

CURRENT ISSUES – PERSPECTIVES AND REVIEWS

Variation in Individual Investment Strategies among Social Animals

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Invited Review**Abstract**

Cooperation and conflict are ubiquitous features of life in the vast majority of animals and can occur over a wide range of functional contents and at various levels. In this review I describe known and less well-known proximate aspects of cooperation and conflict over reproductive behaviour in social animals, where individuals other than the genetic parents contribute to the provisioning of care ('alloparental care'). Traditionally the evolution of alloparental care is viewed as a two-step process: the decision to delay dispersal and independent breeding, usually as a consequence of the existence of constraints on independent breeding, and the decision to behave as alloparents by which individuals that have delayed dispersal gain a net fitness benefit. Behavioural ecological theory generally assumes that all individuals are similar in 'make-up' and that life history and behavioural decisions are facultative. However, there is probably more individual variation in the amount and type of social behaviour than originally anticipated. Here, I demonstrate that some of these differences in behaviours are because of environmental factors, which may be associated with 'reaction norms' or the genotype's quantitative phenotypic variation, or which may yield polyethisms. Most evolutionary models of animal cooperation are based on optimality approaches that do not consider individual genetic variation and maternal effects on the variation in the expression of social behaviour. Further research on the genetic basis of cooperations and subordinate–breeder interactions may be crucial for understanding the evolution of social behaviour. If we take individual differences into account our conclusions and explanations of social behaviour may change. Given the conceptual similarities between the various research disciplines addressing different types of cooperation and conflict over investment, the issues described here should lead to more mutual attraction between the different disciplines and stimulate further development in our understanding of cooperation strategies in general.

Introduction – Variability in Cooperation

Cooperation is a ubiquitous feature of life. Individuals cooperate in hunting, feeding, fending off enemies and migrating from one site to another (Wilson

1975; Dugatkin 1997). Many insects, fish, birds and mammals live and breed in colonies, and males and females cooperate in mating and/or care provisioning. But why do animals cooperate? Behavioural ecologists traditionally addressed this question by

studying adaptation and the effects of environment on behaviour and reproductive success. Individuals may cooperate with their relatives to enhance the reproductive output of their kin (e.g. Koenig et al. 1992; Mumme 1992; Emlen 1995, 1997; Russell & Hatchwell 2001; Richardson et al. 2003), and males and females cooperate to raise young in many insect, fish and bird species (Smiseth & Moore 2004; Houston et al. 2005). Furthermore, if the environment is harsh (e.g. extremely cold or hot) and there is high predation risk, then cooperation among conspecifics is expected in order to cope with the environment, food and enemies. Emperor penguins (*Aptenodytes forsteri*) have developed a social behaviour when it gets cold. During extremely low temperatures, they huddle together in groups that may comprise several thousand penguins. That way, most individuals of the group have a part of their body protected and warmed by the other penguins. However, is this cooperation? There is a continual movement of penguins from the outside of the group to the centre thereby displacing the warmer and more protected penguins to the outside where they will take their turn in the worst places against the wind and raw cold (Ancel et al. 1997).

There are, however, differences between individuals, populations and species in the extent of cooperation. These differences are explained in the context of evolutionary theory, which states that individuals are selected for their ability to efficiently translate resources into their survival and reproductive success, maximizing their genetic contribution to future generations (Hamilton 1964; Maynard Smith 1964). Individuals are thus expected to employ a strategy that maximizes their own fitness, even if it leads to a decrease in fitness of their partner or of other group or family members. A conflict over behaviours between individuals occurs if the evolutionary interests of individuals do not coincide. The evolution of investment should be driven by the relative costs and benefits of investment (e.g. Maynard Smith 1977; Clutton-Brock 1991). For example, a conflict over providing parental care to offspring may arise if the relative value of the offspring to the male and female parents varies with confidence of genetic parentage (Westneat & Sherman 1993).

It has been assumed that the differences in behaviours and strategies employed by individuals to maximize their inclusive fitness are largely because of behaviourally plastic responses to the environment (Sih et al. 2004; Pennisi 2005). Despite the fact that genetic variation lies at the heart of evolution-

ary adaptation, we are usually unaware of the genetic mechanisms underlying the strategies we model or study empirically (Grafen 1991). However, recent studies have demonstrated consistent differences in the extent of behaviour towards the same stimuli between individuals belonging to different populations (Taborsky 1994; Gross 1996; Brockmann 2001) and between individuals of the same population (Dingemanse et al. 2003; Drent et al. 2003). In other words, alternative tactics may be exhibited by different types of individuals (genotypes). For example, in great tits (*Parus major*) some individuals are consistently more aggressive (e.g. towards competitors) than others (Drent et al. 2003). Recent study in a range of species revealed a strong genetic component of behaviour (Bakker 1994; Koolhaas et al. 1999; Pervin & John 1999; Insel & Young 2000; Dingemanse et al. 2002; Fitzpatrick et al. 2005; Hammock & Young 2005). Therefore, both the genetic and environmental determination of behaviour should be incorporated as proximate factors for the evolution of life history and behavioural decisions.

In the last decades, theoretical and empirical studies on cooperation and conflict over reproductive allocation have rapidly proliferated and this area is emerging as one of the central importance in behavioural ecology (Krebs & Davies 1997; Bernard 2004). This increased interest in the patterns of reproductive allocation has also been stimulated by advances in molecular ecology. The revolution in molecular biology has generated techniques that have become relatively cheap and easy and are increasingly used by behavioural scientists. Such techniques include DNA fingerprinting, first multilocus minisatellite fingerprinting and later microsatellite fingerprinting, which provided the opportunity to determine parentage and estimate genetic relatedness between individuals. Molecular sex markers provided the ability to determine the sex of adults and offspring at an early stage before external differences have been developed. The field has progressed conceptually as well as empirically, leading to the establishment of new research disciplines as well as to the ability to quantify and evaluate the short-term fitness consequences of reproductive allocation and investment in offspring for the individuals involved. However, a complication in this field is that long-term individual fitness consequences of reproductive investment and allocation are very hard to measure. This is because individuals often disperse outside the study area and are very hard to monitor. Only few studies on resident species have provided adequate long-term data to quantify how current differences

in reproductive allocation translate into changes in future inclusive fitness.

In this review I will argue that individual variation in social behaviour is not always facultative. This insight may have profound consequences for evolutionary explanations of cooperation and conflict behaviours and their resolution. Here, I focus on phenomena of cooperation and conflict over reproductive strategies in social animals, where provisioning of care to young by other individuals than the genetic parents occurs ('alloparental care'; Riedman 1982). Species with alloparental care are particularly good for investigating the proximate and ultimate factors mediating cooperation and conflict over reproductive strategies because many studies on cooperatively breeding animals are sufficiently long-term that they can provide extensive demographic data and knowledge of the key life history parameters affecting the inclusive fitness functions for the breeding parents and alloparents (Stacey & Koenig 1990; Koenig & Dickinson 2004). I begin with a general outline of cooperation and conflict over investment strategies, in which I discuss conceptual similarities between different disciplines addressing various types of cooperation and conflict over investment. I then focus on the proximate and ultimate factors involved in the evolution of alloparental care and in the individual differences in alloparental behaviours. Finally, I outline some of the unresolved issues and suggest future research objectives.

Levels of Cooperation and Conflict

Cooperation and conflict over investment can occur over a wide range of strategies and at various levels. We can differentiate between three levels of cooperation and conflict. (1) *The intersexual level*: sexual conflict assumes interests of male and female differ and may occur at the intersexual level over mating decisions, parentage or parental investment ('sexual conflict'; Trivers 1972). In most socially monogamous species, both males and females contribute substantially to one or more parental activities, such as incubation, nestling feeding or offspring defence. However, the relative contribution by the sexes to these activities varies dramatically both across and even within species (Silver et al. 1985; Clutton-Brock 1991). Asymmetries in investment may arise if the relative value of the brood to the two sexes varies with confidence of genetic parentage (Westneat & Sherman 1993; Whittingham & Dunn 2001; Westneat & Stewart 2003), opportunity to gain additional social mates or extra-pair copulations (West-

neat et al. 1990; Ketterson & Nolan 1994; Magrath & Komdeur 2003), or if the relative costs of providing care differs between the sexes (e.g. the partner with higher reserves to spare providing more care; Barta et al. 2002). (2) *Intergenerational level*: cooperation and conflict may arise between parents and offspring, for example, about the distribution of resources with the parents' optimal division being different from the offspring's optimal division ('parent-offspring conflict', Trivers 1974). Furthermore, cooperation and conflict may also arise over parental investment in own and extra-pair or adopted offspring in socially monogamous species (Westneat & Sherman 1993; Whittingham & Dunn 2001; Westneat & Stewart 2003; Kalmbach 2006). (3) *The intra-group and intergroup level*: in cooperatively breeding species cooperation and conflict may arise over dispersal or helping by subordinates, over the amount of investment in progeny by subordinates or parents of either sex (Emlen et al. 1991; Emlen 1994; Cockburn 1998; Hatchwell & Komdeur 2000), or over the amount of reproduction between same-sex individuals (Johnstone 2000; Magrath et al. 2004).

Conceptual Similarities between Research Traditions

Across species and taxa, the form of reproductive investment differs but can be compared in a meaningful way. When discussing cooperation and conflict over investment strategies, people often think of issues related to cooperatively breeding species, in which individuals live together in family groups on permanent stable territories and where offspring delay dispersal and become helpers-at-the-nest of subsequent broods on their natal territory, even after they are sexually mature (Brown 1987). However, cooperation and conflict over investment strategies can also occur in non-cooperatively breeding species.

Among vertebrates, cooperative breeding is found in at least 3% of bird and mammal species (Brown 1987), with a particularly high frequency of 19% in oscine passerine species (Cockburn 2003), and in some fish species (Taborsky 1994). The reasons for using social animals to address the diversity of types of conflict and cooperation are twofold. First, the recent experimental and theoretical advance in modelling conflicts over reproduction within-group living animals (see review Johnstone 2000) may also refresh our insights into other types of conflicts. To give an example, the likelihood of subordinates to remain in a group is expected to depend on the long-term relative benefits of remaining at home

(e.g. direct reproduction, kin selection) vs. the benefits of dispersal and independent reproduction (Johnstone 2000). These relative benefits may be modified by, for example, the cost of dispersal to other breeding sites or the availability of independent breeding options ('ecological constraints', Emlen 1982; Koenig et al. 1992) or by cooperative or mutualistic benefits of remaining at home ('benefits of philopatry', Stacey & Ligon 1987, 1991; Ekman et al. 2004; 'benefits of group augmentation', Kokko et al. 2001) instead of dispersing. Conceptually this is very similar to understanding if and when parent males should desert their brood in socially monogamous species, depending on the relative benefits of assisting the current female raising the offspring compared with the benefits of attracting secondary females. Again, these relative benefits may be modified by 'ecological constraints' (e.g. risk of dispersal, availability of secondary nesting sites, operational sex ratio) and the cooperative or mutualistic benefits of assisting the current partner compared with single-parents raising offspring after desertion. Thus, a particular type of ecological constraints can elicit a similar response in terms of cooperation and conflict over investment in group living and socially monogamous species. For example, if the costs of dispersal are low, subordinates in group living species may leave their group and disperse successfully to obtain territories and become independent breeders whereas males in socially monogamous species may leave their mate to gain an additional territory and mate. On the other hand, if the costs of dispersal are high, unsuccessful individuals in both systems may be forced to become 'floaters', living in marginal habitats or moving among interstitial spaces between occupied territories until a suitable vacancy can be found. Under such circumstances individuals should remain in the group or with their mate.

Secondly, the issues whether individuals within a conflict can take control over their situation (i.e. are able to dominate other interactants or circumvent domination by others) and whether individuals can 'manipulate' the behaviour of interactant(s) appears crucial in all theoretical and empirical studies of conflict. However, this concept seems to be reinvented for each type of conflict again and again quite independently. For example, the concept of 'power' is important in our understanding of sexual conflict (e.g. whether males can ensure reproductive success via paternity monopolization by mate guarding or sperm competition vs. whether females can circumvent this by extra-pair copulation behaviour, Birkhead & Møller 1998), sibling conflict (e.g. whether

siblings can dominate other siblings vs. whether parents can interfere with sibling competition, Mock & Parker 1997), and within-group conflict (e.g. whether breeders can suppress the reproduction of subordinates vs. whether subordinates can influence dominants to concede reproduction, Beekman et al. 2003). Again, the concept of 'manipulation' appears in the sexual conflict literature (e.g. whether partners will compensate a reduction in care; Houston & Davies 1985; Winkler 1987; Wright & Cuthill 1989; Markman et al. 1995; McNamara et al. 1999; Barta et al. 2002), but likewise it is important for our understanding of parent-offspring and sibling competition (e.g. whether offspring can manipulate their parents to feed them more, Clutton-Brock 1991; Kilner & Johnstone 1997; Mock & Parker 1997; Wright & Leonard 2002), and within-group conflict (e.g. whether dominant breeders can make subordinates to 'pay-to-stay' for continued group membership, Gaston 1978; Taborsky 1984, 1985; Mulder & Langmore 1993; Kokko et al. 2002; Bergmüller & Taborsky 2005).

It should be clear from this discussion that there are conceptual similarities between the different research disciplines addressing various types of cooperation and conflict over investment. Although this review focuses on individual behavioural differences in cooperation and conflict over investment strategies in social animals, the topics discussed here are also relevant for studies addressing cooperation and conflict of investment strategies at other levels. If individual, consistent behavioural differences play a role in one scenario (alloparental care), the consequences are likely to be similar in other scenarios, too.

Proximate and Ultimate factors involved in the Evolution of Alloparental Care

Apart from cooperative breeding systems, alloparental care also occurs in other reproductive systems, including those with social monogamy and biparental care. An example of alloparental care in socially monogamous species is the occurrence of adoptions of unrelated young in birds and mammals (e.g. Riedman 1982; Eadie et al. 1988; Meek & Robertson 1991; Kalmbach 2006) and 'farming-out' in fish, when parents actively donate their young to another brood (e.g. Yanagisawa 1985; Wisenden 1999). The term adoption has been used in different contexts (communal crèching, brood amalgamations), but is generally defined as a form of alloparental care where one or several foreign young permanently

join another brood, and the parents of the original brood exclusively provide all aspects of parental care to these young (Eadie et al. 1988).

At first sight investing resources into non-genetic offspring appears contradictory to the aim of maximizing one's own genetic contribution to future generations, but this paradox can be resolved by studying the costs and benefits of alloparental care for the donors as well as for the recipients. The evolution of cooperative breeding systems with helpers-at-the-nest is usually viewed as a two-step process: first, the decision of grown offspring to delay dispersal and independent breeding by staying at home; and secondly, the decision of those individuals who have stayed at home to become helpers (Emlen 1982; Fig. 1). The first step in this model is usually attributed to the existence of constraints on independent breeding (Emlen 1982; Arnold & Owens 1998; 1999; Hatchwell & Komdeur 2000). The second step of the model envisages that individuals that have delayed dispersal gain a net fitness benefit by helping.

In this section I will discuss some known and less well-known proximate and ultimate factors responsible for the evolution of alloparental care behaviour in general and for the evolution of individual differences in the type and amount of alloparental care behaviour in particular. I discuss the relationships between factors and discuss how these may affect decisions on alloparental care [for a schematic illustration of (potential) determinants of alloparental care behaviour discussed below, see Fig. 1].

Kin selection

Alloparents may accrue indirect fitness benefits through the increased survival and productivity of their relatives (for reviews, see Brown 1987; Emlen 1991; Cockburn 1998; Clutton-Brock 2002; Roulin 2002; Koenig & Dickinson 2004). These indirect or kin-selected benefits are widely regarded as being of fundamental importance in the evolution of cooperative breeding systems (Emlen 1997), but such benefits can be accrued only if helpers assist their relatives. As a consequence, the ability to discriminate between individuals or groups of individuals plays a major role in the evolution of social behaviour. In societies where offspring remain at home and help, kin discrimination may simply come about by associative learning where help is based on the identity of parents as in the Seychelles warbler (*Acrocephalus sechellensis*; Komdeur et al. 2004), or where help is directed towards nest mates present in the same territory, a rule which is ably exploited by

Galápagos mockingbirds (*Nesomimus parvulus*; Curry & Grant 1990) and slave-maker ants, e.g. *Formica subintegra* (Hölldobler & Wilson 1990). However, in societies where subordinates do not remain at home but nevertheless sometimes associate with dominants and help raising their offspring, the ability to recognize kin from non-kin is critical to target kin for providing assistance (Komdeur & Hatchwell 1999). One such model system is the long-tailed tit (*Aegithalos caudatus*). Mature long-tailed tits try to breed independently, but if their brood fails, these failed breeders preferentially select nests of close kin and help them to raise offspring (Russell & Hatchwell 2001). Long-tailed tit chicks learn specific calls from the adults that rear them in the nest and they use this information later to discriminate between kin and non-kin, which enables them to assist in the rearing of a related pair's chicks (Sharp et al. 2005).

The importance of kin selection as the major driving force behind the evolution of alloparental care has recently been questioned (Emlen 1995, 1997; Cockburn 1998; Dickinson & Hatchwell 2004). The major reasons are threefold. First, several cooperative breeding societies have been described where subordinates do not appear to provide help (Cockburn 1998). Secondly, in some societies subordinates gain direct fitness benefits, e.g. through inheritance of a territory or shared reproduction (Arnold & Owens 1998; Vehrencamp & Quinn 2004). Thirdly, in several societies subordinates preferentially help unrelated dominants raising offspring (Reyer 1980; Clarke 1989; Sherley 1990), or parents provide all aspects of parental care to their own young as well as to several foreign young, which permanently joined the brood (Riedman 1982; Yanagisawa 1985; Eadie et al. 1988; Meek & Robertson 1991; Wisenden 1999; Kalmbach 2006), or subordinates (temporarily) leave groups to join other, unrelated groups and become helpers there (Rood 1990; Creel & Creel 2002; Stiver et al. 2004).

Individual Differences in Helping Behaviour

In some studies where subordinates do not appear to provide help, subordinates might have been wrongly categorized as non-helpers. This is because subordinates can participate in different types of helping behaviour, ranging from nest building, offspring provisioning to predator defence (Heinsohn 2004), and most studies have focused solely on subordinate offspring provisioning and ignored other types of subordinate investments, such as sentinel or mobbing behaviours. In some cooperatively breeding systems

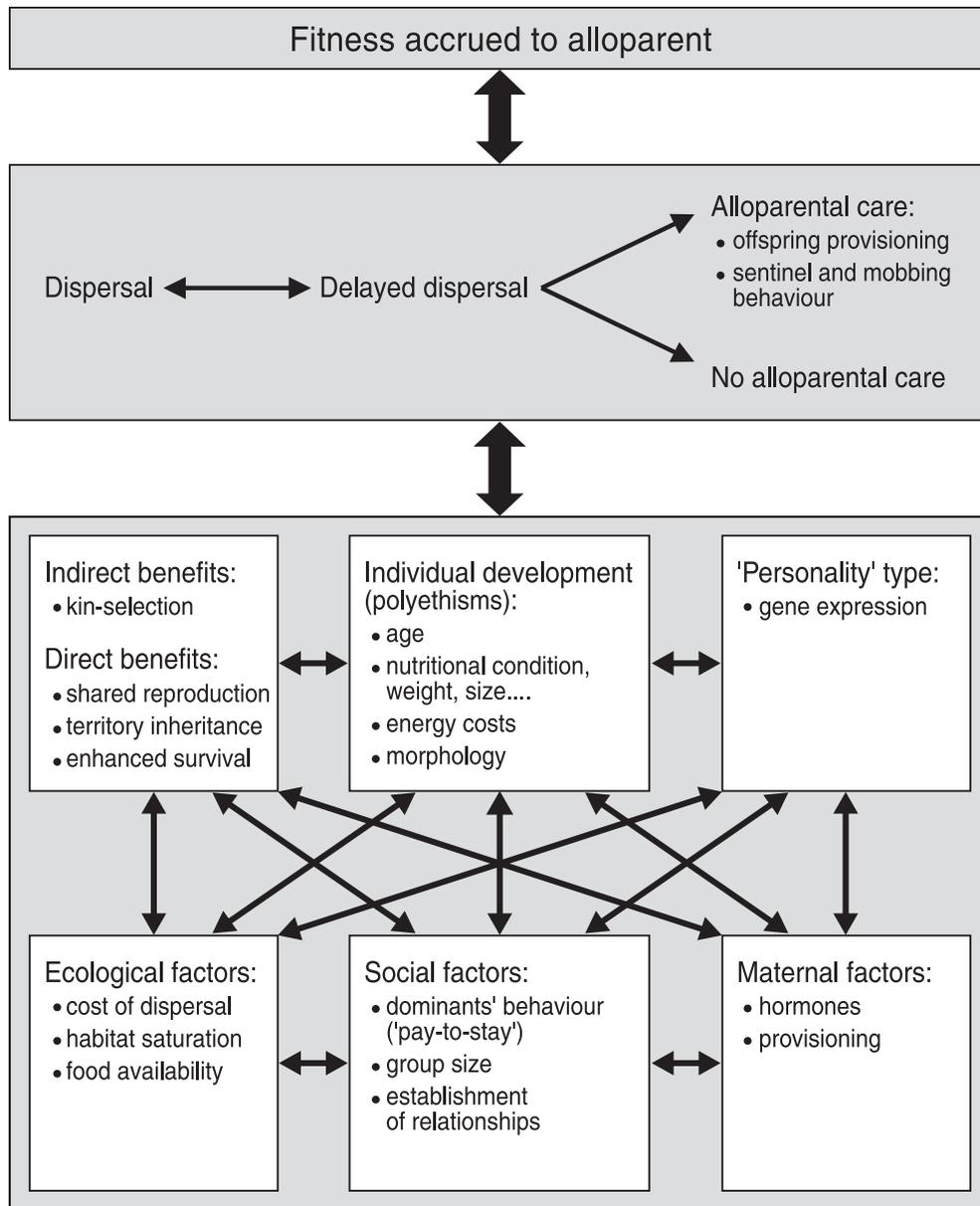


Fig. 1: Schematic illustration of some components of the evolution of alloparental care and interactions between them (arrows depict interactions)

individuals presumed to be non-helpers are not as uncooperative as they appear. For example, in the cooperatively breeding noisy miner (*Manorina melanoccephala*) a considerable number of subordinates that were never seen to provision the young, did help intensively with predator mobbing. Furthermore, bad provisioners contributed more to mobbing than good provisioners (Arnold et al. 2005). In blue jays (*Cyanocitta cristata*), laboratory tests have shown that some individuals were consistently more cooperative for mutual gain in food than others

(Stephens et al. 2002). Social groups can thus be made up of individuals who specialize in certain helping behaviours or those who perform a number of behaviours to differing degrees. So far, division of labour among members of cooperatively breeding groups has mainly been studied in eusocial insects, where individuals often show morphological differentiation into separate castes associated with extreme specialization for particular tasks (Wilson 1971; Schmid-Hempel 1990; Keller & Vargo 1993; Bourke & Franks 1995; Calderone 1995; Traniello &

Rosengaus 1997). Among cooperatively breeding vertebrates, morphological differences that are not a consequence of differences in age are unusual between breeders and helpers, as well as between helpers (Brown 1987; Solomon & French 1997). In vertebrates, the only known example of morphological specialization for a specific role comes from the naked-mole-rats (*Heterocephalus glaber*), where complete physical dimorphism has evolved between reproductive females and non-breeding helping females. Dimorphism is a consequence of the lumbar vertebrae lengthening after the onset of reproduction in females (O'Riain et al. 2000). However, division of labour in cooperative animals can arise even in the absence of extreme specialization (Lacey & Sherman 1990, 1997; Heinsohn & Cockburn 1994; Clutton-Brock et al. 2003; Stiver et al. 2005; Arnold et al. 2005; Heg et al. 2005), and therefore may be an important aspect of alloparental care behaviour in vertebrate societies too. An individual may show consistent propensities for performing specific alloparental behaviours. Such consistent individual differences in helping are suggestive of behavioural syndromes, or 'personality types', based on underlying endocrinal or physiological mechanisms (Sih et al. 2004), and thus might represent alternative strategies of subordinates to optimize lifetime fitness. However, one should bear in mind that if there is evidence for individual consistency in the performance of a specific behaviour, this does not necessarily mean that there is evidence for a genetic basis of behaviour. On the other hand, apparent lack of consistency in behaviour does not preclude a strong genetic component in the parameters of the reaction norms of different individuals. In other words all individuals may show variability in helping behaviour under different circumstances, but the propensity to help under each state, or the threshold for help, may be determined mainly by the genes.

Recent study in a range of species revealed a strong genetic component of behaviour (Bakker 1994; Koolhaas et al. 1999; Pervin & John 1999; Insel & Young 2000; Dingemanse et al. 2002; Fitzpatrick et al. 2005; Hammock & Young 2005). It has been shown that in *Microtus* voles the length polymorphisms in the regulatory regions of genes have important impact on gene expression and thereby on the expression of social behaviour variation (Hammock & Young 2005). Voles may show dramatic species differences in social structure. Prairie voles form lifelong attachments with a mate, are biparental, and show high levels of social interest (Getz et al. 1981), whereas the closely related mon-

tane vole does not pair bond, the males do not contribute to parental care, and they are socially indifferent (Jannett 1982). There is now interesting evidence that length polymorphisms in the regulatory regions of genes have important impacts on the expression of genes that affect social behaviour. In male prairie voles, long-allele individuals engaged in social interactions more readily, and generally were more inquisitive about social cues than short-allele individuals. Microsatellite DNA variation not only appears to be a strong correlate of differences in social behaviour among prairie vole males, but also between the species of prairie voles and montane voles (Hammock & Young 2005). It is therefore plausible also that genetic variation will influence individual variation in the propensity to cooperate within species.

Alternatively, the individual differences in the frequency and type of helping behaviour (division of labour) might not be fixed for life, but might be the result of age- and weight-dependent polyethisms (Taborsky & Limberger 1981; Taborsky et al. 1986; Lacey & Sherman 1990, 1997; Von Siemens 1990; Heinsohn & Cockburn 1994; Boland et al. 1997; Clutton-Brock et al. 2000, 2001a, 2003). Table 1 shows examples of species for which there is evidence that the occurrence of individual variability in the amount and type of social behaviour depends on morphological specialization, the condition (weight, nutritional status), size or the age of individuals. For example, in (sub)social spiders the weight of spiders is shown to be a proximate factor influencing dispersal behaviour (e.g. *Celotes terrestris*, Krafft et al. 1986; *Amaurobius ferox*, Kim 2000; *Stegodyphus mimosarum*, Bodasing et al. 2001). In *A. ferox* a lack of prey in the maternal nest decreased body condition and accelerated dispersal behaviour, whereas the addition of prey items increased body condition and lengthened the dispersal period in previous non-fed clutches (Kim 2000). In *S. mimosarum* significantly more spiders left a colony when they were larger (Bodasing et al. 2001). In cooperative cichlids (*Neolamprologus* species; Taborsky & Limberger 1981; Taborsky et al. 1986) and in the naked-mole-rats (Lacey & Sherman 1990, 1997) large helpers contributed more to territory/colony defence and less to brood care and maintaining the breeding shelter/burrow system than small helpers. In meerkats (*Suricata suricatta*), younger helpers contributed more than older animals to pup feeding and social digging than to babysitting or nest guarding (Clutton-Brock et al. 2003). When controlled for the influence of age and weight, the level of contributions that

Table 1: Evidence for morphological specialization, body size, weight and age variation in dispersal behaviour and the amount and type of social behaviour

Species	Factor	Variation in behaviour	Source
Birds			
White-winged chough (<i>Corcorax melanocephalus</i>)	Age	Offspring provisioning	Heinsohn & Cockburn (1994); Boland et al. (1997)
Noisy miner (<i>Manorina melanocephala</i>)	Unknown	Offspring provisioning, mobbing	Arnold et al. (2005)
Blue jay (<i>Cyanocitta cristata</i>)	Unknown	Mutual gain in food	Stephens et al. (2002)
Mammals			
Voles (<i>Microtus</i> sp.)	Gene expression	Parental care	Hammock & Young (2005)
Naked-mole-rat (<i>Heterocephalus glaber</i>)	Size	Brood care, colony defence, maintenance burrow system	Lacey & Sherman (1990, 1997); O'Riain et al. (2000)
Meerkat (<i>Suricata suricatta</i>)	Age	Pup feeding, social digging, nest guarding	Clutton-Brock et al. (2001a,b, 2003)
Fish			
Lake Tanganyika cichlid (<i>Neolamprologus pulcher</i>)	Size	Brood care, territory defence, maintenance breeding shelter	Taborsky & Limberger (1981); Taborsky et al. (1986); Von Siemens (1990)
Lake Tanganyika cichlid (<i>Neolamprologus pulcher</i>)	Size	Dispersal behaviour	Stiver et al. (2004); Bergmüller et al. (2005a)
Invertebrates			
Subsocial spider (<i>Cæloptes terrestris</i> , <i>Ammaurobius ferox</i>)	Weight	Dispersal behaviour	Krafft et al. (1986); Kim (2000)
Social spider (<i>Stegodyphus mimosarum</i>)	Size	Dispersal behaviour	Bodasing et al. (2001)
Social insects	Morphology	Work load	Wilson (1971); Schmid-Hempel (1990)
Honey bee (<i>Apis mellifera</i>)	Morphology	Food provisioning	Calderone (1995)
Ants	Morphology	Food provisioning	Bourke & Franks (1995)
Termites	Morphology, age	Nest construction	Rosengaus & Traniello (1993)
Eusocial insects	Morphology	Reproductive roles	Keller & Vargo (1993)

meerkat helpers made to rearing pups was not significantly correlated with variation in kinship to the litters they were rearing (Clutton-Brock et al. 2001b). In white-winged choughs (*Corcorax melanorhamphos*) the amount of help in large groups increases sharply with age of helpers (Heinsohn & Cockburn 1994).

Distinguishing between certain behaviours and weight- and age-related polyethisms is not easy. For example, in *A. ferox* spiderlings the level of aggression among spiderlings rather than the weight could be a proximate factor influencing dispersal behaviour. This is because the weights of spiderlings and levels of aggression among spiderlings in the maternal web were inversely correlated with the amount of prey in the maternal nest (Kim 2000). On the other hand, supplementary feeding experiments performed in the social spider *S. mimosarum* showed that dispersal is influenced by spider size and not by variability in access to resources and intragroup competition (Bodasing et al. 2001). In cooperative vertebrates, where helpers have not reached adult size, age is likely to affect the overall level of contributions to cooperative activities whether or not specialization occurs (Heinsohn & Cockburn 1994). Furthermore, the type of helping behaviour, too, is likely to change with age, because some activities are more energetically costly than others, and these differences are more likely to translate into larger fitness costs at some stages of life than others (Clutton-Brock et al. 2003). For the same reasons, helpers that vary in weight at a given age might be expected to adjust their overall level of contributions and their relative contributions in relation to the varying costs of cooperative behaviour to their fitness (McNamara & Houston 1992), and empirical studies suggest that this is the case (Boland et al. 1997; Clutton-Brock 1998, 2001b). For example, the amount of help provided per helper may decrease with group size because the cost-benefit ratio of group living increases with group size. On the other hand, the amount of help may also decrease with group size because competition for resources increases with increasing group size and individuals may attain lower weights and lower nutritional reserves to spare for helping activities. One should bear in mind that weight- and age-related transition in helping levels does not preclude the existence of a phenotypic or genetic basis of helping levels. Weight- and age-related transition in helping levels could well be viewed as genetically programmed, phenotypically adjusted, or most likely, a combination of both.

It should be clear from the above examples that attempts to investigate the influence of particular

variables (such as kinship) on individual contributions to social activities need to incorporate genetic factors as proximate factors for the evolution of cooperation.

Ecological Factors

The variation in the expression of helping activities may not only depend on the degree of flexibility in individuals' abilities to execute the helping tasks, but may also depend on ecological factors that constrain individuals from dispersal. The ecological constraints hypothesis proposes that prolonged associations with kin occur when ecological factors cause dispersal costs to be high (Emlen 1994). It is difficult to test the direct role of dispersal costs on the incidence of helping (Brown 1987; Zack 1990). Most studies investigating the factors that set the scene for helping behaviour have suggested ecologically mediated dispersal costs to be the causal factor (Koenig et al. 1992; Emlen 1994). However, most of such studies have been correlational and conducted in typical cooperative breeding systems where dispersal costs and breeding constraints appear to be positively coupled (Pruett-Jones & Lewis 1990; DuPlessis 1992; Komdeur 1992; Walters et al. 1992; Heg et al. 2004a). To test whether dispersal costs directly set the scene for helping behaviour, it is essential that direct tests are conducted in both 'typical' and 'atypical' systems. A good example of a study that investigates whether dispersal costs set the scene for helping comes from the atypical cooperatively breeding long-tailed tit. In this species there are no constraints on independent breeding (Hatchwell 1999), but dispersal costs are greater between isolated habitats than within contiguous habitats. The incidence of helping was higher in isolated habitats suggesting dispersal costs set the scene for cooperative breeding in long-tailed tits (Russell 2001).

Social Factors

In species where dominants gain from subordinate helpers and helpers gain from remaining in the group, dominants may make subordinates help to be allowed to stay in the group by which the dominants accrue benefits. Dominants can threaten subordinates with punishment or eviction from the group if subordinates do not help or engage in reproduction. A good example for the occurrence of dominance suppression is the cooperatively breeding Lake Tanganyika cichlid *N. pulcher*. In this species helping behaviour is influenced by size differences

between subordinates and dominants (Taborsky & Limberger 1981). Prolonged group membership provides substantial survival benefits to subordinate *N. pulcher* (Taborsky 1984), particularly if they live in groups protected by a large number of adults (Heg et al. 2004a). Reproductively mature subordinates invested more in helping and submissive behaviour towards same sex large breeders than small breeders (Hamilton et al. 2005). Help may serve as payment to the breeders to stay inside the group, as helpers received reduced aggression if they provided more help (Bergmüller & Taborsky 2005). Given that submissive and helping behaviour is energetically costly (Grantner & Taborsky 1998), subordinates may restrain their own growth to avoid running the risk of harassment and expulsion by dominants (Heg et al. 2004b; Skubic et al. 2004). On the other hand, in situations where dominants gain from helping whereas subordinates do not gain from helping, dominants may offer reproductive staying incentives to subordinates who might otherwise do better to leave (e.g. Emlen & Vehrencamp 1983; Vehrencamp 1983). However, in many vertebrate societies dominant individuals do not have full control of subordinate helping and reproduction (Clutton-Brock 1998; Reeve et al. 1998; Dierkes et al. 1999; Clutton-Brock et al. 2001b; Beekman et al. 2003; Hager & Johnstone 2004; Langer et al. 2004; Skubic et al. 2004). This suggests that reproductive sharing is the outcome of within-group conflict over reproduction, which is likely to occur when subordinate helpers increase their fitness by becoming reproductives themselves within groups at a cost to the fitness of the dominant. Lack of dominant control might be due to high costs to the dominants of exerting such control or lack of abilities that are needed to apply control (e.g. egg recognition capacity).

Variation in the expression of helping may also depend on group size. If individuals survive or reproduce better in large groups, cooperative behaviour can be explained by group augmentation (Brown 1987; Kokko et al. 2001; Clutton-Brock 2002). In this case, individuals benefit from raising new group members even if these are unrelated (Kokko et al. 2001). On the other hand, with an increasing number of subordinates in the group, the fitness yield of helping per subordinate may decline, and for some subordinates the option of stopping helping and dispersing may probably prove more successful. An experimental reduction of group size in the field of the cichlid fish *N. pulcher*, resulted in increased brood care effort by small helpers, but not by large helpers (Brouwer et al. 2005). It has been

suggested that in small, generally young helpers, kin selection may be an important evolutionary cause of cooperation in this species (Taborsky 1984). Large helpers, however, who are generally older and less related to the breeders than small helpers (Dierkes et al. 2005) are suggested to pay to be allowed to stay in the territory by helping (Taborsky 1985; Balshine-Earn et al. 1998; Bergmüller et al. 2005a) and they do not need to increase their amount of help when living in smaller groups (Brouwer et al. 2005).

In some societies unrelated subordinates invest in costly help to avoid being evicted from groups by the breeders (the 'pay-to-stay' hypothesis; Gaston 1978). A theoretical study demonstrated that in such systems the threat of eviction alone is sufficient to enforce helping (Hamilton & Taborsky 2005). However, helping will only be favoured if helpers do impose costs on breeders. Helpers may have some control over the costs of eviction for breeders. If breeders are confined to a territory, they cannot easily move away from costly subordinates, and whether a subordinate leaves is, at least in part, its own decision. An obstinate subordinate may impose higher eviction costs, and thus such an individual may be more likely to be tolerated. It has been suggested that in such systems the level of help provided by unrelated subordinates should be lower than the costs they impose on breeders when help is payment to avoid eviction. In their model constraints on dispersal and dispersal costs have no effect on the amount of help provided (Hamilton & Taborsky 2005).

Furthermore, less well appreciated has been the role of between-group dispersal and helping in unrelated groups or helping of unrelated individuals. In several societies, subordinates not only maintain social relationships and helping activities towards members of their own group, but also (temporarily) leave groups to join other unrelated nearby groups and become helpers there (Rood 1990; Creel & Creel 2002; Stiver et al. 2004). The goal of helping in such cases may be the establishment of familiarity and social relationships with other individuals (Croft et al. 2004). Subordinates use these neighbouring groups' territories as safe havens when the risk of staying in the home territory increases (Bergmüller et al. 2005b), and may successfully migrate into other groups (Stiver et al. 2004). This suggests subordinates may be prepared to risk expulsion after engaging in reproduction, because other groups are available to disperse to, and they may strategically chose which groups to join and which breeders to help. If dominants gain fitness by accepting addi-

tional helpers, helpers might trade their helping contribution for being accepted in a territory that provides beneficial conditions (Bergmüller et al. 2005b). This is expected in a biological market scenario, which predicts that animals will play off potential partners against each other if they have the opportunity to do so, and by doing so they influence their net gains from cooperation (Noë & Hammerstein 1994, 1995; Noë 2001). This effect was first shown for male baboons forming coalitions to gain access to females (Noë 1990), and has since been corroborated for exchanges of grooming against tolerance and access to babies in several primate species (Barrett & Henzi 2001). The investments and returns in cooperation are not only concerning the tangible rewards that are obtained and eventually split, but also the social dimension. Previous studies were all observational, therefore it is essential to test the biological market paradigm using experiments.

Not only adult subordinates, but also very young individuals may disperse to other groups to get adopted in the group and receive parental care by foster parents. In wild populations, adopters appear to be almost exclusively successful breeders who have young of their own at the time of adoption (McKaye & McKaye 1977; Zicus 1981; Williams 1994; Larsson et al. 1995). This observation has led to the traditional explanation of adoptions as 'reproductive error' due to imprecision of parent-offspring recognition at an early age (Jamieson 1986; Emlen et al. 1991). However, adoptions cannot only be explained by a recognition mistake between parents and offspring (McKaye & Oliver 1980). In several species of geese, for example, adoptions of goslings have been observed throughout the whole brood-rearing period of 2–3 months (Prevett & MacInnes 1980; Choudhury et al. 1993; Williams 1994), whereas individual recognition of own offspring is developed by the age of 10–15 days (Prevett & MacInnes 1980). In general, unrelated young should only be accepted, if the benefits to the own offspring or to the parents outweigh the costs. The fitness consequences and adaptiveness of adoption are little studied and understood (Emlen et al. 1991; Kalmbach et al. 2005; Kalmbach 2006). In colonially nesting birds, which nest very close to each other, last hatched chicks sometimes avoid being harassed by their older siblings by climbing out of their nest to join younger offspring in other nests where they become dominant chicks (Mock 1984; Redendo et al. 1995). Greylag goose (*Anser anser*) goslings chose dominant foster families within a few days after hatching. It pays a gosling to choose the best 'par-

ents', because goslings stay with their parents throughout their first winter and gosling growth and survival increase with dominance of the foster parents (J. Komdeur, M. W. Kleefman, E. Kalmbach & M. J. J. E. Loonen, unpublished data). Geese in general tend to tolerate the integration of unrelated goslings within their own group of offspring, suggesting that not only the goslings, but also the parents may benefit from adoption. Costs of additional offspring should be low in geese, because goslings are not actively fed by their parents (so-called 'shared investment', Lazarus & Inglis 1978). On the plus side, an increase of gosling group size may not only increase the safety of own offspring through for example, predator dilution (Dehn 1990), but also the company of a large offspring group may also benefit parents in terms of fewer agonistic interactions, higher chance to win agonistic encounters through active social support and higher food intake when compared with small families in the same situation (Scheiber et al. 2005). In addition, stress, measured by the excretion of corticosterone metabolites, was significantly decreased in large families as an effect of passive social support because of the parents receiving social support from their related and unrelated goslings leading to an increase in dominance and energy balance, and ultimately an increase in residual reproductive value of the parents (Scheiber et al. 2005).

Hormones

Hormones are involved in mediating virtually all aspects of an organism's life and affect functions as reproductive and agonistic behaviours. It is therefore expected that hormones will also regulate various kinds of cooperative and competitive interactions characteristic of social breeding systems (Schoech et al. 2004). Breeding females can create inequalities in their offspring, by producing eggs that differ in the level of nutrients and hormones (e.g. testosterone) that stimulate growth and competitiveness of last hatched chicks (Groothuis et al. 2005). These maternal influences can have profound effects on the offspring's behaviour later in life (Eising et al. 2001).

Within the context of cooperative breeding, several hormones could be involved. For example, the steroid hormone testosterone (T) is essential for mediation of aggression and the maturation of sperm in males (Raouf et al. 1997). T levels, and with that aggression and gonadal maturation in subordinates can be kept low due to the presence and behaviours of dominants, and this might result in the failure of a subordinate to express sexual behaviours. Cortico-

sterone is secreted in response to stressful stimuli in order to cope with stress (Wingfield 1988; Moore et al. 1991). While corticosterone is essential in facilitating responses to environmental challenges, it could cause an animal to shift from reproductive to survival effort. Elevated corticosterone levels in birds can result in incomplete gonadal developments (Moore & Zoeller 1985). Within the context of social breeding, corticosterone could be elevated in response to dominant–subordinate interactions by which non-breeding helpers may remain reproductively inactive (Reyer et al. 1986; Wingfield et al. 1991; Schoech et al. 1997). Examination of corticosterone and testosterone levels might, therefore, reveal a mechanism whereby reproductive quiescence is enforced upon non-breeders. Another hormone that has stimulated interest in the context of cooperative breeding is prolactin. Given the role of prolactin in multiple aspects of parental behaviour (Buntin 1996), it could well be that prolactin has a function in mediating alloparental or helping behaviours.

As with genetic causation it is also likely that variation of hormone levels will influence individual variation in the propensity to cooperate within species. For example, the influence of testosterone can vary markedly between individuals. In the cooperatively breeding superb fairy-wren (*Malurus cyaneus*), males were shown to maintain high levels of testosterone throughout the breeding season, but still provide substantial care for their broods (Peters 2001). Nevertheless, experimental elevation of testosterone, within the natural range, resulted in a marked decline in provisioning rate (Peters et al. 2002). It seems that male fairy-wrens maintain testosterone at individually optimal levels that do not interfere with parental duties, but which enable them to continue pursuing extra-pair copulations, the primary avenue for paternity in this species (Peters et al. 2002). The major difficulty that makes drawing conclusions difficult is that most of the research on endocrinology and cooperative behaviour carried out to date is correlational. Experimental manipulations in social species are needed before one can conclude that a given hormone causes a behavioural response.

Implications and Recommendations

In this review I described and discussed empirical studies to identify the proximate and ultimate causes underlying individual differences in animal cooperation and social breeding in particular, and their evolutionary consequences. The bottom line is that

we now have more questions, and fewer answers, to the central questions in the field of social breeding systems than we had a decade ago. There is probably a lot more individual variation in the amount and type of social behaviour performed than originally anticipated. Some of these differences in behaviours are due to environmental factors, which may be associated with ‘reaction norms’ and/or the genotype’s quantitative phenotypic variation, or to environmental factors that may yield polyethisms. However, in either case it is unlikely that these differences in social behaviour are entirely due to plastic behavioural responses to the environment. The ‘switch’ mechanism between different types of social behaviour is thought to be genetically or maternally (hormonally) regulated.

Empirical studies are needed to investigate the genetic and maternal bases of social behaviour and the role of development of social behaviour. Parameter estimation should be conducted using ‘animal models’ (Lynch & Walsh 1998; MacColl & Hatchwell 2003) and should be assisted by experiments. Given that much behaviour is dependent on environmental factors, behaviours of cross-fostered young (raised in non-natal territories) should be compared with behaviours of control young (raised in natal territories). More studies are needed on how genetic variation will influence individual variability in the propensity to cooperate within- and between-species. Variation in cooperative behaviour may also be determined by developmental and maternal effects. Endocrine studies of cooperative breeding are rare (Schoech et al. 2004), and more (viz. experimental) research into hormonal mechanisms responsible for variation in cooperative behaviours is necessary.

Most evolutionary models of animal cooperation are based on optimality approaches that do not consider the influence of individual genetic variation and maternal effects on the variation in the expression of social behaviour. In contrast, behavioural ecological models in general do consider genetic variability as a source of variation in behaviour among individuals. For example, a co-evolutionary model of parent–offspring conflict has demonstrated an environmental and a genetic basis of this conflict (Kölliker & Richner 2001). New theoretical models are needed to incorporate the additional features of genetic and maternal components to understand the evolution of alloparental care and advanced sociality. However, some theoretical models did consider genetic variability as a source of variation in social behaviour among individuals, and demonstrated that genetic variability of cooperative behaviour might

explain some variation in help by different stages along a dynamic equilibrium of genetic cooperators, discriminators and defectors (e.g. Nowak & Sigmund 2000). Further theoretical and empirical research is needed on the genetic bases of cooperation and subordinate–breeder interactions for a better understanding of the evolution of social behaviour.

If we take individual differences into account our explanation of social behaviour may change. Many ‘condition-dependent’ (phenotypic) strategies can produce consistent variation among individuals as a result of consistent differences in condition. Such consistent variation in condition may be genetic, or because of the individual’s personal history. This is well known in the field of sexual selection, for example, where variation in male display and ornamentation can be very consistent, or even hormonally based, and yet ‘condition-dependent’. Some variation in the propensity to help may be based on similar mechanisms. This implies that consistency should not necessarily be interpreted as the opposite of phenotypic adjustment. If some individuals are predisposed to behave differently than others, we should not necessarily assume that all individuals possess optimized facultative responses. There may be scenarios where selection has not generated an ‘optimal genotype’ underlying certain behaviours because of changing selection pressures or other constraints. If so, this may lead to the exhaustion of genetic variation in social traits. It may be that we shall find a similar situation as with ‘the lek paradox’ (Ritchie 1996): why is their still genetic variation left in populations despite the fact that some individuals perform better than others and there is a genetic component to the underlying traits? Important factors, which may preserve genetic variation in populations, could be frequency-dependent selection (Roff 1996) and environmental heterogeneity (Larsson et al. 1997).

In general, behavioural traits are expected to have intermediate levels of heritability (Stirling et al. 2002). It has been claimed that phenotypic correlations have similar sign and magnitude to the underlying genetic covariances, as might be expected if the identified phenotypic correlations are adaptive (Cheverud 1988; Roff 1996). However, this conclusion is controversial (Willis et al. 1991; Lynch & Walsh 1998). Individual differences in social behaviour need our special attention, which may greatly increase our understanding of variation in helping and ultimately the maintenance of social behaviour (e.g. cooperative breeding and adoption behaviour).

In this review, I have tried to summarize new empirical findings and ideas for future research on cooperation and conflict in animal societies. I hope that this discussion leads to more mutual attraction between the different disciplines addressing various types of cooperation and conflict in animals and that it will promote the development in our understanding of cooperation strategies in general, e.g. how power and manipulation determine the outcome of conflict and who will benefit, whether individuals negotiate about their level of investment and whether this reduces conflict and increases cooperation, and whether individuals punish uncooperative individuals and retaliate upon individuals taking a larger share of the resources than the partner is willing to give. It should also be clear that individual variability in cooperation could be genetically or maternally influenced, and therefore it is important to integrate studies of social behaviour with research on genetics, maternal and ontological influences on behaviour (e.g. the early social environment).

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