Cooperation and conflict over investment strategies in animals

Modern evolutionary theory is based on the idea that individuals are selected for their ability to efficiently translate resources into reproductive success, maximising their genetic contribution to future generations. Individuals are thus expected to exploit the strategy that maximises their own reproductive fitness, and this can often lead to associated decreases in fitness of their partner, and/or of other group or family members. 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 central importance in behavioural ecology (Krebs & Davies, 1997; Barnard, 2004). This increased interest in the patterns of reproductive allocation has been stimulated by advances in two fields. First, 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, which provided the ability to determine parentage and estimate relatedness between individuals, and molecular sex markers, which provided the ability to determine the sex of adults and offspring at an early stage before external differences have developed. Second, in parallel, new concepts were developed, such as inclusive fitness, costs and benefits of behaviour, individual decision making, evolutionarily stable strategies, and female mating preferences. The field has progressed conceptually as well as empirically, leading to the establishment of new research fields as well as to novel ways of analysing new and old data.

A conflict over investment 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). Cooperation and conflicts of this sort can occur over a wide range of investment strategies and at various levels. In this special issue we differentiate between three levels of cooperation and conflict. (i) The inter-sexual level. Sexual conflict may occur over mating

decisions, parentage or parental investment (Trivers, 1972). (ii) The intergenerational level. Cooperation and conflict may arise between parents and offspring about the distribution of resources with the parents' optimal division being different from the offspring's optimal division ('parent-offspring conflict', Trivers, 1974) and over parental investment in own and extra-pair or adopted offspring in socially monogamous species. (iii) The intra and inter-group level. Cooperation and conflict may arise over dispersal or helping by subordinates in cooperatively breeding species, over the amount of parental investment by subordinates or parents of either sex, or over the amount of reproduction between same-sex individuals in breeding groups of cooperatively breeding species.

The goal of this special issue is to discuss cooperation and conflicts over these three levels of investment strategies, and the ultimate and proximate factors involved for the different kinds of conflicts. The reasons for drawing together studies addressing such a wide diversity of types of conflicts 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) versus the benefits of dispersal and independent reproduction (Johnstone, 2000). These relative benefits may be modified by, for example, the availability of independent breeding options ('ecological constraints': Emlen, 1982) or by cooperative or mutualistic benefits of remaining at home ('benefits of philopatry': Stacey & Ligon, 1991; 'benefits of group augmentation': Kokko et al., 2001) instead of dispersing. Conceptually this is very similar to understanding if and when parent males (or females) should desert their brood, depending on the relative benefits of assisting the current female raising the offspring compared to the benefits of attracting secondary females. Again, these relative benefits may be modified by 'ecological constraints' (e.g., availability of secondary nesting sites, operational sex ratio) and the cooperative or mutualistic benefits of assisting the current female compared to single-parents raising offspring after desertion.

Second, the issue whether individuals within a conflict can take 'power' 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, but 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 guards like mate guarding or sperm competition versus whether females can circumvent these by extra-pair copulation behaviour, Birkhead & Møller, 1998), sibling conflict (e.g., whether siblings can dominate other siblings versus whether parents can interfere with sibling competition, Mock & Parker, 1997), and within-group conflict (e.g., whether breeders can suppress the reproduction of subordinates versus whether subordinates can force 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), 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; Mulder & Langmore, 1993; Kokko et al., 2002; Bergmüller & Taborsky, 2005). We hope this introduction and issue will help to highlight these conceptual similarities and lead to more cross-fertilisation between the various disciplines addressing various types of conflicts. The issue is divided into three sections which correspond with the levels at which cooperation and conflict over investment strategies can occur.

1. Cooperation and conflict over investment strategies at the inter-sexual level

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), and these differences remain poorly understood (Ketterson & Nolan, 1994; Møller, 2000; Balshine-Earn et al., 2002). The evolution of parental care should be driven by the relative

costs and benefits of providing care (Maynard Smith, 1977; Clutton-Brock, 1991). Asymmetries in investment may arise if the relative value of the brood to the two sexes vary with confidence of genetic parentage (Westneat & Sherman, 1993; Whittingham & Dunn, 2001; Westneat & Stewart, 2003), opportunity to gain additional social mates or extra-pair copulations (Westneat 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). Initially, it was assumed that each parent had to choose simultaneously and independently about the amount of parental care to provide (Yamamura & Tsuji, 1993; Balshine-Earn & Earn, 1997; Webb et al., 1999). However, this is unlikely to apply in many breeding systems, where parental care is provided over a prolonged time period and accordingly can be adjusted much more dynamically to, for example, environmental circumstances and contributions by the partner. Thus, some studies suggested that the optimal contribution by one parent should also depend on the level of investment by their partner, with a reduction in effort by one parent often resulting in (partial) compensation by the other (e.g., Houston & Davies, 1985; Winkler, 1987; Wright & Cuthill, 1989; Markman et al., 1995; McNamara et al., 1999).

The papers in this section reflect sexual conflicts over parentage and parental care and their interactions. Bouwman & Komdeur (2005) provide evidence that the occurrence of extra-pair paternity (EPP) in the socially monogamous reed bunting (*Emberiza schoeniclus*) is not likely to be a result of only the female deciding whether or not to engage in extra-pair copulations, but of the interactions between the female, social male and extra-pair male and that the outcome of this interaction is dependent on age and experience. Young males, but not old males, were cuckolded more by old females than by young females. This increase in EPP with female age is not due to an increased capacity of older females to raise a brood without male help, as neither males nor females changed their share in parental care with age, but probably due to older females becoming more experienced at circumventing paternity assurance tactics of young males. Three striking examples of conflict over parental care are presented in various songbird species. In the penduline tit (*Remiz pendulinus*) three patterns of parental care occur, female care, male care, and no care, and there is a major risk involved: bi-parental desertion with the cost of a lost clutch (Persson & Öhrström, 1989). Each sex may mate with up to seven different partners over a breeding season. Since

each of the parents will prefer its mate to face the costs of parental care, a sexual conflict over care arises. Bleeker et al. (2005) provide evidence that male penduline tits perform most of the nest building and that nest building is energetically more demanding than incubation. As a consequence, the body condition of males, but not females, influenced parental care decisions. Males in poor condition may care because incubation is energetically less expensive than nest building, and they cannot afford the energy requirements of building a new nest. Magrath et al. (2005) demonstrate that in the European starling (*Sturnus vulgaris*), females with a more developed brood patch than males are more sensitive and responsive to clutch temperature than males. In experimentally warmed clutches females responded to reduce incubation attendance while males increased attendance to compensate for the reduction by the female. Draganoiu et al. (2005) show that the amount of post-fledging care in black redstarts is closely linked to partial or complete brood desertion. Males are more likely to completely desert the brood during the post-fledging period. They report a close positive association between the relative parental feeding effort and the relative numbers of fledglings exclusively cared for by the male, with brood division more often occurring when both parents have similar feeding contributions. No evidence for bi-parental cooperation determining the amount of post-fledging care provided was found. Intriguingly, an across-species comparison shows no clear correlation between the relative male investment during the nestling phase and the post-fledging phase, suggesting male feeding-contributions during both phases are independently adjusted. The conclusion is that more effort should be made to experimentally disentangle the costs and benefits of shared investment versus (partial) brood desertion, but at the same time we need to keep in mind that this conflict may have different solutions depending on the age of the brood. These studies suggest that the strategy of one of the parents may influence the care decision made by the other parent, and that these are not independent choices of both parents.

2. Cooperation and conflict over investment strategies at the inter-generation level

The provisioning of care to young by other individuals than the genetic parents has been described in many animals and is referred to as alloparental care (Riedman, 1982). Apart from cooperative breeding systems, alloparental care also occurs in socially monogamous species with bi-parental

care, for example adoptions in birds and mammals (e.g., Riedman, 1982; Eadie et al., 1988; Kalmbach et al., 2005) and 'farming-out' in fish (e.g., Wisenden, 1999). At first sight investing resources into non-genetic offspring appears contradictory to the aim of maximising one's genetic contribution to future generations, but this paradox can be resolved by studying the costs and benefits of alloparental care. Unfortunately, the fitness consequences and adaptiveness of these kinds of alloparental care are little studied and understood (Emlen et al., 1991; Kalmbach, in press). In this issue Kalmbach et al. (2005) provides experimental evidence that within a few days after hatching lone goslings of the greylag goose (*Anser anser*) might choose foster families according to quality. Goslings chose dominant families when given the choice between a dominant and a subordinate foster family. The fact that with increasing gosling age foster parents were more aggressive towards lone goslings and less willing to adopt could be due to improved individual recognition and may reflect decreasing benefits of gaining an additional family member, suggesting intergenerational conflict. It may pay in the long-term for a gosling to choose the best parents, because goslings stay with their parents throughout their first winter. Also in this issue, Scheiber et al. (2005) provide experimental evidence that individual greylag geese benefited more when present in large families than in small families in terms of fewer agonistic interactions, higher chance to win agonistic encounters through active social support, and higher food intake, as compared to small families in the same situation. In addition, stress, measured by the excretion of corticosterone metabolites, was significantly decreased in large families as an effect of passive social support. These data may also explain the apparent paradox that geese in general, and greylag geese in particular, tend to tolerate the integration of unrelated goslings within their own group of offspring. In general, unrelated young should only be accepted, if the benefits to the own offspring or the parents outweigh the costs. This indeed seems to be the case. 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 (Dehn, 1990), but the company of a large offspring group may also benefit parents. This may happen due to the parents receiving social support from their related, and unrelated, goslings, leading to a reduction in the number of stressful events, an increase in dominance and energy balance, and ultimately an increase in residual reproductive value of the parents.

3. Cooperation and conflict over investment strategies at the intra- and inter-group level

Cooperative breeding, where subordinates assist others in the rearing of offspring, has stimulated a great deal of research and continues to engender considerable interest among behavioural ecologists (Brown, 1987; Stacey & Koenig, 1990; Jennions & Macdonald, 1994; Emlen, 1995; Cockburn, 1998; Hatchwell & Komdeur, 2000; Koenig & Dickenson, 2004). The importance of kin selection (indirect fitness benefits) driving the evolution of cooperative breeding has recently been questioned (Emlen, 1995; Cockburn, 1998; Dickinson & Hatchwell, 2004). The major reasons are fourfold. First, subordinates do not always provide help (Cockburn, 1998). Second, in several societies subordinates preferentially help unrelated dominants raising offspring (Reyer, 1980; Clarke, 1989; Sherley, 1990). Third, in some societies subordinates are engaged in reproduction by which they gain direct fitness benefits (Arnold & Owens, 1998; Vehrencamp & Quinn, 2004). This either suggests dominants are less able to control reproduction in subordinates than previously thought, or dominants are more willing to concede reproduction to subordinates as an incentive to keep them as helpers. Alternatively, reproductive sharing may be the outcome of within-group conflict over reproduction. Clearly, studies are needed showing whether dominants and/or subordinates can exert direct or indirect control over reproduction ('power'), whether dominants concede reproduction and/or subordinates restrain themselves from doing so, and whether dominants can manipulate the amount of help received by subordinates. Finally, subordinates can leave groups to join other unrelated groups and become helpers there (Rood, 1990; Creel & Creel, 2002). Hitherto, 'ecological constraints' and 'benefits of philopatry' have been major paradigms in our understanding why subordinates remain in groups and do not breed independently (e.g., Koenig et al., 1992; Komdeur, 1992; Emlen, 1994; Heg et al., 2004a), but less well appreciated has been the role of between-group dispersal and helping in unrelated groups. The final papers in this issue are touching on all four major points mentioned above.

First, indirect fitness benefits would be maximized if subordinates preferentially help more closely related kin. 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 and the 'rule-of-thumb' of help directed at nest mates (a rule which is ably exploited by e.g. slave-maker ants, e.g. *Formica subintegra* (Höll-dobler & Wilson, 1990)). However, in societies were subordinates do not, or do not necessarily remain at home, but nevertheless sometimes associate with dominants and help raising offspring, the ability to recognise kin from non-kin becomes critical to target kin for assistance (Komdeur & Hatch-well, 1999). One such a unique model system is provided by the long-tailed tit (*Aegithalos caudatus*). Mature long-tailed tits try to breed independently, but if their brood fails, these failed breeders preferentially seek out nests of close kin and help them to raise offspring (Russell & Hatchwell, 2001). In this issue, Sharp & Hatchwell (2005) show that of some vocalisations in the long-tailed tits the inter-individual variation was significantly greater than the intra-individual variation. This may be used as potential reliable cues to identity, allowing individuals to discriminate between related and unrelated conspecifics and adjust their amount of alloparental care accordingly.

Second, several cooperative breeding societies have been described where subordinates do not appear to provide help. In some of these studies, subordinates might have been wrongly catagorized 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. Alternatively, in some societies helpers might not show active, direct help, but nevertheless increase the fitness of the breeders due to indirect effects like predator dilution. In a study on the cooperatively breeding noisy miner (*Manorina melanocephala*) in this issue, Arnold et al. (2005) demonstrated nicely that individuals presumed to be non-helpers or bad helpers are not uncooperative as they appear. A considerable fraction 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. Social groups can thus be made up from individuals who specialise in certain helping behaviours or who perform a number of behaviours to differing degrees. Such consistent individual differences in helping are suggestive of behavioural syndromes based on e.g. underlying physiological mechanisms (Sih et al., 2004), and thus might represent alternative subordinate strategies to optimize lifetime fitness. Alternatively, these consistent individual

differences might be age-related polyethisms, as occurs in for instance in cooperatively breeding cichlids (Taborsky et al., 1986). Either way, individual differences in helping behaviour need our continued attention and may greatly increase our understanding of variation in helping and ultimately the maintenance of cooperatively breeding societies.

Fitness payoffs are optimized by group members in relation to the survival and productivity advantages of living in a group. In species where dominants gain from helping subordinates and helpers gain from remaining in the group, dominants may make subordinates help to be allowed to stay in the group by which the dominant accrue benefits. On the other hand in situations where dominants gain from helping subordinates and subordinates do not gain from helping, dominants may offer reproductive staying incentives to subordinates who might otherwise do better to leave. A good example for the occurrence of dominance suppression is presented by Hamilton et al. (2005) in the cooperatively breeding African cichlid *Neolamprologus pulcher*. In this species helping behaviour is influenced by size differences between subordinates and dominants. Reproductive mature subordinates invested more in helping and submissive behaviour toward same sex large breeders than small breeders. Given that submissive and helping behaviour is energetically costly (Grantner & Taborsky, 1998), subordinates may restrain their own growth to avoid running the risk of harrassment and expulsion by dominants (Heg et al., 2004b). Help may serve as payment to the breeders to stay inside the group (e.g., Bergmüller & Taborsky, 2005), as helpers received reduced aggressions if they provided more help. Prolonged group membership may provide substantial benefits to the subordinate *N. pulcher*, particularly if they live in groups protected by a large number of adults (Heg et al., 2004a). In this issue, Heg et al. (2005) showed in the field that *N. pulcher* subordinates gain long-term survival benefits from living in groups. Especially smaller subordinates had higher survival if they remained in larger groups and local extinction rates of groups declined significantly with group size.

Third and finally, the amount of dominant control over subordinate activities and group membership is one of the key features of most theoretical frameworks for explaining variation in allocation of activities and reproduction between same-sex individuals living within social groups (Magrath et al., 2004). Dominants can threaten subordinates with punishment and/or eviction from the group if subordinates engage in reproduction. But what if

subordinates have alternatives available beyond independent breeding when they risk expulsion from the group, or what if dominants do not completely control reproduction within groups? The two final papers in this issue provide examples of both. Bergmüller et al. (2005) show that subordinates in *N. pulcher* not only maintain social relationships with members of their own group, but also with members of other groups. Helpers use these neighbouring groups' territories as safe havens when the risk of staying in the home territory increases, and may successfully migrate into other groups (see also Stiver et al., 2004). This suggests subordinates may risk expulsion after engaging in reproduction, because other groups are available to disperse to, and may strategically chose which groups to join and which breeders to help. New theoretical models are needed to incorporate these additional features of group dynamics and their effects on within-group relatedness, reproductive sharing and helping behaviour. An intriguing apparent lack of dominant control is provided by Komdeur (2005) in the Seychelles warbler (*Acrocephalus sechellensis*). Seychelles warbler dominant females do not apply behavioural mechanisms to prevent subordinates from laying in the dominant's nest in situations when suppression of subordinate production would be adaptive. Lack of dominant control might be due to high costs to the dominants of exerting such control or lack of abilities needed to apply control (e.g. egg recognition capacity).

Concluding remarks

In conclusion, the symposium provided a welcome opportunity to discuss the past, present and future of research into investment strategies. The papers contained in this issue summarize some of the highlights of the meeting, including new empirical findings and ideas for new research, and discussions of current controversies and unsolved problems. We hope that the research described in this issue stimulates many further developments in our understanding of investment strategies, e.g. how power and manipulation determine the outcome of conflict and who is to gain, whether individuals are able to negotiate about their level of investment and whether this reduces conflict and increases cooperation, and whether individuals are able to pun-

ish uncooperative individuals and retaliate against individuals taking a larger share of the resources than the partner is willing to give.

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Guest editors

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