjoerg Kunc, Joah Madden and I designed and conducted the playback experiment; and T. H. Clutton-Brock contributed to discussion. I analysed the data and wrote the paper.

6.2 ABSTRACT

In species where young are provisioned by both parents, males commonly contribute less to parental care than females and are less responsive to variation in begging rates. Similar differences in the care of young occur among adults in cooperative breeders but fewer studies have investigated whether these are associated with differences in responsiveness. Here, we present results from a playback experiment investigating responsiveness to begging in the meerkat, a cooperatively breeding mammal. Although increased begging rate raised the feeding rate of adults of both sexes, there was no consistent tendency for females to be more responsive than males. However, when we examined changes in the proportion of food items found that were fed to pups (generosity), we found that females were more responsive than males to increased begging rate. These results can be explained in terms of sex differences in dispersal: in meerkats, females are philopatric and receive considerable benefits from investing in young, both directly, by increasing group size, and indirectly, by recruiting helpers if they inherit the breeding position. In addition, they emphasize that generosity provides a more sensitive measure of responsiveness to begging than feeding rate, as it accounts for variation in foraging success.

6.3 INTRODUCTION

In vertebrates, where both parents provision their young, females often contribute more to parental care than males (Clutton-Brock, 1991). In addition, females are commonly more sensitive to signals of offspring need (Kolliker et al., 1998, Kilner, 2002, Quillfeldt et al., 2004) such as begging rate, which has been shown to reflect hunger state in a number of species (Kilner and Johnstone, 1997). Sex differences in responsiveness to begging may

arise because parents respond to different signals, vary in their response to the same signal or modify their behaviour differently according to their partner's response (Hinde, 2006). These differences are likely to reflect sex differences in the costs and benefits of parental care (Lessells, 2002), with the sex that accrues greater fitness benefits per unit of investment exhibiting higher sensitivity to offspring need.

Sex differences in contributions to care of young have also been demonstrated in many cooperative breeders (reviewed in Cockburn, 1998, Clutton-Brock et al., 2002). As in biparental systems, these differences may be a consequence of variation in the costs and benefits of care, and are likely to be associated with variation in responsiveness to offspring begging rate. While some studies have investigated how adults in a group vary in their responsiveness to begging according to breeding status or condition (Wright, 1998, Bell, 2008), only one study has demonstrated sex differences (MacGregor and Cockburn, 2002). To our knowledge, there is no evidence from cooperative breeders that the sex which invests more in the care of young also demonstrates greater responsiveness to increases in begging rate.

We investigated responsiveness to begging in a cooperatively breeding mammal, the meerkat, which has a mobile begging system where begging calls are audible to all group members (Manser and Avey, 2000, Kunc et al., 2007). Meerkats are small (<1 kg) carnivores living in groups of 3–50 individuals, with a dominant pair monopolising reproduction and helpers of both sexes contributing to the care of young (Clutton-Brock et al., 2001a). Pups start foraging with the group from about 30 days of age and receive prey items by helpers until they are nutritionally independent, at around three months old. There is high variation in pup feeding: females feed more than males and dominants contribute less than subordinates (Brotherton et al., 2001). Pups emit a continuous begging call to solicit feeding from adults, the rate of which indicates their hunger level (Manser et al., 2008).

We conducted a playback experiment to determine whether there were sex or status differences in responsiveness to increased signals of need from pups. We manipulated a

single component of the begging signal (call rate), and measured the response of a focal individual. Most previous studies of the responses of adults to variation in juvenile begging rate have measured adult feeding rate, rather than the proportion of food found that is fed to offspring (generosity), which gives a measure of food allocation to young relative to that eaten by the adult. In this study, we examined the effects of begging rate on both the absolute feeding rate and generosity of dominant and subordinate adults of both sexes. We predicted that females would be more responsive than males and that dominants would be less responsive than subordinates, as suggested by natural variation in contributions to feeding young (Brotherton et al., 2001).

6.4 MATERIALS AND METHODS

The study was conducted between December 2005 and May 2006 on a population of wild meerkats in the Northern Cape, South Africa (26°58'S, 21°49'E) (Clutton-Brock et al., 2001a). All individuals in the population were identifiable by unique dye marks and were habituated to ignore observers at close range (<1 m).

We played 30 minutes low rate and 30 minutes high rate begging, in a random order, to focal individuals in 11 groups with pups during the peak feeding age (40–65 days). Playback stimuli were created from recordings of 11 female pups of similar ages from 11 different groups, using a different playback stimuli for each group. We manipulated the begging rate of stimuli by either adding or removing periods of background noise between calls to create the low (40 calls/minute) and high (120 calls/minute) treatments. These values lie within the natural range of begging rates (mean ± SE begging rate: 83.26 ± 2.69, range: 23.35–137.15, from calculations based on 87 pups of 26 litters from 11 groups). In each group, the experiment was conducted on the dominant pair and a subordinate individual of each sex, over two consecutive days. The amplitude of the begging playback was kept to natural levels (Manser and Avey, 2000) and no more than two experiments were played consecutively to a group in one session, to avoid individuals habituating to calls and ceasing to respond. During the experiment, we followed the focal individual at a distance of 2 m with the speaker, recording the size of all prey items found, which was later used to estimate their biomass (as in Brotherton et

al., 2001). Whenever the focal individual found a prey item, we noted whether it ate the item or took it to within 1 m of the loudspeaker and/or fed it to a pup (cf. Kunc et al., 2007). As pups in a group may respond to the begging call by guarding helpers more closely, we also recorded the presence of any pups within 2 m of the focal individual.

Statistical tests were performed using R (R Development Core Team, 2009). We used four general linear mixed models (GLMMs) to investigate the influence of begging rate, and its interaction with sex and dominance status, on adult feeding rate (biomass fed per hour), generosity (proportion of biomass found fed to pups) and foraging success (total biomass found). With the blocked design of our experiment (four focal individuals in each group), we could compare individuals within a group by fitting individual and group as random effects. Model simplification was conducted following Crawley (2002), with proportional data arcsine-transformed and feeding rate data log-transformed. Assumptions for normality and homogeneity of variances were fulfilled. All three-way interactions were non-significant and thus deleted from the final model.

6.5 RESULTS

Adult feeding rate was influenced both by playback treatment and sex, being higher in females (as in Clutton-Brock et al., 2001a) and during the high begging rate playback, whereas it did not differ between dominants and subordinates (Table 6.1a). In addition, there were no significant treatment-by-sex or treatment-by-status interactions (Table 6.1a, Figure 6.1a).

Similarly, the proportion of food items found that were fed to pups (generosity) increased during the high begging rate treatment and was higher in females, while there was no difference between dominants and subordinates (Table 6.1b). However, there was a significant treatment-by-sex interaction, indicating that females were more responsive to increased begging rate than males (Table 6.1b, Figure 6.1b).

Finally, dominants of both sexes had higher foraging success than subordinates ($F_{1,32}=4.87$, $p=0.027$), although there were no significant differences in foraging success

between the sexes ($F_{1,32}$=0.93, p=0.33) or between low and high rate playback treatments ($F_{1,43}$=0.22, p=0.64).

response term	explanatory terms	F	p-value	effect (s.e.)
(a) *feeding rate* (g fed / h)	**treatment**	**7.82**	**0.008**	**high: 0.0 (0.0), low: -0.48 (0.17)**
	sex	**4.44**	**0.043**	**female: 0.0 (0.0), male: -0.39 (0.18)**
	status	0.36	0.551	
	treatment*sex	0.95	0.334	
	treatment*status	1.14	0.291	
	status*sex	2.08	0.160	
(a) *generosity* (g fed / g found)	**treatment**	**14.1**	**< 0.001**	**high: 0.0 (0.0), low: -0.41 (0.11)**
	sex	**8.06**	**0.008**	**female: 0.0 (0.0) male: -0.31 (0.11)**
	status	0.81	0.375	
	treatment*sex	**4.80**	**0.034**	
	treatment*status	0.23	0.631	
	status*sex	2.39	0.133	

Table 6.1 Effect of low and high call rates on (a) feeding rate and (b) generosity. Shown are the results of GLMMs including group and individual identity as random terms. Non-significant terms were deleted from the final model.

(a)
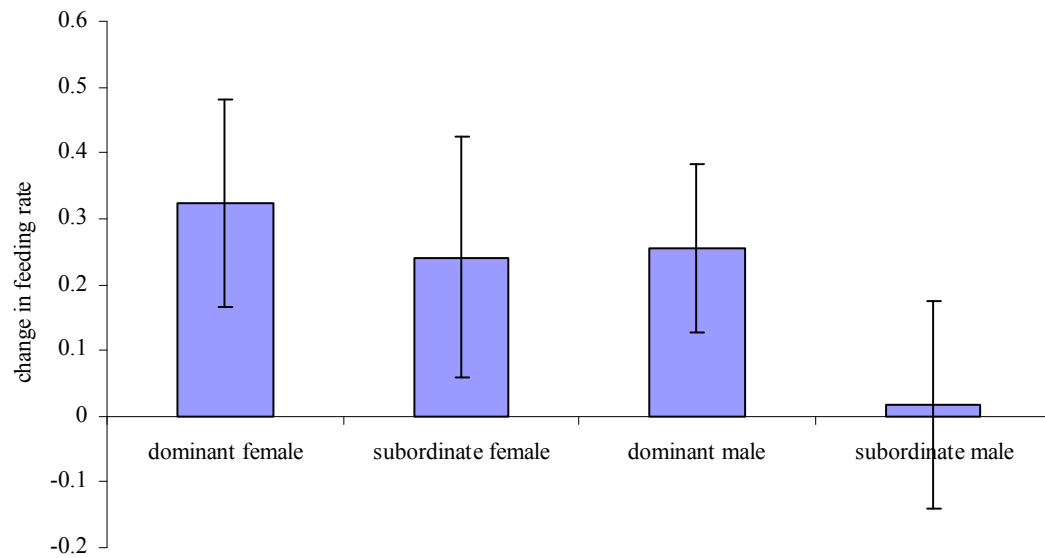
(b)

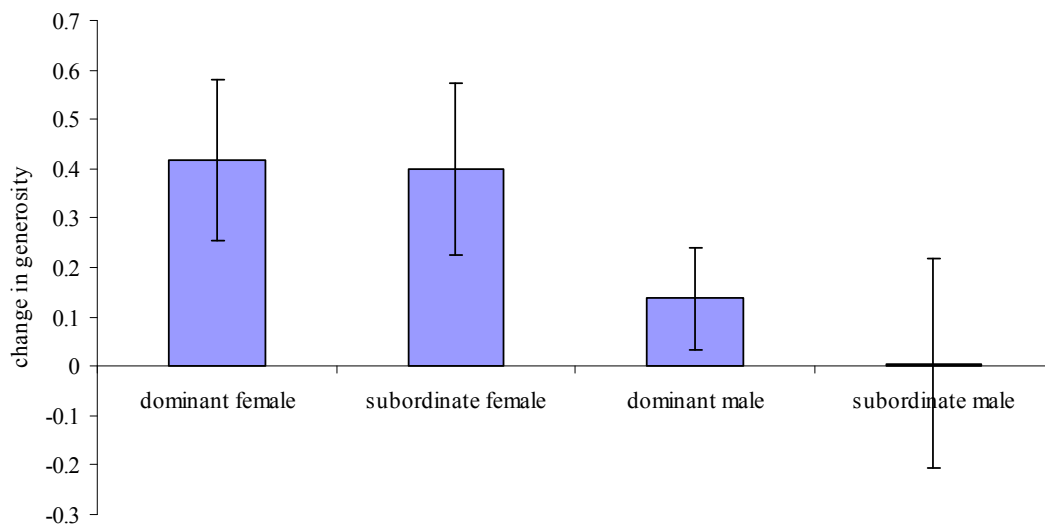**Figure 6.1.** Change in (a) feeding rate or (b) generosity from low to high rate begging treatments for different adults depending on their sex and dominance status. Each bar depicts mean (± 1 SE) within-individual difference in response.

6.6 DISCUSSION

Increased begging rate raised both overall feeding rate and generosity, as predicted by theoretical and empirical studies (e.g. Godfray, 1991, Burford et al., 1998, Glassey and Forbes, 2002). However, when we considered variation in the level of response, our results differed depending on the measure considered: we found sex differences in responsiveness to increased begging rate in terms of generosity but not feeding rate, while dominants and subordinates did not differ in responsiveness for either measure. Generosity is a more sensitive measure as it accounts for variation in foraging success. Even though foraging success did not differ between the sexes or across treatments, dominants were more successful at finding food than subordinates. Consequently, the contrast between subordinate females, who found less food but fed more of it to pups, and dominant males, who found more food but fed less of it to pups, is only evident when considering generosity. This demonstrates the importance of controlling for foraging success in studies of responsiveness to begging. Where direct observations of foraging behaviour are unfeasible, foraging success may be estimated through changes in body mass (e.g. Martins and Wright, 1993).

Both dominant and subordinate females were significantly more responsive to increased begging rate than males. Sex differences in responsiveness to increased begging rate are likely to be a true reflection of variation in sensitivity to offspring need, since begging rate indicates pup hunger level (Manser et al., 2008). Our results differ from those of MacGregor and Cockburn (2002), who found that male superb fairy wrens were more responsive to the playback of begging even though females contribute more to offspring care. They suggested that, as males spend less time at the nest, they have less information than females on offspring need and may consequently be more sensitive to increased vocal begging, whereas females may also respond to postural signals. Such information asymmetry is unlikely to explain differential responsiveness to begging in meerkats, since pups forage with the group and their begging calls can be heard throughout the group (Manser and Avey, 2000).

Sex differences in responsiveness to begging are probably a consequence of differences between males and females in the costs and benefits of investing in young. Sensitivity to the nutritional demands of pups is adaptive to adults as pups which receive more food have improved chances of survival (Clutton-Brock et al., 2001a). Females, being the philopatric sex, have more to gain than males by maximizing pup survival, both through direct benefits of group augmentation and future benefits of recruiting helpers that may later assist them if they inherit the breeding position (Clutton-Brock et al., 2002). Sex differences in dispersal, therefore, could explain why females are both more generous to pups and more responsive to increases in begging rate.

As dominants contribute less to pup care than subordinates (Brotherton et al., 2001), we had expected them to be less responsive to begging. However, we found no difference between dominant and subordinate individuals of the same sex in responsiveness to increased begging rate, similar to Arabian babblers, where both helpers and breeders increased their feeding rate in response to begging (Wright, 1998). The lack of difference in responsiveness between dominants and subordinates here may be because dominants were more successful at foraging and consequently incurred fewer costs by increasing their generosity to hungrier offspring.

In conclusion, we found that females were more responsive to increased begging rate, in terms of generosity but not feeding rate. Females receive greater future pay-offs from investing in young than males, which may explain both why they invest more in young in general and respond more than males to changes in a pup's signal of need.

7 • THE EFFECT OF PUPS ON CARER FORAGING BEHAVIOUR AND VOCALIZATIONS

7.1 ABSTRACT

Many studies have shown that carers increase their feeding rate in response to the begging calls of dependent young, but less is known about whether they alter their foraging behaviour to find more food. In addition, while most studies on carer-offspring communication have focused on carer responses to offspring vocalizations, little is known about changes in the vocalizations produced by carers themselves. In this study, I investigated the way in which the presence of dependent pups influenced carers in three ways. First, I asked if carers altered their foraging behaviour in order to find more food during periods of provisioning pups. I conducted a playback experiment to test whether carers that contributed more to pup care altered their foraging behaviour to a greater degree on hearing begging calls. Second, I investigated the vocalizations produced by carers and asked whether they gave different types of calls, depending on their purported function, when followed by begging pups. Finally, I focused on the factors that influenced specific vocalizations given by carers when provisioning pups, and conducted an experiment to elucidate the effect of pup age on the probability that carers gave these feeding calls. I found that, first, pups had no detectable effect on the foraging behaviour of carers, regardless of their natural contributions to cooperative care. Second, when carers were followed by a begging pup, they gave fewer close calls, which mediate distance between foraging individuals, and more joining and lead calls, which are used in the context of coordinating group movement. Vocalizations during feeding events were more likely when pups were younger and closer to another adult, which suggests that these calls serve to draw the attention of pups to the prey item and minimize the cost of it being stolen by another adult. This study adds to the growing body of research investigating carer-offspring communication in social mammals with mobile, begging offspring.

7.2 INTRODUCTION

Carers commonly respond to the begging signals of young by increasing their feeding rate (Wright and Leonard, 2002) and, as a result, may increase their foraging effort in order to find more food. As different categories of carer vary in the extent to which they

respond to begging (MacGregor and Cockburn, 2002, English et al., 2008, Madden et al., 2009), the degree to which carers adjust their foraging behaviour may depend on how much they respond to the begging of young. The question of whether carers alter their foraging behaviour in response to begging, and how this changes depending on investment in young, has received little attention. As most studies on carer response to begging have been based on feeding rates at the nest in birds (e.g. Glassey and Forbes, 2002), activity-time budgets away from the nest may be difficult to observe. Indirect measures of the total amount of food found, and the way in which this is allocated by parents between self-feeding and nestling provisioning, have been estimated from changes in body mass (Martins and Wright, 1993). To my knowledge, studies on monogamous seabirds have provided the only examples of direct measures of parental foraging behaviour during periods of provisioning young (Davoren and Burger, 1999) and the way in which this varies according to levels of investment (Thaxter et al., 2009).

As well as needing to find more food, carers may alter their foraging behaviour by increasing their vigilance when young are present, as younger individuals may be more susceptible to predation (e.g. Sullivan, 1989) and may have yet to develop their own anti-predator responses (Curio, 1993). Investigating how carers change their foraging behaviour would therefore require a consideration of both prey pursuit behaviour and anti-predator vigilance. Cooperatively breeding systems, in which individuals vary in their contributions to caring for young (e.g. Clutton-Brock et al., 2001a, Legge, 2000, Woxvold et al., 2006), provide an ideal opportunity to ask both how carers change their foraging behaviour, in general, and whether this depends on their levels of investment in cooperative behaviour.

In addition to changing their foraging behaviour, carers may modify their vocalizations in the presence of attendant begging young. In species that forage in social groups, individuals often vocalize to communicate with other group members, to regulate foraging distance between potential competitors (Radford, 2004b, Radford and Ridley, 2008), to recruit other group members to a shareable food source (Brown et al., 1991, Di Bitetti, 2005) or to coordinate group movement from one foraging patch to another

(Boinski and Campbell, 1995, Radford, 2004a). As the social environment plays an important role in the type or rate of call given, the presence of dependent young in the group is likely to influence the production of call types according to their function. For example, carers may give more food-associated calls to recruit young individuals to food patches when the young's foraging skills have not yet fully developed (Radford and Ridley, 2006). If young individuals are themselves emitting loud begging vocalizations, carers may give fewer calls to regulate foraging distance or coordinate group cohesion as these calls may no longer be audible over the sound of begging.

Finally, the presence of young can elicit specific vocalizations in adults during provisioning events. Such feeding calls have been reported in avian systems, where calls on arrival at the nest stimulate chicks to beg (Madden et al., 2005, Leonard et al., 1997, Clemmons, 1995b) and are therefore suggested to increase the efficiency of nest visits. Less is known about feeding calls when mobile young follow adults, although recent evidence in cooperatively breeding pied babblers suggests that these calls function to promote fledgling movement (Raihani and Ridley, 2007). Feeding calls may also play a role in the development of foraging skills in young. In cooperatively breeding golden lion tamarins, for example, carers give food-offering calls when provisioning young with large or live prey items (Rapaport, 2006), which are suggested to motivate juveniles to approach adults. Feeding calls may increase the efficiency of food transfer both by drawing the attention of young to the food item and, in animals that forage in social groups where prey items donated to young may be stolen by other adults in the vicinity, reducing the likelihood of losing prey to nearby adults.

Here, I investigated the influence of attendant dependent young on both the foraging behaviour and vocalizations of carers in groups of cooperatively breeding meerkats. From around 21 days of age until nutritional independence (around 90 days), meerkat pups follow adults in the foraging group emitting continuous begging calls, to which carers of both sexes respond by provisioning them with prey items (Manser and Avey, 2000). There is high variation between group members in provisioning rates (Clutton-Brock et al., 2001a) and differences among helpers in responsiveness to increased begging rate

(English et al., 2008, Madden et al., 2009). No study has yet considered the extent to which carers change their foraging behaviour either according to the presence or absence of dependent young in the group, or when exposed to continuous stimulation by begging calls. Here, I used observational data on foraging behaviour to compare carers when pups were present in the group compared to when there were no pups in the group. I conducted a playback experiment on pairs of focal individuals which exhibited contrasting contributions to cooperative pup care, to investigate differences between generous and selfish individuals in the extent to which begging modified their foraging behaviour.

Foraging group members emit a range of vocalizations (Manser, 1998), the most common of which is the 'close' call, which is thought to maintain cohesion among group members. They also give 'joining' calls when catching up with the foraging group and 'lead' calls to initiate group movement (Manser, 1998). A previous study demonstrated that carers give fewer close calls when pups are present in the group than in the non-breeding season (Manser, 1998). I used acoustic recordings of individuals and, restricting the comparison to within the breeding season, investigated whether helpers modified their rate of close, joining and lead calls depending on whether or not they are being followed by a begging pup. Finally, adults occasionally give a quiet call as they approach pups with food (pers. obs.), similar in structure to a joining call, hereafter termed 'feeding' calls. I used observational data to investigate what factors influenced the probability a helper would give a feeding call. I then conducted a provisioning experiment where I followed a focal helper with a microphone after experimentally provisioning it with a scorpion, in groups with pups in the early provisioning period (within first fortnight of foraging with adults) or when pups had been foraging with adults for at least three weeks.

In this chapter, I consider three questions. First, do adults modify their foraging behaviour in the presence of pups? I predicted individuals would increase their digging effort or vigilance rate, or both, when pups were present in the group and on hearing pup begging, with such an increase being greater for individuals that contributed more to cooperative pup care. Second, do carers change the rate of vocalizations when followed by begging pups? I predicted that they would give fewer calls primarily directed to other

adults, and increase calls that function in carer-offspring communication. Third, I asked what factors influenced the probability a carer gave a feeding call. I was specifically interested in whether these calls served to increase the efficiency of transferring prey items liable to be lost, which would be the case for young and naïve pups, if another adult was nearby or if the prey item was mobile and likely to escape.

7.3 METHODS

7.3.1 Do adults modify their foraging behaviour in the presence of pups?

Observations of foraging behaviour

I investigated the extent to which adults changed their foraging behaviour in the presence of pups by conducting continuous focal watches. Focal watches lasted for 20 minutes, occasionally terminated early if more than half the group stopped foraging or if the focal helper stopped foraging for more than two minutes (mean ± SE focal watch duration: 19.1 ± 0.3 min). During each focal watch, I collected continuous data on the foraging behaviour of the focal individual (see ethogram in appendix II), including the time it spent digging, searching the surface and vigilant (bipedally and quadrupedally). In addition, I recorded every prey item found by the focal individual, and, if there were pups in the group, whether this prey item was fed to a pup. In total, I compared 119 focal watches from 15 individuals in 4 groups (3–15 focal watches per individual).

To investigate whether pups influenced carer foraging behaviour, I compared the foraging behaviour of individuals when pups were in the group (pups present) and when not (pups absent). 'Pup present' was defined as the period when pups aged 30–75 d were foraging with the group and 'pup absent' was defined as the period from 30 d prior to the birth of the pups until the day they were born. These time periods were chosen to minimise seasonal differences that may influence foraging behaviour. I used linear mixed models (LMMs) to investigate the effect of pups on the following four measures calculated per focal watch: foraging effort (relative time spent digging compared to searching), mean foraging bout duration, total biomass found and vigilance rate. In all models, I controlled for any confounding effects of sex, age category (younger or older

than 365 d), group size or rainfall in the 30 d prior to the focal watch, with group and individual identity as random terms.

Playback experiment

I conducted a playback experiment to investigate the effect of begging on the foraging behaviour of carers and whether any effect depended on an individual's natural contributions to pup care. In total, 19 pairs of helpers from 10 groups were selected such that they were of the same age and sex but differed consistently in both babysitting and provisioning of the current litter, and categorised as 'generous' or 'selfish' accordingly. A post-hoc *t*-test of their contributions to care for the duration of dependency of the litter confirmed that individuals were indeed different in both cooperative activities (paired *t*-test, babysitting: $t_{18} = 8.28$, $p < 0.0001$; provisioning: $t_{18} = 5.19$, $p < 0.0001$)

Experiments were conducted while pups in the group were begging (aged 30–75 d) to avoid habituation of animals to the sound of begging from the speaker. During the experiment, two observers each followed a single focal adult, with both adults exposed to 30 minutes of begging and 30 minutes of background noise. The order in which adults received the treatments was randomised and both adults received treatments in the same order. Begging playback files were randomly selected from a pool of recordings of seven different pups of both sexes from two different litters in two groups during the peak begging period (30–75 d). During the experiment, we continuously recorded the behaviour of the focal individuals, noting details of foraging behaviour (whether searching the surface or actively digging) and vigilance behaviour (head down or scanning the environment). In addition, each time the focal helpers found food, we recorded the type and size of the prey item, to calculate biomass found (following Brotherton et al., 2001) and whether it was fed to a nearby pup or eaten by the helper. The experiment was paused if the group alarmed or ceased foraging for more than two minutes.

I compared differences between selfish and generous helpers in terms of foraging (relative foraging time spent digging and amount of biomass found) and vigilance rate

during begging and background noise playback treatments. Behaviours were compared through LMMs, with treatment (begging or noise), category (selfish or generous) and their interaction as fixed effects; and experimental pair as a random effect (which accounted for pseudoreplication, given the fixed effects structure, as each individual was only measured once per treatment per experimental pair). In addition, I investigated the influence of playback treatment on the whether the focal adult donated a prey item to the pup (yes or no), as well as the interaction between treatment and category, using a GLMM with binomial error structure. A binary measure was used rather than the absolute number of feeds as feeding events were rare.

7.3.2 Do adults modify their vocalizations in the presence of pups?

During the period of peak pup-provisioning (pups aged 30–80 d), I followed foraging adults to record their vocalizations using a Sennheiser KE66/M6 directional microphone, connected to a Marantz PMD670 digital sound recorder (.wav format, sample frequency 44.1 kHZ, resolution 16 bit). The focal carer's vocalizations were recorded through one channel, while I described its behaviour and distance to the nearest pup or adult through a second channel. Calls were later transcribed using CoolEdit 2000 v.1.1 (Syntrillium Software Corporation, Phoenix, U.S.A.) and spectograms were created using Praat (Boersma and Weenink, 2005) (frequency resolution: 20 Hz, time resolution: 2 ms, Gaussian window shape).

I analysed transcriptions of these recordings to find out if helpers gave different vocalizations depending on whether an individual was social foraging with a pup (SF) or not (Not SF). Social foraging was defined as an adult being within 2 m of a pup (which, generally, would be following the adult and begging for food, Brotherton et al., 2001). Three main call types were identified as in Manser (1998) according to their sound and spectral image, although the continuum of calls meant some were ambiguous and therefore only non-ambiguous calls were used for further analysis. In general, 'close' calls were given at regular intervals and comprised several syllables, 'joining' calls were a brief squeak and 'lead' calls were longer and more tonal (figure 7.4.1). Of the 2,666

calls recorded, 433 (16 %) could not be categorised and 280 (11 %) of these were during social foraging context.

In total, I analysed 81 recordings taken from 42 adults in six groups (1–5 recordings per adult, mean ± SE length of focal recordings: 6.3 ± 0.5 min, range: 1.1–22.7 min). I created three separate GLMMs on the number of close, joining and lead calls, with Poisson error family and an offset function for log-transformed duration (as not all focal watches lasted the same length) with context (SF or Not SF) as a fixed effect, to compare calls given when social foraging and not social foraging. Comparisons were paired within focal recording and individual (fitted as random terms), to control for any other effects such as an individual's age, sex, or condition, and also litter age.
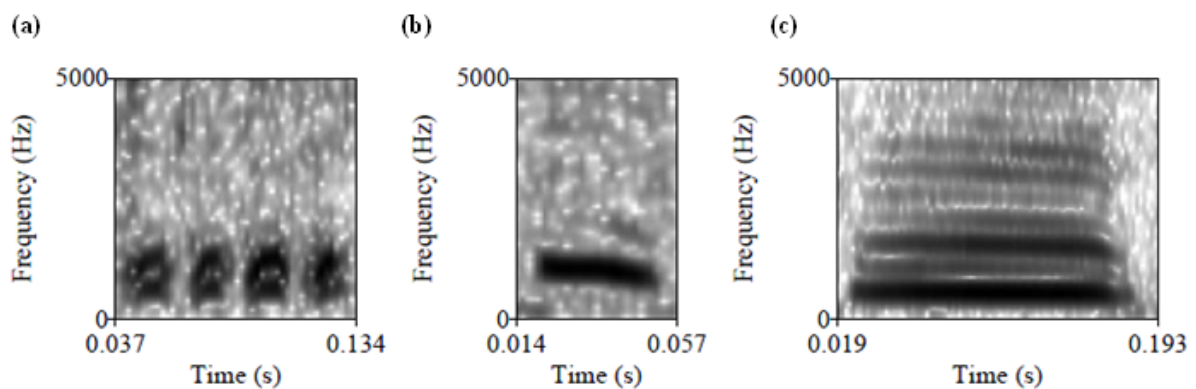
Figure 7.1 Spectrogram showing typical (a) contact call (which comprises several syllables); (b) joining call and (c) lead call.

7.3.3 What is the function of feeding calls?

Context in which feeding calls are given

During *ad libitum* recordings of provisioning events, I noted whether the carer feeding the pup vocalized as it approached with food, the presence of another carer within 1 m of the pup being fed (yes/no), the type and size of prey item and the identity of the pup and carer. In total, I observed 831 feeds from 135 carers to 64 pups in 11 groups during which I could determine whether the carer had vocalized or not. To investigate the factors influencing feeding calls, I conducted a binomial mixed model with vocalize or not (1/0)

as the response variable, and carer age category, carer sex, pup age, pup sex, prey mobility, and whether another carer was within 1 m as fixed variables; including group, carer and pup identities as random terms. Carer age category was defined as being <1 y, 1–2 y or >2 y, excluding individuals less than six months of age as they rarely feed pups (Clutton-Brock et al., 2002). Prey mobility was categorised as 'moving' or 'stationary' depending on the probability of the item escaping: for example, scorpions, geckos and beetles are more likely to move away if dropped compared to larvae, pupae or millipedes.

Scorpion provisioning experiment

To investigate further the influence of pup age on the probability of giving feeding calls, I experimentally provisioned 19 helpers with scorpions (genus *Opisthalamus*) during two periods of pup provisioning: 'Early', when pups had been foraging with the group for less than two weeks (pups aged 32–38 d), and 'Late', when pups had been foraging with the group for at least three weeks (pups aged 58–78 d). The experiment was conducted by two observers: one observer processed the scorpion to remove its sting and dropped it in front of the focal helper from a distance (such that the helper did not associate finding the scorpion with the presence of the observer), while the second observer stood by the nearest pup, which was most likely to be fed (Brotherton et al., 2001), with a Sennheiser KE6/M66 attached to a Marantz PMD670 to record any vocalizations made when the pup was fed. As the size of prey items influences an individual's decision to give food to young (Brotherton et al., 2001), we standardized the size of the scorpions, as far as possible, with scorpions of 4.25 g on average (range: 1–9 g). Each carer was given a series of five scorpions over the course of the morning, but the proportion of scorpions fed to pups varied among carers. In total, we observed 85 provisioning events (46 during the early period and 39 during the late period) from 19 carers to 25 pups in seven groups. I conducted a GLMM with the response term as whether or not a pup-feed was accompanied by a vocalization (0/1) and fixed effects of pup-feeding period (early or late) and whether or not an adult was within 1 m of the pup. Group, carer and pup identity were included as random terms.

7.4 RESULTS

7.4.1 Do adults modify their foraging behaviour in the presence of pups?

Focal observations

I found no effect of pup presence in the group on foraging behaviour (relative time spent digging, LMM: $\chi^2 = 0.20$, $p = 0.254$; mean foraging bout length, LMM: $\chi^2 = 0.01$, $p = 0.907$; biomass found, LMM: $\chi^2 = 0.90$, $p = 0.342$) or vigilance rate (LMM: $\chi^2 = 0.26$, $p = 0.610$).

Playback experiment

There was no measurable effect of playback treatment (begging or noise) on relative time spent digging (LMM: $\chi^2 = 0.0016$, $p = 0.968$), biomass found (LMM: $\chi^2 = 1.2$, $p = 0.271$) or vigilance rate (LMM: $\chi^2 = 0.51$, $p = 0.476$); nor were there any significant interactions with helper category (all treatment-by-category interactions, $p > 0.3$). Vigilance rate was influenced by helper category, however, with generous helpers exhibiting higher vigilance rates than selfish helpers (LMM: $\chi^2 = 5.50$, $p = 0.019$). While generous helpers were more likely to donate a food item regardless of treatment (GLMM: $\chi^2 = 8.90$, $p = 0.003$), selfish and generous helpers were both more likely to donate a food item to pups during the begging playback treatment than the control (GLMM: $\chi^2 = 4.21$, $p = 0.040$), with no difference between categories in the effect of treatment (GLMM: $\chi^2 = 0.29$, $p = 0.593$, figure 7.2).

7.4.2 Do adults modify their vocalizations in the presence of pups?

Paired comparisons within focal recordings on the same individual during the two social contexts (social foraging versus not social foraging) revealed that individuals gave fewer close calls (GLMM: $\chi^2 = 142$, $p < 0.0001$), more joining calls (GLMM: $\chi^2 = 296$, $p < 0.0001$) and more lead calls (GLMM: $\chi^2 = 81.2$, $p < 0.0001$) when they had a pup foraging within 2 m of them compared with more than 2 m from any pups (figure 7.3).
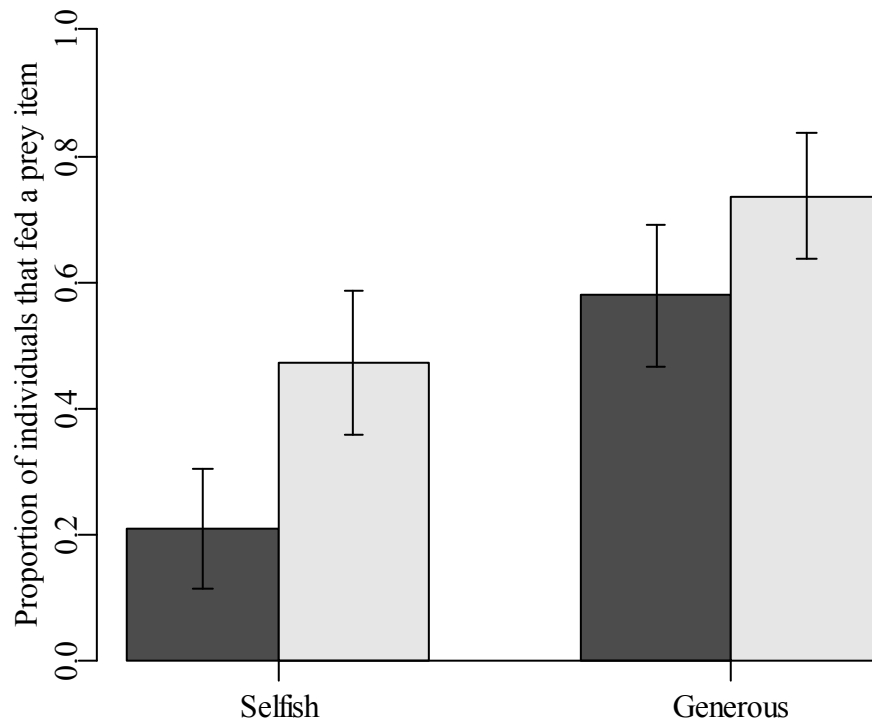
Figure 7.2 Proportion of individuals (n = 19 for each category) that donated a prey item during the playback treatment of control noise (dark grey) or begging calls (pale grey), with standard error of the proportion calculated following Crawley (2005). The probability of donating a prey item increased during the begging playback treatment, and there was no significant interaction between treatment and category (see text for details).

7.4.3 What is the function of feeding calls?

Context in which feeding calls given

Feeding calls were more likely to be given to younger pups and in cases where another carer was within 1 m of the pup being fed (table 7.1, figures 7.4 and 7.5). In addition, younger carers (<1 y old) were more likely to give feeding calls than those 1–2 y and >2 y of age (figure 7.5). Pup identity was a significant random term, while neither group nor adult identity explained significant variation and were therefore excluded from the final model.

Scorpion provisioning experiment

Carers were more likely to give feeding calls during the early period of pup-provisioning than when pups were older (GLM: χ^2 = 81.2, p < 0.0001, figure 7.6), although in this analysis there was no effect of the presence of another adult <1 m (GLM: χ^2 = 1.89, p = 0.17). GLMs were conducted rather than GLMMs as group, carer and pup identity did not constitute significant random terms. Indeed, of the 39 pup-feeds during the late provisioning period, only two of these were accompanied by a vocalization, in comparison to 28 of 46 feeds accompanied by a vocalization during the early provisioning period.

Explanatory terms	LRT-χ	p-value	effect (s.e.)
Pup age	**112**	**<0.0001**	**-0.104 (0.012)**
Distance to another carer	**9.43**	**0.002**	**>1 m: 0.000 (0.000)**
			<1 m: 0.576 (0.185)
Carer age category	**7.62**	**0.022**	**<1 y: 0.000 (0.000)**
			1-2 y: -0.588 (0.301)
			>2 y: -0.955 (0.345)
Carer sex	2.56	0.110	
Prey mobility	1.43	0.230	
Pup sex	0.88	0.348	

Table 7.1 Results from a GLMM of factors predicting feeding calls. Analysis was based on 831 feeds from 135 carers to 64 pups in 11 groups, with pup identity as the only significant random term.
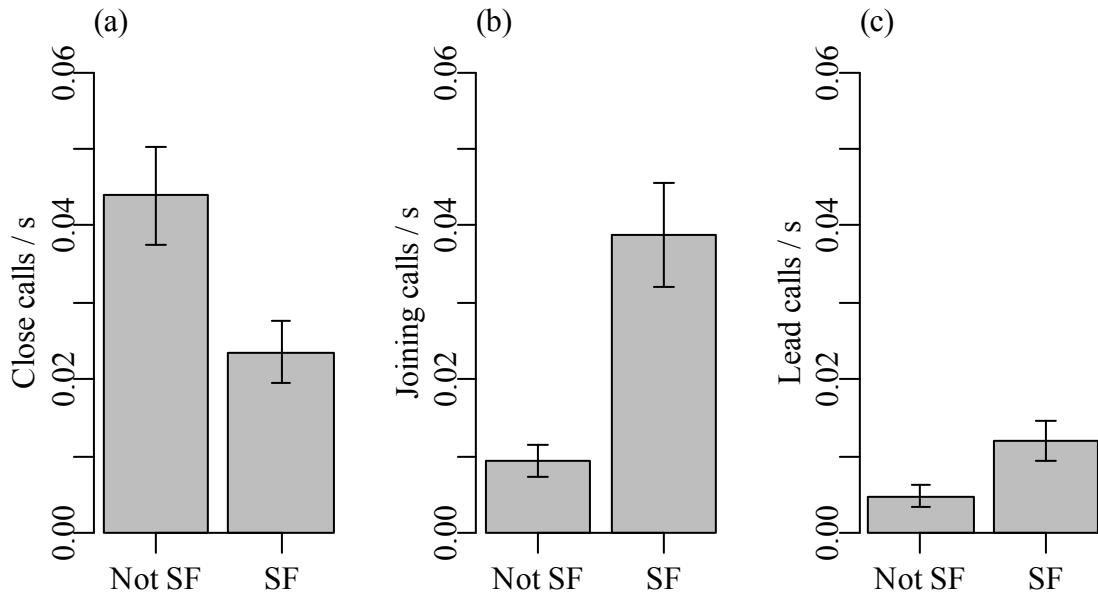
Figure 7.3 Individuals gave (a) fewer close calls, (b) more joining calls and (c) more lead calls when social foraging (SF) with a pup than when not social foraging. Shown are mean ± SE rate of vocalizations given by 42 adults.
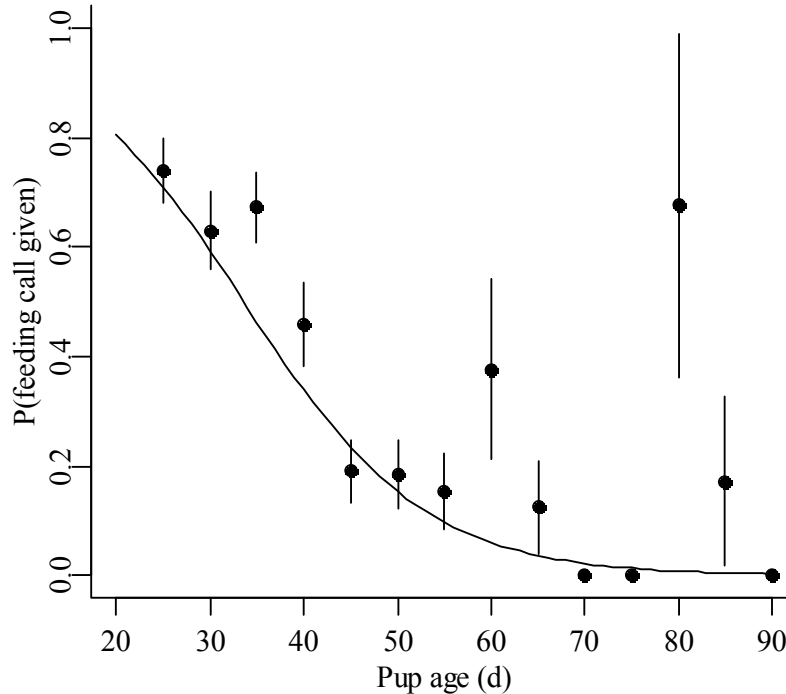
Figure 7.4 Probability of carer giving a feeding call declined with pup age. The line denotes the predicted effect from a GLMM (see text for details). Large error bars, or lack thereof, for age > 65 d, assumed to be the result of low sample sizes.
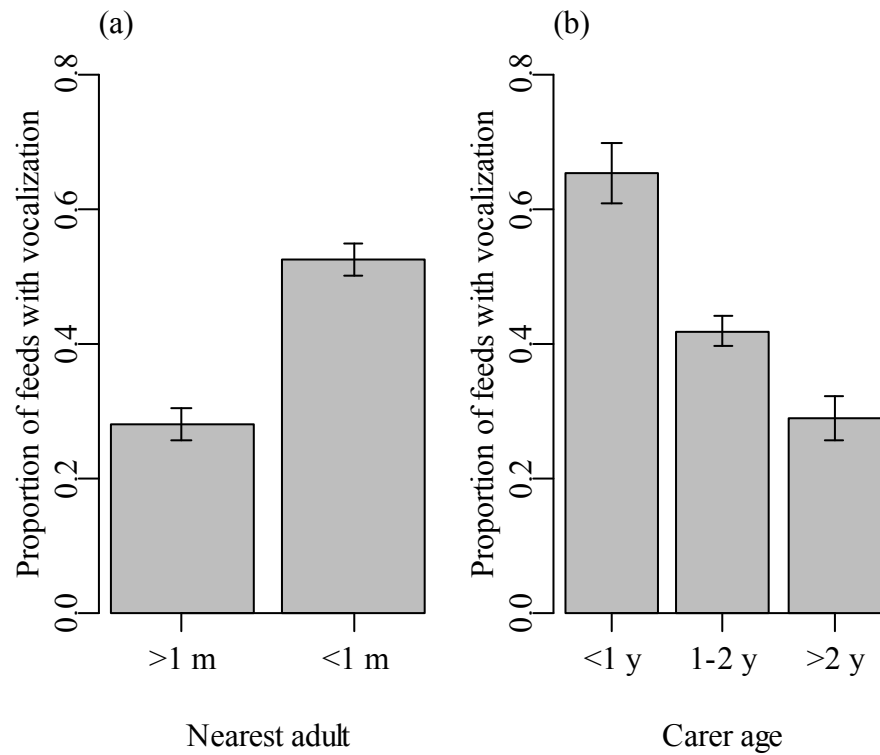
Figure 7.5 The proportion of feeds accompanied by a vocalization from the carer (a) increased if the nearest adult was <1 m from the pup being fed, and (b) decreased with age of carer bringing the food item.
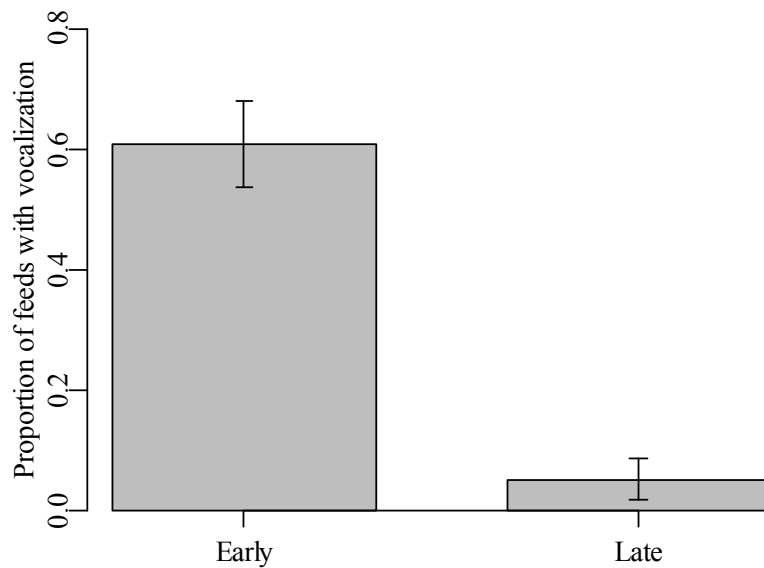
Figure 7.6 Proportion of feeds accompanied by a vocalization during experimental feeding of adults with scorpions, during early and late periods of pup-provisioning.

7.5 DISCUSSION

In this chapter, I investigated the extent to which carers modified their foraging behaviour and vocalizations when followed by begging pups. In general, the presence of pups did not have any measurable effect on the foraging behaviour of carers, either when comparing their behaviour within and outside the breeding season, or when considering the shorter timescale of when they were followed by a begging pup or not. In contrast, carers modified their vocalizations according to the presence or absence of pups (Manser, 1998) and, in this study, proximity to pups. Finally, feeding calls were more likely to be given to younger pups and those within 1 m of another adult, hence potentially serving to reduce the likelihood of the prey item being stolen by another adult in the vicinity.

I had predicted that carers would increase their foraging effort to accommodate the costs of feeding young. Carers did not change their foraging behaviour, however, either when pups were in the group or when carers were continuously exposed to begging calls. The lack of effect of pups on carer foraging behaviour may be explained by considering meerkat foraging strategy. Meerkats are opportunistic foragers, searching for subterranean prey using olfactory cues and digging when they have located a potential prey item (Doolan and Macdonald, 1996). Although I had expected carers to spend more time actively digging during the provisioning period or on hearing begging, it is possible that they do not have this flexibility because digging time simply depends on the distribution of prey items in the ground. Instead of increasing foraging effort, carers may spend more time foraging in total, compared to non-foraging behaviours such as resting and playing, when pups are in the group. It was unfeasible to test this possibility by conducting playback experiments when the group was not foraging, however, as pups tended not to beg at this time (personal observation) and the sound of begging from a speaker would seem artificial. The constraint of their foraging system suggests that provisioning pups comes at a high cost to carers, as they cannot compensate by finding more food, and may explain variation in the carer-pup associations between banded mongooses and meerkats. In banded mongooses, which live in tropical areas of high prey abundance, long-term associations between pups and helpers are maintained; whereas

meerkat helpers, foraging in arid environments, do not have the capacity to maintain high generosity and pups therefore switch between helpers (Hodge et al., 2007).

When comparing carers that varied in their contributions to cooperative pup care, I found no evidence that generous individuals changed their foraging behaviour to a greater extent than selfish individuals. In the common guillemot, Thaxter et al. (2009) found that, although nestling provisioning was female-biased, there was no difference between the sexes in their foraging efficiency. I found similar results in meerkats where, although generous helpers provide more food to pups, they do not compensate for this by increasing their foraging effort to a greater extent on hearing begging. In addition, there was no increase in vigilance behaviour during the begging treatment, although generous helpers were more vigilant overall. In chapter 4, I demonstrated that individual differences in vigilance rate when pups were not present in the group were positively correlated with provisioning rate in general. The relationship between vigilance and helping may be explained if vigilance indicates increased levels of anxiety (Rushen, 2000) and more generous individuals have higher levels of stress, which is supported by a recent study where exposure to begging calls raised cortisol levels of male meerkats (Carlson et al., 2006a).

There were striking differences in the rate and type of vocalizations given by carers depending on whether a pup was present within 2 m or not. Manser (1998) found that individuals gave fewer close calls when pups were foraging in the group compared to outside the breeding season. Like Manser (1998), I found that carers gave fewer close calls while social foraging with pups compared to >2 m from the nearest pup. In addition, when I considered the rate at which adults gave joining and lead calls, which Manser (1998) suggested played a role in group movement, I found that carers increased their rate of both types of calls when followed by a pup. Together, these results suggest that social context plays an important role in both the type and frequency of calls given, as has been demonstrated in a number of studies on primate vocal communication (e.g. Harcourt et al., 1993, Palombit, 1992, Slocombe and Zuberbuhler, 2005).

Receiver properties can have a large influence on the characteristics of a signal (Johnstone, 1997) and, here, I discuss how variation in the types of calls given may be explained in terms of whether the carer is signalling to another adult or to a dependent pup. It is important to note that, in contrast to detailed studies on alarm-calling behaviour and offspring vocalizations in meerkats (e.g. Manser, 2001, Manser et al., 2008), there has only been one, unpublished description of carer vocalizations when foraging (Manser, 1998). As such, purported functions of the different types of calls are currently speculative. Close calls have been suggested to regulate distances between foraging members (Manser, 1998), as in other species (Harcourt et al., 1993, Palombit, 1992, Radford, 2004b). As they are primarily directed towards other carers, individuals being followed by a begging pup may replace close calls for call types targeted to pups, such as lead calls. Lead calls have been described as long, tonal calls often given by dominant individuals when mobilizing the foraging group (Manser, 1998), but here similar calls were given by carers when followed by a pup. Pups were not competent at keeping up with the group so these calls may have served to increase offspring mobility, as in pied babblers (Radford and Ridley, 2006, Raihani and Ridley, 2007), although, unlike babblers, lead calls were not associated with the delivery of food in meerkats.

It is difficult to hypothesize why carers give more joining calls in the presence of pups, as little is known about the function of this type of call, which appears to be given when lost individuals have relocated the group or when the group is moving (Manser, 1998). Joining calls are similar in structure to submission calls given by subordinate individuals in the presence of more dominant individuals (pers. obs.), and may therefore indicate stress. The structure of vocalizations can often indicate underlying endocrinological state, as has been extensively studied in the context of song structure in passerines (Marler et al., 1988, Galeotti et al., 1997). Results from work currently underway to investigate the hormonal correlates of meerkat vocalizations will help explore this possibility (S. Townsend & M. Manser, pers. comm.). In addition, although comparison of vocalization rates was paired within carers to account for individual differences (owing to small sample size), future work could investigate whether more generous helpers give a higher frequency of lead or joining calls in the presence of pups, particularly in the light of a

recent study demonstrating that pups follow more generous helpers (Madden et al., 2009).

Adults occasionally gave quiet vocalizations while provisioning young with prey and here I show that they were more likely to give these calls when pups were younger, if another adult was within 1 m of the pup being fed or if the carer providing food was less than one year of age. The effect of pup age was evident in both observational data and an experiment where adults were provisioned with standardized prey at two stages of the pup-feeding period. Previous studies investigating vocalizations by adult birds feeding chicks at the nest have demonstrated that food-associated calls are more frequent when chicks are younger (Clemmons, 1995b, Leonard et al., 1997), hence supporting the idea that these calls serve to draw the attention of young to food at an age when they are less responsive to the presence of the carer. While it would have been interesting to investigate offspring responsiveness to the feeding call (as in Clemmons, 1995a, Leonard et al., 1997, Madden et al., 2005, Raihani and Ridley, 2007), a pilot experiment was discontinued as pups were highly unresponsive to the sound of vocalizations from a loudspeaker, indicating that they relied strongly on the visual stimulus of the adult.

I had predicted that feeding calls may perform a function in the development of foraging skills in young meerkats. Recently, Thornton and McAuliffe (2006) demonstrated that meerkats teach young individuals prey-handling skills: as pups get older, carers gradually introduce them to live prey, which older pups are in turn less likely to lose. In golden lion tamarins, food-offering calls have been suggested to play a role in the development of foraging skills, as adults are more likely to vocalize when provisioning live prey (Rapaport, 2006). I did not, however, find any effect of prey mobility on the probability that a feeding call was given, which indicates that these vocalizations may not play a role in teaching of prey-handling skills in meerkats. Instead, the fact that these low-amplitude vocalizations are more likely to be produced if another adult was present within 1 m of the pup being fed indicates that they may play a role in drawing the attention of a naïve pup to a prey item before it gets stolen by a nearby adult. To my knowledge, there has been little investigation of kleptoparasitism by other adults of food provided to young in

cooperative breeders, and the role of feeding calls in reducing this behaviour merits further exploration.

To conclude, while several studies have demonstrated that parents respond to begging by increasing the amount of food delivered, few studies have investigated how parents alter their behaviour to achieve this. Here I found that meerkat carers do not compensate for giving food to pups by increasing the amount of food found, which underlines the cost of helping in this system. In contrast, there were striking differences in the vocalizations produced by carers when followed by begging young, which indicates the importance of social context on vocal communication. Finally, I suggest that feeding calls play a role in increasing the efficiency of food transfer to naïve young. Investigating the influence of attendant, begging young on adult behaviour and vocalizations, particularly in species with mobile begging young following adults, can help broaden our understanding of the costs of caring for young and the complexities of adult-offspring communication.

8 • GENERAL DISCUSSION

8.1 Overview

In virtually all cooperative species, there are large individual differences in cooperative behaviour, the causes and consequences of which remain poorly understood despite thirty years of research on the evolution of cooperation (Komdeur, 2006). In this dissertation, I investigated the causes of individual variation in cooperative offspring care in meerkats and its consequences for carer-offspring communication. My primary aims were to determine, first, whether individual variation in cooperative behaviour was consistent over time and across different types of cooperation (chapter 3); second, whether individual variation in cooperative behaviour could be explained by behaviour in other contexts or experiences in early life (chapters 4 and 5); and, third, the way in which the presence of pups influenced the cooperative behaviour of adults (chapters 6 and 7). In this chapter, I discuss the implications of my findings while offering suggestions for further work.

8.2 Individual variation in cooperative behaviour: consistency over time and correlations across contexts

There is growing recognition that behavioural variation is not always plastic but may be consistent within individuals and constrained across contexts (Wilson, 1998, Sih et al., 2004a). As natural selection acts on variation in behaviour, understanding the causes and consequences of limited behavioural plasticity is important in studies of ecology and evolution. In meerkats, individuals differed from one another in their contributions to babysitting and provisioning, and these differences were consistent over time (chapter 3). Babysitting and provisioning were positively correlated within individuals (chapters 3 and 4), but variation in cooperative offspring care was not strongly correlated with behaviour in other contexts (chapter 4). Individual variation in helping behaviour was negatively correlated with care received when young, in females but not in males (chapter 5). In the introduction to this dissertation, I described how consistent individual differences and correlations across contexts may be explained by considering mechanistic constraints, life-history trajectories or individual specialisation. Here, I will discuss my results in the framework of these potential explanations.

8.2.1 Mechanisms constraining variation in behaviour

Heritability of cooperative behaviour

Underlying genetic variation among individuals may result in consistent individual differences. I found that babysitting and provisioning were repeatable within individuals over the course of their life-time (chapter 3). Under certain circumstances, repeatability can provide an estimate of heritability (Boake, 1989, Dohm, 2002) which may help us understand selection on behavioural traits. Although there is evidence that parental care is heritable (MacColl and Hatchwell), only one study has investigated the heritability of cooperative behaviour, as measured by propensity to help in facultatively cooperative western bluebirds (Charmantier et al., 2007). Using the techniques of quantitative genetics on the meerkat database (Kruuk, 2004), we could extend this research by investigating whether variation in helping behaviour is heritable in an obligate cooperative breeder. Genetic factors could also explain the positive correlation between babysitting and provisioning (chapters 3 and 4), whereby a single gene or set of genes has pleiotropic effects on multiple cooperative behaviours.

Hormonal mechanisms drive correlated traits

Behavioural syndromes, or suites of correlated traits, may be driven by the action of hormones on multiple phenotypic traits (Sih et al., 2004b). Individual differences in babysitting and provisioning were positively correlated (chapters 3 and 4), which could be explained if both types of cooperative behaviour were controlled by the same neuroendocrinological mechanism. Recent studies on meerkats do not support this prediction, however. Neither prolactin nor testosterone were found to be correlated with long-term variation in contributions to either babysitting or provisioning in male meerkats (Carlson et al., 2006a, Carlson et al., 2006b), although short-term changes in prolactin preceded decisions to babysit (Carlson et al., 2006b). Moreover, cortisol levels were positively correlated with provisioning rates but not babysitting effort (Carlson et al., 2006a, Carlson et al., 2006b). Common hormonal mechanisms may instead provide a better explanation for the positive correlation between vigilance rate and provisioning (chapters 4 and 7). Vigilance behaviour may be an indicator of anxiety (Rushen, 2000). Consequently, higher cortisol levels, which underlie increased provisioning rate (Carlson

et al., 2006a), may be associated with increased vigilance behaviour. There is much scope for further work both to elucidate the influence of hormones on suites of behaviour in cooperative breeders and to explain how individual differences in hormonal levels arise and are maintained.

Foraging efficiency and condition

Recent theory has described how variation in state variables, such as energy reserves or body size, can result in consistent individual differences in behaviour (Dall et al., 2004). The repeatability of babysitting and provisioning may therefore be attributed to underlying differences in foraging efficiency and condition, both of which influence cooperative behaviour in meerkats (Clutton-Brock et al., 2000, Clutton-Brock et al., 2001a). The importance of foraging efficiency is further underlined by the finding that provisioning is more repeatable than babysitting (chapter 3) and provisioning is directly linked to foraging ability (a carer needs to find food before deciding whether to feed it to young). Although there were consistent individual differences in foraging effort (chapter 4), however, these differences did not explain variation in cooperative behaviour. As it was not clear how foraging effort related to foraging success, a fruitful avenue for further research would be to quantify the repeatability of growth rates and investigate whether this correlates with individual variation in cooperative behaviour.

8.2.2 Life-history trade-offs and variation in helping

Life-history trade-offs may result in correlations across different behavioural traits and consistent individual differences in a single trait (Stamps, 2007, Wolf et al., 2007). In cooperative breeders, life-history strategies are associated with decisions about whether to remain in the group or disperse, whether or how much to help, and whether to attempt to breed (Russell, 2004), with the relative influence of each option varying across individuals according to factors such as condition in early life (e.g. Russell et al., 2007). There is evidence that trade-offs influence variation in cooperative behaviour in meerkats: males who spend more time prospecting outside the group for reproductive opportunities contribute less to cooperative behaviour (Young et al., 2005). Here, I examined whether the trade-off between current investment in helping and future

reproduction resulted in behavioural syndromes. I had predicted that individuals following a strategy of maximising their chance of future reproduction would help less and take more risks to maximise food intake, given the importance of relative body size in attaining the dominant position (Hodge et al., 2008).

In contrast to previous research demonstrating that life-history strategies result in behavioural syndromes in cichlids (Bergmüller and Taborsky, 2007), I found little evidence for correlations across risk-taking and cooperative behaviour in meerkats (chapter 4). This suggests that risk-taking and cooperative behaviour may be governed by independent mechanisms. Instead, life-history strategies may result in correlations between cooperative behaviour and aggression, which could be explored in future work. Several studies in non-cooperative species have demonstrated that individual differences in aggression are consistent over time and correlated with behaviour in other contexts (e.g. Bell, 2005, Garamszegi et al., 2009). Within meerkat groups, there is striking aggression directed from dominant individuals toward same-sex individuals (Clutton-Brock et al., 2005, Kutsukake and Clutton-Brock, 2006a, Kutsukake and Clutton-Brock, 2008), which can serve to suppress reproduction by subordinate females (Young et al., 2006). It is not yet known, however, whether individual differences in aggression among dominant individuals are consistent and the extent to which they correlate with their contributions to cooperative behaviour prior to attaining dominance.

The trade-off between allocating resources to helping other individuals' offspring versus saving resources for future direct reproduction may explain why females raised in larger groups reduce their contributions to helping (chapter 5). Hodge (2007) suggested that male-biased care in banded mongooses could be explained by the trade-off between helping and reproductive success. Young males rarely gained access to reproductive females and instead maximised net inclusive fitness by caring for young, whereas females helped less to maintain condition for reproduction (Hodge, 2007). Similarly, maintaining good body condition is important for female meerkats, as females compete intensely for access to the breeding position and success partly depends on body size relative to other same-aged females in the group (Clutton-Brock et al., 2006). Given that

helper-mediated weight in early life influences later breeding success (Russell et al., 2007), females born into larger groups may reduce their cooperative behaviour to maintain body condition and increase their chance of successfully attaining the dominant position. The influence of future fitness on variation in helping has been best explored in primitively social wasp societies (Cant and Field, 2001, Field and Cant, 2006), where experimentally increasing an individual's position in the breeding queue results in a concomitant decrease in its helping behaviour. These ideas could be further tested in meerkats, by manipulating a female's likely chance of becoming dominant (for example, through long-term feeding experiments to manipulate the body size of females from the same litter) and measuring any changes in cooperative behaviour.

8.2.3 Individual specialisation and group composition

Investigating correlations across different types of cooperative behaviour can indicate whether individuals specialise in particular roles within a social group. For example, in noisy miners, individuals which contribute more to provisioning chicks exhibited reduced mobbing effort (Arnold et al., 2005) and cichlids which defend the territory more spent less time maintaining it (Bergmüller and Taborsky, 2007). In contrast, meerkats do not appear to specialise according to different types of behaviour, and in fact individuals that babysit more are those that contribute more to provisioning (chapters 3 and 4, Clutton-Brock et al., 2003). Positive correlations across helping behaviours are suggestive of 'helping types', with some individuals contributing disproportionately more to cooperative offspring care than others. In banded mongooses, Hodge (2007) found that some males were 'super-helpers' and exhibited disproportionately higher babysitting and provisioning effort than the average level for their sex and age class. The existence of such super-helpers raises questions about why all individuals do not cheat and why selfish individuals are tolerated in the group at all. Although we still do not fully understand the causes of such variation (chapters 4 and 5), we can speculate about the consequences of specialised helper types for group dynamics.

In cooperative breeders that live in stable social groups, such as meerkats, the existence of both consistent individual differences in helping behaviour (chapter 3) and

specialisation of particularly generous or selfish helpers (chapters 3 and 4) may provide some empirical support for models of the evolution of personality based on game theory (Dall et al., 2004). Frequency-dependent selection, in which the success of a particular strategy depends on what the rest of the population is doing, can result in the evolution of stable behavioural types (Dall et al., 2004). A recent model described how consistent individual differences in cooperation can evolve when individuals monitor the cooperative behaviour of others (social awareness), at a cost, and these stable differences in turn select for social awareness (McNamara et al., 2009). While cooperative pup care in meerkats is not strictly comparable to the dyadic games between matched players as described in these models, there is much scope for further theoretical investigation of the causes and consequences of consistent helping behaviour in cooperatively breeding groups.

Specialisation of individuals as being more or less cooperative across a range of behaviours has consequences for the optimal composition of a group. For example, in group-living water striders, groups with a high number of aggressive males have been found to be less successful (Sih and Watters, 2005). This leads to the intriguing possibility that helper number, a common measure for the benefits of cooperative breeding (Ridley, 2007, Russell et al., 2003a), may not be the most sensitive measure for group productivity. Future studies may therefore benefit from considering the specific composition of different types of individuals in the group. If having a particular composition of types of individuals leads to increased reproductive success in a group, there may be selection for breeders to modify group composition in their favour. It may be possible for mothers to adjust the cooperative tendencies of their young (e.g. through pre-natal hormones, Groothuis et al., 2005). Maternal effects have, until recently, been largely overlooked in studies on cooperative breeders (Russell and Lummaa, 2009) but raise the exciting possibility that mothers may predict the future social environment of their offspring and mediate their cooperative behaviour accordingly.

8.3 How the presence of begging pups influences adult behaviour and vocalizations

Variation in investment in young may influence how carers respond to signals of need from dependent offspring, although few studies have explicitly tested variation in responsiveness in cooperative breeders (e.g. Wright and Dingemanse, 1999, McDonald et al., 2009). In meerkats, females were more sensitive than males when exposed to increased begging rate (chapter 6, English et al., 2008), which signals increased hunger state (Manser et al., 2008). Variation in responsiveness to begging is likely to be a result of sex differences in philopatry (Clutton-Brock et al., 2002): female meerkats do not disperse and therefore have more to gain from investing in young, both through the direct benefits of group augmentation and by recruiting helpers for future direct breeding attempts (Clutton-Brock et al., 2002).

Increased generosity towards pups comes at a cost to carers, as they do not compensate for giving away more food to young by finding more food. Three different comparisons support this conclusion: carers do not find more food when exposed to high-rate begging compared to low-rate begging (chapter 6), when exposed to begging compared to background noise (chapter 7) or when foraging in groups with attendant begging pups compared to outside the breeding season (chapter 7). This suggests that the foraging strategy of meerkats is such that they cannot increase their foraging effort to accommodate the cost of feeding young, and may explain differences in carer-pup associations between meerkats and banded mongooses. In banded mongooses, which live in tropical areas of high prey abundance, pups form long-term associations with a single carer (Gilchrist, 2004), whereas meerkat pups switch between carers frequently (Hodge et al., 2007). Further work comparing the foraging ecology and costs of cooperative behaviour between these species may shed light on this intriguing difference.

If carers vary in their generosity to young and more generous carers are more responsive to begging, then offspring receive greater payoffs from increased begging rate if they target their begging toward more generous carers (Bell, 2008, Madden et al., 2009). This leads to the question whether offspring actively seek out more generous carers, and, if so, the mechanism by which they choose certain individuals to follow. Meerkat pups spend

more time following generous helpers (Hodge et al., 2007), which indicates that they may discriminate among helpers according to their provisioning rate. Vocalizations produced by carers could play a role in this process, as has been shown in banded mongoose carer-pup associations (Muller and Manser, 2008). Although Madden et al. (2009) found that pups do not discriminate between carers according to their recent history of being fed a prey item, they did not test whether pups are more likely to follow helpers that give more lead calls. In chapter 7, I investigated the vocalizations produced by carers and found that carers produced fewer close calls and more lead and joining calls when followed by begging pups. Owing to small sample size, I did not explore whether more generous helpers were more likely to give lead and joining calls, although this is a potential mechanism by which pups can target more generous helpers.

8.4 How recent statistical developments can inform future work

In this dissertation, I applied multivariate statistical techniques to investigate individual variation in cooperative behaviour, using linear mixed models and generalised linear mixed models with fixed and random effects. Over the three-year period of this study, developments in these techniques have resulted in some controversy and confusion among both statisticians and ecologists (Bolker et al., 2009). There is an increasing call to shift away from typical null hypothesis significance testing, such as the stepwise regression approach used here, and instead to use multi-model averaging (Burnham and Anderson, 2002) or Bayesian inference (Gelman and Hill, 2007), although such approaches are beyond the scope of this dissertation. Future work would benefit from applying such analyses on traditional models on variation in helping behaviour to see whether they are robust to other types of inference.

Most mixed models in the ecological literature, including those presented in this dissertation, generally fit random terms as intercepts rather than slopes, although this may not always be appropriate (Schielzeth and Forstmeier, 2009). Here, I used random intercepts to ask whether individuals were different from one another and consistent within themselves in cooperative behaviour and other traits (chapters 3 and 4). Random slopes models could extend this investigation to determine whether individuals vary in

their plasticity (Nussey et al., 2007, Dingemanse et al., in press). Random slopes models could also be used to investigate whether there are individual differences in the development of cooperative behaviour over age, thus extending the findings of Clutton-Brock et al. (2002) at a finer scale. At the same time, values for cooperative behaviour could be centred within individuals to separate within-subject and between-subject effects (van de Pol and Wright, 2008): for example, to see whether helping increases with age in general across all individuals compared to how it increases within individuals.

8.5 Conclusion

Individual variation in cooperative behaviour is striking yet often disregarded in studies on the evolution of cooperative behaviour. In this dissertation, I examined the extent to which individual variation in meerkats was consistent within individuals, and how it could be explained in terms of behaviour across contexts and by experiences in early life. The study of behaviour should not consider traits in isolation but should take into account other time-points (both early life and future decisions) as well as other contexts. As such, life-history strategies provide an informative framework with which to understand individual variation. By examining the link between carer-offspring communication and variation in helping, I also emphasize how behavioural decisions in a social group can be influenced by the behaviour of other individuals.

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Appendix I

Species common and scientific names

Kingdom Animalia

Phylum Arthropoda

Class Insecta

Order Hymenoptera
Hover wasp (hairy-faced)   *Liostenogaster flavolineata*
Paper wasp   *Polistes dominulus*

Order Hemiptera
Water strider   *Aquarius remigis*

Phylum Chordata

Class Actinopterygii

Order Cichlidae
Cichlid   *Neolamprologus pulcher*

Order Gasterosteiformes
Threespined stickleback   *Gasterosteus aculeatus*

Order Perciformes
Bluegill sunfish   *Lepomis macrochirus*
Peacock wrasse   *Symphodus tinca*
Perch   *Perca fluviatilis*

Class Aves

Order Accipitriformes
Gabar goshawk   *Melierax gabar*
Martial eagle   *Polemaetus bellicosus*
Pale chanting goshawk   *Melierax canorus*
Steppe buzzard   *Buteo vulpinus*
Tawny eagle   *Aquila rapax*

Order Coraciiformes
Laughing kookaburra   *Dacelo novaeguineae*
Yellow-billed hornbill   *Tockus leucomelas*

Order Falconiformes

Lanner falcon	*Falco biarmicus*

Order Passeriformes

Apostlebird	*Struthidea cinerea*
Arabian babbler	*Turdoides squamiceps*
Bell miner	*Manorina melanophrys*
Blue jay	*Cyanocitta cristata*
Carrion crow	*Corvus corone*
Collared flycatcher	*Ficedula albicollis*
Crimson-breasted shrike	*Laniarius atrococcineus*
Dark-eyed junco	*Junco hyemalis*
Fork-tailed drongo	*Dicrurus adsimilis*
Great tit	*Parus major*
House sparrow	*Passer domesticus*
Long-tailed tit	*Aegithalos caudatus*
Noisy miner	*Manorina melanocephala*
Pied babbler	*Turdoides bicolor*
Seychelles warbler	*Acrocephalus sechellensis*
Superb fairy wren	*Malurus cyaneus*
Western bluebird	*Sialia mexicana*
White-winged chough	*Corcorax melanorhamphos*

Order Piciformes

Acorn woodpecker	*Melanerpes formicivorus*

Order Strigiformes

Tawny owl	*Strix aluco*

Class Mammalia

Order Artiodactyla

Bighorn sheep	*Ovis canadensis*
Blue wildebeest	*Connochaetes taurinus*
Common eland	*Taurotragus oryx*
Gemsbok	*Oryx gazella*
Red deer	*Cervus elaphus*
Springbok	*Antidorcas marsupialis*

Order Carnivora

African wild cat	*Felis silvestris lybica*
Banded mongoose	*Mungos mungo*
Bat-eared fox	*Otocyon megalotis*

Cape fox	*Vulpes chama*
Caracal	*Caracal caracal*
Domestic dog	*Canis lupus familiaris*
Dwarf mongoose	*Helogale parvula*
Meerkat	*Suricata suricatta*
Slender mongoose	*Galerella sanguinea*

Order Primates

Golden lion tamarin	*Leontopithecus rosalia*
Rhesus Macaque	*Macaca mulatta*

Order Rodentia

Brown rat	*Rattus norvegicus*
Cape ground squirrel	*Xerus inauris*
Eastern chipmunk	*Tamias striatus*
House mouse	*Mus musculus*
Naked mole-rat	*Heterocephalus glaber*
Red squirrel	*Tamiasciurus hudsonicus*

Class Reptilia

Order Squamata

Mole snake	*Pseudaspis cana*
Puff adder	*Bitis arietans*
Water python	*Liasis fuscus*

Class Sauropsida

Order Squamata

Cape cobra	*Naja nivea*

Kingdom Plantae

Phylum Magnoliophyta

Class Magnoliopsida

Order Capparales

Shepherd's tree	*Boscia albitrunca*

Order Fabales

Blackthorn	*Acacia mellifera*
Camelthorn	*Acacia erioloba*

Order Lamiales
Drie doring   *Rhigozum trichotomum*

Order Malvales
Raisin bush   *Grewia flava*

Order Poales
Kalahari sourgrass   *Schmidtia kalahariensis*

Appendix II

Ethogram for foraging focal observations

Behaviour	Description
Searching	Walking around looking for food, scratching at surface
Digging	Actively pursuing prey item
Look up	Vigilant on all fours
Stand up	Vigilant on hind legs
Raised guard	Vigilant from elevated position
Eating	Eating and processing food
Marking	Scent-marking, defecating or urinating
Social digging	Renovating bolt-hole or sleeping burrow
Resting	Resting
Social	Playing or allogrooming
Moving	Running
Groom self	Grooming self
Termite feeding	Eating several tiny items from same patch
Re-foraging	Returning to same hole (or <10 cm)

For all successful foraging bouts, the size of the prey item was recorded relative to an adult's mouth, and estimated mean wet biomass per category (Thornton, 2008a)

Category	How measured	Biomass
Tiny	Swallowed down immediately	0.05
Small	Item not protruding from mouth at all	0.11
Medium	Less than half the item protruding from mouth	0.58
Large	Over half the item protruding from mouth	2.86
Extra-large	80% of the item protruding from mouth	9.56