CHAPTER 12

Cooperative breeding systems

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12.1 Introduction

Cooperative breeding is a type of social system in which some group members (referred to as 'helpers') routinely provide care for offspring that are not their own, but retain the potential to reproduce themselves either currently or in the future. This broad definition (which derives from those suggested by Cockburn 1998; Crespi and Yanega 1995; Emlen 1991) includes a range of species, from primitively eusocial insects such as paper wasps, hover wasps, halictid bees, and ambrosia beetles; to avian, mammalian, and fish 'helper-at-the-nest' systems in which offspring delay dispersal and help dominant breeders with subsequent breeding attempts; and also larger animal societies with multiple male and female breeders and helpers per group (Fig. 12.1). From current information, 9% of birds (852 species; Cockburn 2006) around 2% of mammals (Lukas and Clutton-Brock in press; Riedman 1982), <0.5% of fishes (20–38 species; Taborsky 1994; Taborsky 2009), and hundreds of species of insect can be classed as cooperative breeders. There are also examples from arachnids (Salomon and Lubin 2007) and crustaceans (Duffy and Macdonald 2010). These societies, while very diverse in terms of social structure and basic biology, share some common features. Populations are usually subdivided into groups of kin (although non-kin individuals may also be present) with strong ecological constraints on dispersal or independent breeding (Hatchwell 2009). Within groups, there is usually (but not always) a reproductive division of labour in which high ranked or socially dominant individuals breed, and lower ranked individuals help (Field and Cant 2009b). Because helpers retain the ability to reproduce themselves, their behaviour reflects a trade-off between current and future fitness, and between direct and indirect components of their inclusive fitness. In this way cooperative breeders differ from eusocial species which have distinct reproductive and worker castes and helpers remain functionally or morphologically sterile throughout their lives (Bourke 2011).

Cooperative breeders have been the focus of intense research in behavioural ecology for two main reasons. First, they embody a major puzzle of evolutionary theory: how can altruistic behaviour be favoured by natural selection? Helpers pay a fitness cost to boost the reproductive output of other group members. For example, subordinate foundresses of the paper wasp Polistes dominulus risk their lives foraging to feed larvae to which they are often unrelated (Leadbeater et al. 2010; Queller et al. 2000). Using the classification of social behaviours introduced by Hamilton (1964), helping is a form of altruism when it involves a lifetime direct fitness cost to the helper, and results in a lifetime direct fitness benefit to the recipient of help. In the case of paper wasps, foraging involves clear fitness costs because foundresses that do more foraging suffer higher mortality (Cant and Field 2001). Cooperative breeding systems provide concrete examples of altruism together with the possibility of measuring the fitness consequences of helping, and hence an opportunity to test evolutionary theories of cooperation.

Second, cooperative breeders have proved to be excellent models for the study of evolutionary conflict and its consequences for behaviour and group dynamics. Evolutionary conflict arises whenever the optimum fitness outcomes for the participants in an interaction cannot all be achieved simultaneously. In the case of cooperative breeders, the role of breeder is usually more profitable (in terms of fitness) than the role of helper, which generates
evolutionary conflict over reproductive roles and shares of reproduction. Conflict arises over helping effort because investment in helping usually trades off against a helper’s own residual reproductive value, so each helper would prefer other group members to invest more. Studies of within-group conflicts in cooperative breeders have provided insights into how groups remain stable despite selection for selfishness, and the ways in which evolutionary conflicts of interest within groups can be resolved on an evolutionary time scale, for example, by the evolution of morphological specialization (Bourke 1999), or fertility schedules which eliminate reproductive overlap within groups (Cant and Johnstone 2008); and also on a behavioural time scale, through mechanisms of ‘negotiation’ (Cant 2011; McNamara et al. 1999). The general principles arising from these studies can help us to understand how conflict is resolved in a range of contexts, such as sexual conflict over mating and conflict between parents (Chapter 9), and between parents and offspring over parental investment (Chapter 7).

The topic of cooperative breeding has been well-reviewed in birds (Cockburn 1998; Hatchwell 2009; Koenig and Dickinson 2004; Stacey and Koenig 1990) and mammals (Russell 2004; Solomon and French 1997). Insect cooperative breeders are usually described as ‘primitively eusocial’ (because they lack sterile castes) and are not usually considered alongside vertebrates, although there are clear similarities between insect and vertebrate systems (Field and Cant 2009a). Here I focus on four questions that are of interest to researchers working on both taxa. First I discuss current understanding of evolutionary routes to cooperative breeding, and the constraints on dispersal that can lead to the formation of cooperative groups. Second, I outline the main hypotheses for the evolution of helping.

Figure 12.1 Examples of cooperative breeding systems. (a) Tropical hover wasps (Stenogastrinae; such as this group of Parischnogaster alternata) breed year round in South East Asia in semi-permanent mud nests. Females mate and either attempt to breed independently or form a strict age-based queue to inherit the position of breeder (Field et al. 2006; Photo by Adam Cronin). (b) A group of cooperatively breeding spiders Stegodyphus dumicola preying upon a cricket. This species forms colonies of tens to hundreds of individuals in which a large proportion of females are non-breeders. These females help by regurgitating food for the offspring of other females, and are eventually consumed by them (Salomon and Lubin 2007; photo by Mor Salomon-Botner). (c) The African cichlid Neolamprologus pulcher forms cooperative groups in which reproduction is monopolized by a single breeding pair. Subordinates delay dispersal and help if there is a shortage of suitable breeding habitat, and prefer to settle with non-kin over kin (Heg et al. 2008; photo by Michael Taborsky). (d) Pied babblers Turdoides squamiceps form cooperative groups of 2–10 individuals in the Kalahari Desert. Helpers engage in sophisticated sentinel behaviour, vocal negotiation over cooperation, and active teaching of fledglings (Raihani and Ridley 2008; photo by Alex Thornton). (e) Banded mongooses Mungos mungo in Uganda live in groups of 8–60 individuals in which multiple females give birth together in each breeding attempt. After pups emerge from the den they form one-to-one relationships with adult ‘escorts’ who guard and provision them (Bell et al. 2010; Cant et al. 2010; photo by the author). (f) Human reproductive life-history is characterized by a short-interbirth interval and long period of offspring dependency (Mace and Sear 2005). Offspring are reliant upon the investment of their parents, grandparents, and older siblings for many years, and are cooperative breeders par excellence (photo of members of the forager-horticulturalist Phari Konwa tribe, India, by Shakti Lamba).
behaviour based on direct and indirect fitness benefits, and assess the evidence for these in insects and vertebrates. I focus in particular on recent developments in kin selection theory which examine the impact of demography on the evolution of social behaviour and life-history in cooperative species. Third, I discuss recent attempts to incorporate behavioural negotiation into evolutionary models of parental care and cooperation. Fourth, I consider reproductive conflicts that arise within groups over helping effort and reproduction, and theory and empirical tests of how evolutionary conflict over reproduction is resolved. Much of this conflict theory applies equally well to non-cooperative species and can be used to derive insights into how within-family conflict over parental care is resolved on evolutionary and behavioural time scales (see also Chapters 7, 8, and 9).

12.2 Routes to cooperative breeding

In most cooperatively breeding fish, birds, and mammals, groups form when offspring delay dispersal and remain on their natal territory to help their parents rear subsequent broods. In birds, 852 out of 9268 bird species for which parental care systems are known or can be inferred are cooperative breeders (Cockburn 2006). Avian cooperative breeders almost always evolved from socially monogamous biparental ancestors, the mating system exhibited by around 80% of extant birds (Cockburn 2006; Cornwallis et al. 2010). The ancestral mating system of mammals is polygyny rather than social monogamy (Clutton-Brock 1989), but recent phylogenetic analysis suggests that most cooperatively breeding mammals evolved from monogamous ancestors (Lukas and Clutton-Brock in press). In both birds and mammals, therefore, monogamy appears to set the stage for the evolution of cooperative breeding.

In many cooperative insect lineages an important precursor to cooperative breeding is the evolution of progressive provisioning, where mothers remain to guard and provision their offspring during development (Field and Brace 2004). Progressive provisioning and extended parental care facilitate the evolution of cooperation because additional helpers can provide insurance against the death of the mother and defend offspring against predators and parasites while mothers forage (Field and Brace 2004; Gadagkar 1990).

In insects two main evolutionary routes to cooperative breeding and eusociality have been proposed. The subsocial route (Wheeler 1928) is similar to that proposed for cooperative vertebrates, namely, that transitions to cooperation occurred through offspring remaining in their natal nest to help their mother (or mother and father, in the case of termites; Korb 2008). The second, semisocial route (Lin and Michener 1972; Michener 1958), suggests that cooperation arose among same-generation females who could gain mutualistic and kin-selected benefits from breeding together. Same-generation associations are commonly seen in some bees, ants, and polistine wasps (Lin and Michener 1972). Phylogenetic analysis suggests that high relatedness as a consequence of monogamy is associated with evolutionary transitions from solitary breeding to cooperative breeding and eusociality in Hymenoptera (Hughes et al. 2008) and in termites (Boomsma 2009). Ancestral monogamy in Hymenoptera has been taken as evidence in support of the subsocial route to cooperative breeding, because in subsocial associations helpers can expect to raise full rather than half siblings, whereas monogamy would appear to offer no clear advantage to sociality via the semisocial route (Boomsma 2009).

These comparative analyses emphasize the importance of kin structure for cooperative transitions, but it is clear that ecological conditions also play a major role in the origin and maintenance of cooperative breeding. In birds, offspring delay dispersal when there is a shortage of suitable breeding habitat (e.g. Komdeur et al. 1995), where there are high indirect or direct fitness benefits of philopatry, for example through inheritance of breeding positions (Dickinson and Hatchwell 2004); and, across species, where ecological environments are temporally variable, since this allows groups to breed in both harsh and benign years (Rubenstein and Lovett 2007). Similar factors may also promote group formation in cooperatively breeding cichlids (Wong and Balshine 2011). In mammals, delayed dispersal of offspring does not appear to be the result of habitat saturation, since vacant habitat
From this brief survey it is clear that multiple factors may contribute to delayed dispersal of offspring and subsequent evolution of cooperative breeding. Monogamy makes the transition to cooperative breeding easier for both insects and vertebrates, and in insects progressive provisioning sets the stage for cooperative breeding because helpers then become particularly useful. In vertebrates, delayed dispersal arises where there is a shortage of suitable habitat or mates or strong barriers to group entry. In insects helpers may do best to remain in their natal group because independent nesting entails high mortality, and in Hymenoptera from a life-history in which solitary breeders have a high chance of dying before their offspring are fully developed. In each case the consequence of constraints on dispersal is a genetically structured population, in which relatedness to local group members is on average greater than relatedness to the breeding population at large (Hatchwell 2010). In the next section I explore how population structure influences selection for any traits that have social effects, such as helping or breeding.

### 12.3 Selection for helping behaviour

 Helpers contribute to the rearing of offspring in a variety of ways: assisting with nest construction, provisioning of offspring, babysitting young, and defence of a nest or territory against conspecifics and predators. These behaviours involve measurable survival costs or costs to attributes which are likely to correlate with direct fitness, such as mating success or condition. A central challenge has been to explain how these behaviours can evolve and persist in populations despite these costs. Selection will favour alleles for helping behaviour only if the fitness costs are offset by benefits either to the helper themselves or to other individuals in which copies of the ‘helping’ alleles reside. This has led to four main hypotheses to explain helping behaviour, the first two of which are usually lumped together as forms of ‘kin selection’: 1) indiscriminate helping may be favoured if dispersal is limited so that the recipients of help are on average more closely related than the population at large (Hamilton 1964); 2) individuals may recognize kin and preferentially direct care towards them (Hamil-
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Figure 12.2  Sweat bees (Halictinae) include both solitary and cooperatively breeding species, and in some species cooperative behaviour varies between populations. Females of Halictus rubicundus dig a nest burrow in spring. In southern Ireland, Halictus rubicundus (Wicklow, Eire) breeds cooperatively. Mated overwintering females dig a burrow nest in spring and produce a first brood of 5–7 offspring which remain to help their mother raise a second, larger brood of reproductives. In Northern Ireland populations (Belfast), nests are started later in spring and only one brood is produced per season, with no helping among offspring. Transplantation of overwintered females to southern and northern latitudes of Great Britain (a) resulted in females switching from cooperative to non-cooperative life-histories (b) and (c). Panel (b) shows the percentage of nests from the cooperative Wicklow population that became cooperative at the source site (SO) and at the site to which they were transplanted (TR). Panel (c) shows the results for the transplant experiment on the Belfast population. Reproduced from Field et al. (2010) with permission from Elsevier.

Given that the great majority of cooperatively breeding species are composed of groups of genetic relatives, mechanisms based on kin selection seem to offer a plausible and general explanation for the evolution of helping behaviour. However, the discovery of hardworking, unrelated helpers in both insect (Leadbeater et al. 2010; Queller et al. 2000) and vertebrate (Clutton-Brock et al. 2000; Reyer 1984) systems indicates that direct fitness benefits or coercion must also be important in maintaining helping behaviour, at least in some systems. Moreover, it is important to remember that the factors that could have initially promoted cooperative breeding may be very different from those that select for cooperative behaviour in extant systems.

12.3.1 Demography and indiscriminate altruism

Altruistic traits can be favoured by natural selection if they satisfy Hamilton’s rule (Hamilton 1964)

\[ r_{xy} B - C > 0 \]  

(12.1)

In which \( C \) is the lifetime direct fitness cost to the focal bearer of a trait; \( B \) is the lifetime direct fitness benefit to social partners resulting from the trait; and \( r_{xy} \) is the coefficient of relatedness of the focal individual \( x \) to its social partner \( y \), that is, their genetic similarity relative to the population mean (Hamilton 1964). Since costs and benefits are defined in terms of lifetime fitness effects, acts which involve immediate costs need not be altruistic. For example, an actor who pays an immediate cost to help another is not behaving altruistically if this cost is repaid later, for example, through reciprocation by the recipient. Failure to consistently
employ Hamilton’s definition of altruism in terms of lifetime fitness effects has caused much misunderstanding in the past, and is one of the sources of confusion underlying recent attacks on Hamilton’s theory (e.g. Nowak et al. 2010; but see Rousset and Lion 2011 for a counter-critique). Note also that a focus on Hamilton’s rule doesn’t mean ignoring the role of ecology in the evolution of cooperation, such as whether animals build a safe nest or live in saturated habitats. Factors such as these can raise the benefits, B, and lower the costs, C, of helping, and thereby favour the evolution of altruism (Alexander et al. 1991).

From the outset Hamilton recognized two distinct ways in which altruism may evolve. First, actors might recognize and preferentially direct help toward their genetic relatives. Second, and more controversially, constraints on dispersal may ensure that actors interact primarily with close kin. The problem with this second mechanism is that limited dispersal (or population ‘viscosity’) increases both average relatedness between social partners and the intensity of local competition for resources or reproductive opportunities. To illustrate, suppose that an actor engages in some behaviour (such as guarding the nest, or provisioning young) which results in b extra offspring for a recipient, at a cost of c fewer offspring for the actor. As a consequence of the act, the overall change in the number of offspring produced locally is (b − c). Will this act be favoured by natural selection? If all these extra offspring disperse away from the patch and compete with unrelated individuals, there are no further fitness consequences of helping and the bs and cs (which measure numbers of offspring) can be used as reasonable proxies for the Bs and Cs in Hamilton’s rule (which measure lifetime fitness effects) to determine the direction of selection on the helping act. If, however, there are constraints on dispersal then extra offspring produced may remain locally and compete with offspring to which the actor may be related (through local density dependent regulation). Selection will then favour helping if the following extended version of Hamilton’s rule is satisfied (Queller 1992):

\[
 r_{xy}b - c - r_{xy}(b - c) > 0 \quad (12.2)
\]

where \( r_{xy} \) is mean relatedness of the actor to the offspring that are displaced by competition as a result of the helping act. Note that this inequality can equally be used to predict selection for ‘harming’ behaviour or traits, which are defined as traits that reduce the fecundity of local breeders, such that b is negative (Johnstone and Cant 2008; West et al. 2002). Where competition is global \( r_{xy} = 0 \) because displaced individuals are a genetically random sample of the population. When competition is local \( r_{xy} > 0 \), and hence inequality (12.2) is harder to satisfy for a given (positive) b and c. In fact the first model to examine explicitly the consequences of local kin competition for the evolution of altruism (Taylor 1992, building on the ‘infinite island’ population genetic model of Wright 1943) found that the positive effect of limited dispersal on selection for altruism was exactly cancelled by the negative effects of increased competition. In other words, according to Taylor’s model, Hamilton’s second mechanism for the evolution of altruism didn’t work.

Subsequent theoretical work by Taylor and others has shown that this ‘cancelling’ result arises because of the simplifying assumptions of the model, and that incorporating plausible demographic and life-history features (e.g. overlapping generations, sex-biased dispersal, budding dispersal, individual variation in fecundity) recovers the prediction that dispersal constraints select for helping (Lehmann and Rousset 2010). Empiricists know that experimental manipulation of ecological constraints can affect individual dispersal and helping decisions on a behavioural time scale (see Section 12.2 above)—what the new models suggest is that severe ecological constraints on dispersal over many generations can favour the evolutionary origin of local helping. Indeed, not only helping behaviour but any social trait which increases the fecundity of local group members is more likely to evolve when there are strong dispersal constraints.

Two factors which promote the evolution of indiscriminate altruism are particularly relevant to both insect and vertebrate systems: sex-biased dispersal and budding dispersal. These are considered below.

12.3.1.1 Sex biased dispersal

In most cooperative breeders one sex disperses more frequently, or further, from their natal patch than the other (Lawson Handley and Perrin 2007). Sex biased dispersal of this kind likely evolved as
a strategy to reduce inbreeding and its associated deleterious effects, and because the advantages of philopatry are often different for males and females (Lawson Handley and Perrin 2007). But it also has profound consequences for the evolution of social behaviour in males and females, and hence social structure and mating system.

Johnstone and Cant (2008) extended Taylor’s (1992) approach to explore how sex differences in dispersal influence selection for ‘helping’ and ‘harming’ behaviour. They showed that where there is a strong sex bias in dispersal, selection favours harming behaviour among adults of the dispersing sex; and in general favours helping among adults of the philopatric sex. This prediction agrees with observations of dispersal and helping in cooperatively breeding birds and mammals, where in general it is the philopatric sex which provides most help (Cockburn 1998; Russell 2004). In cooperatively breeding cichlids, both sexes disperse and both sexes provide help (Stiver et al. 2004). Extending the model to haplodiploid organisms (Johnstone et al. 2012) show that male-biased dispersal, which is widespread in social Hymenoptera, strongly selects for helping among females. Thus, incorporating sex biased dispersal and local competition into Hamilton’s rule suggests that Hamilton (1964) was in fact correct in his original claim that ‘family relationships in Hymenoptera are potentially very favourable to the evolution of reproductive altruism’.

An important message of these models is that not only behaviour but also life-history traits are shaped by kin selection in the same way as are acts of helping or harming. Decisions such as whether to breed or not and how many offspring to produce, and life-history traits such as the rate of senescence, will affect the fitness of other local group members and thus constitute forms of indiscriminate help or harm. Consider, for example, the timing of reproduction. Where selection favours helping early in life and harming later, females may gain from delaying reproduction and instead helping early in life; where the reverse is true, females may gain from early reproductive cessation and late-life helping, in other words, menopause (Cant and Johnstone 2008). It turns out that sex biased dispersal and patterns of mating interact to determine the strength of selection for helping and harming across the lifespan (Johnstone and Cant 2010). Specifically, local mating and male-biased dispersal, the demographic pattern exhibited by most cooperative mammals, results in females becoming less closely related to local group members as they get older, and hence stronger selection for helping early in life compared to later. However, two unusual (and different) demographic patterns result in the opposite pattern. Specifically, a pattern of female-biased dispersal and local mating (thought to characterize ancestral humans), and non-local mating with low dispersal by both sexes (characteristic of pilot whales Globicephala spp and killer whales Orcinus orca, the two other species which exhibit menopause), results in selection for early reproductive cessation and late life helping.

12.3.1.2 Budding dispersal

The usual assumption of infinite island models is that individual offspring disperse alone and join groups in which there are no other relatives present. Gardner and West (2006), however, explored selection for helping under ‘budding dispersal’, that is, when juveniles disperse in groups. Budding dispersal is conducive to the evolution of helping behaviour because it decouples the positive and negative consequences of dispersal: extra offspring produced as a result of help can disperse away from their parents (so avoiding competition with kin) but still form groups in which relatedness is high.

This model helps to explain the evolution of group dispersal in cooperative insects and vertebrates. In many species, young adults form dispersal coalitions to seek out or compete for vacant territories, or to take over existing groups. In acorn woodpeckers (Melanerpes formicivorus), for example, helpers form sibling groups which compete intensely for any reproductive vacancies that appear (Koenig et al. 1998; similar dispersal coalitions are found in other cooperatively breeding birds and mammals, e.g. Port et al. 2010; Sharp et al. 2008). Dispersal coalitions may also arise because multiple young adults are evicted by older dominant breeders (e.g. Cant et al. 2010). A form of budding dispersal occurs in ‘independent-founding’ social vespid wasps of the genera Polistes,
Belonogaster, Mischocyttarus, Parapolybia, and Ropa-  

lidia, in which colonies are founded by multiple inseminated foundresses, independently of any workers (Gadagkar 1991; Reeve 1991). The benefits of joining a dispersal coalition will depend on social structure and the distribution of reproduction within groups, for example, whether breeding is monopolized by a single individual (as is the case in most independent founding wasps) or shared more evenly among group members (as occurs in banded mongooses). The evolution of group dispersal may also involve an element of positive feedback: once group dispersal is common, dispersers may be selected to join larger coalitions which can compete more effectively; or evictors selected to expel larger numbers of their offspring, but these benefits will eventually be offset by the costs of elevated within- 
group competition. Group dispersal in cooperative breeders is a promising area for further theoret- 
ical and empirical work, and may have hitherto unexplored impacts on individual behaviour, group 
structure, and population dynamics.

12.3.2 Discriminate altruism: kin directed care

Kin discrimination should promote the evolution of helping because Hamilton’s rule is easier to sat- 
ify if helpers can direct care towards more closely related group members. In this case relatedness $r_{xy}$ is by definition higher than the average related- 
ness to all potential recipients. Since the ability to preferentially aid kin increases the inclusive fitness pay-off of costly helping, we might expect selection for mechanisms which enable helpers to single out close relatives among members of their social group. Helpers could learn to recognize kin if other factors ensured that individuals with whom helpers interact most frequently, or those in closest physical proximity, were reliably genetically related. In cooperatively breeding birds, kin recognition is typically based on cues that are learnt during development in the nest (Komdeur et al. 2008). There is less evidence that genetic similarity can be recognized directly and there are some theoretical difficulties with this idea. Selection could in principle favour the spread of ‘marker’ alleles which allow relatives to recognize and direct care toward each other, but

the more common such markers became the less useful they would be in distinguishing kin from non-kin (Crozier 1986). For genetic kin recognition systems to work and to promote the evolution of altruism requires that genetic ‘rarity’ is associated with some other fitness advantage, such as resis- 
tance to parasites or pathogens (Rousset and Roze 2007). This may explain why known examples of genetic kin recognition in mice and humans involve detection of similarity at major histocompatibility (MHC) genes which are highly polymorphic and involved in immune function (Rousset and Roze 2007).

Helpers may potentially be able to discriminate kin from non-kin using learned or genetic cues, but do they use these cues when allocating help? In cooperative birds and mammals, some studies find evidence of kin-directed care while others do not: across 9 species, variation in relatedness explains 10% of the variation between helpers in the prob- 
ability of helping (Cornwallis et al. 2009; Griffin and West 2003). One result to emerge from these comparative analyses is that there is typically no relationship between relatedness and helping effort (as opposed to the probability of helping; Corn- 
wallis et al. 2009; Griffin and West 2003). This suggests that the costs and benefits of helping are more important determinants of individual helping effort than is variation in relatedness (Cornwallis et al. 2009).

In cooperatively breeding insects, there is little evidence that helpers discriminate between kin and non-kin within groups. Typically helpers disting- 
uish between nestmates and non-nestmates, but do not distinguish degrees of relatedness among nestmates (Keller 1997). In Polistes dominulus, for example, 20–30% of helpers are non-relatives but there is no difference between related and unrelated helpers in foraging effort, nest defence, aggression or inheritance rank (Leadbeater et al. 2010; Queller et al. 2000). As with vertebrates, kin-biased helping may not be favoured because of the costs of recog- 
nition errors. In insects that share a nest, there may be few environmental cues to distinguish kin from non-kin. In paper wasps, for example, it has been argued that cues based on cuticular hydrocarbons (implicated in kin discrimination among larvae in solitary insects) may be unreliable since these can be
acquired from contact with the nest (Gamboa 2004). However, recent studies have shown that unrelated helpers in *Polistes dominulus* have measurably different hydrocarbon profiles (E. Leadbeater and J. Field, personal communication). While cues to discriminate kin exist, therefore, they are not used by wasps in helping decisions.

### 12.3.3 Direct fitness benefits

Examples of species with hardworking, unrelated helpers (for example, *Polistes dominulus*, Leadbeater et al. 2010; Queller et al. 2000) suggest that helping can also yield direct fitness benefits, and that in some cases these direct benefits alone may be sufficient to outweigh the fitness costs of helping. When considering direct fitness benefits of helping it is useful to distinguish those benefits that are non-enforced or enforced (Gardner and Foster 2008). In both cases helping is more profitable than non-helping, but in the case of enforced benefits it is the threat or action of social partners that reduces the pay-off of the non-helping option.

#### 12.3.3.1 Non-enforced benefits

Helping can be readily explained if it results in some form of immediate or delayed direct fitness benefit which offsets the initial cost of the helpful act. In this case helping is a form mutualism (Gardner and Foster 2008; West et al. 2007). Several behavioural mechanisms which result in delayed benefits of helping have been proposed to operate in cooperative breeders, including the acquisition of parenting skills; the recruitment of offspring into the group which later become helpers themselves; and elevated social status or dominance (reviewed by Dickinson and Hatchwell 2004; Koenig and Walters 2011). The last two mechanisms have received some theoretical attention under the terms ‘group augmentation’ (Kokko et al. 2001) and ‘prestige’ (Zahavi 1995) respectively.

An actor can gain group augmentation benefits if the extra offspring produced as a result of helping remain in their natal group and boost the actor’s future survival or reproductive success (Kokko et al. 2001). The delayed direct fitness of helping will be especially important where helpers have a good chance of inheriting breeding status, and where large group size is associated with elevated survival or reproductive output—two conditions which commonly hold in cooperatively breeding insects and vertebrates. The key assumptions to test are 1) that helping leads to increased recruitment and larger future group size, and 2) that a larger group size is beneficial to the direct fitness of helpers (Wong and Balshine 2011). Studies of insect and vertebrate cooperative breeders often report an association between group size and breeder productivity, but do not show that helping per se leads to elevated future fitness for helpers. In paper wasps and hover wasps group augmentation benefits do not appear to be a major determinant of helper effort: helpers reduce their helping effort as they get closer to inheriting, a pattern which is opposite to that predicted by the group augmentation hypothesis (Field and Cant 2007). In birds there is also scant evidence that variation in group augmentation benefits underlies variation in helping effort (but see Kingma et al. 2011 for one such case).

The prestige hypothesis suggests that helping evolves as a costly signal of quality, and that the costs of helping are offset by the fitness benefits of improved mating access or dominance status that result from this honest advertisement of quality. Initial evidence for the hypothesis came from observations of Arabian babbler *Turdoides squamiceps* helpers competing with each other to help (Carlisle and Zahavia 1986); although a subsequent study on the same species did not replicate this finding (Wright 1999). The key predictions of the prestige hypothesis are 1) that helpers should help more in the presence of an audience; and 2) that elevated helping effort should causally increase social status or mating success. McDonald et al. (2008) tested the first of these predictions in cooperatively breeding bell miners, but found that helpers did not adjust their helping effort to the presence or absence of an audience (the breeding male or female). In other species, helpers that invest most have a higher probability of obtaining breeding status, but this may simply reflect variation in helper quality rather a causal link between helping and future mating success (Cant and Field 2005). Overall, evidence for the prestige hypothesis is scarce.
12.3.3.2 Enforced benefits

Much theoretical interest in evolutionary biology has focused on the use of punishment and threats to induce cooperation and helping (Cant 2011; Ratnieks and Wenseleers 2008). In the context of cooperative breeding, the pay to stay hypothesis (Gaston 1978) suggests that dominants can exploit the gains that subordinates derive from group membership to charge ‘rent’ in the form of help. This mechanism is based on the use of a threat or ‘last move’ in the interaction: helpers work to rear the offspring of dominants to avoid expulsion from the group. When the threat is clear and credible, no evictions will be observed, so an effective threat is a highly cost-effective means of social control (Cant 2011). Alternatively, dominants might coerce subordinates into helping via the use of punishment. Punishment differs from threat in that it involves a repeated interaction rather than a last move: dominants might pay an immediate cost to punish a lazy helper if this act induces the helper to reciprocate by working harder in the future.

The key prediction of the pay to stay hypothesis is that experimental reduction of helper effort should lead to eviction from the group. In splendid fairy wrens and cooperative cichlids, experiments to temporarily remove subordinates helpers or reduce their helping effort typically led to increased aggression from dominants and higher rates of subordinate helping thereafter (Balshine-Earn et al. 1998; Bergmüller and Taborsky 2005; Mulder and Langmore 1993). However, none of these experimental manipulations led to helpers being expelled from the group, as would be expected if aggression is used to enforce help. In Polistes for example, ‘dart’ behaviour is usually classed as aggression but may instead serve as a cooperative signal to coordinate worker activity (Nonacs et al. 2004). In P. dominulus, dominants are often aggressive to subordinates, but this appears to be linked to conflict over social rank rather than conflict over help (Cant et al. 2006).

In summary, patterns of helping in cooperative breeders provide general evidence for Hamilton’s first mechanism based on indiscriminate altruism, namely that increasing constraints on dispersal and the presence of relatives should promote helping and inhibit harming behaviour. Inclusive fitness models which incorporate demography and population structure are also an important step toward an evolutionary theory of ‘cooperative life history’. Variation in relatedness does not correlate well with helping effort within groups, which parallels findings on the relationship between parentage and parental care (Chapter 11). There is little evidence that threats of eviction induce helping, although dominants in some species do use punishment to enforce helping. In some cooperatively breeding insects, helpers adjust their effort according to their expected future fitness (Field and Cant 2009b). However, more research is required to understand individual variation in helping and, importantly, variation in the consistency of individual contributions to helping (their ‘cooperative personality’ Bergmüller et al. 2010; English et al. 2010).

12.4 Negotiation over help

The preceding discussion highlights the evolutionary conflicts that exist within cooperatively breeding groups over levels of investment. Coercion—via punishment and threats—is one behavioural manifestation of this conflict. In many species, however, coercion may be impractical or inefficient: in birds,
for example, the targets of punishment can fly away. Nevertheless, individuals may be able to induce others to help more by adjusting their own helping effort contingent on the helping effort of their social partners, in a process of bargaining or ‘negotiation’. Negotiation is by definition a behavioural interaction: a process of bid and counter-bid. By contrast, classic models of parental care exclude bargaining because they solve for evolutionarily stable combinations of genetically specified fixed ‘sealed bid’ efforts, so called because it is assumed that players can’t change their effort after observing that of their partner (Houston and Davies 1985). Sealed bid models have the advantage of mathematical tractability, but their assumptions are at odds with a wealth of evidence that animals typically observe and adjust their helping effort to that of their social partners (Johnstone 2011; McNamara et al. 1999). Allowing players to observe and respond to each other’s helping effort on a behavioural time scale can render sealed bid equilibria evolutionarily unstable, at least in cases where there is some variation in individual efforts due to noise or variation in quality (McNamara et al. 1999; Johnstone 2011).

To address this issue, McNamara et al (1999) developed one type of ‘negotiation’ model (again in the context of biparental care) in which they solved for evolutionarily stable levels of behavioural responsiveness or ‘rules for responding’, rather than evolutionarily stable fixed efforts. Where increasing investment brings diminishing productivity returns, and each party has perfect information about offspring need, the ESS rule for responding is to partially compensate for changes in each other’s effort levels. However, other response rules (for example, effort ‘matching’, where an increased effort by one parent results in increased effort by its partner) can be evolutionarily stable where parents have incomplete information about the level of offspring need, and use each other’s effort levels to estimate this (Johnstone and Hinde 2006). Variation in how parents obtain information may help to explain the range of responses to experimental manipulation of parental effort that have been observed in biparental birds, including no change in partner effort level, partial or full compensation, and effort matching (Hinde 2006; Chapter 9).

In the context of cooperative breeding, Johnstone (2011) adapted McNamara’s negotiation approach to show that helping may often benefit mothers and fathers (via ‘load lightening’) as much as offspring, so that relatedness of helpers to each parent and the responsiveness of parents may be a more important determinant of helping effort than average relatedness to the brood. The predictions of this model have not yet been tested. Moreover, there have been no tests of the assumptions or predictions of any negotiation model in cooperatively breeding insects.

McNamara et al.’s (1999) model is an important first step towards an evolutionary theory of behavioural negotiation, but there are many other forms that bargaining or negotiation might take. Some biological interactions, for example, can be thought of as consisting of a sequence of ‘moves’, in which one player commits to a level of investment which is observed and responded to by their social partners. For example, in birds and mammals mothers effectively make a ‘first move’ by allocating resources to the egg, while their mate (or a helper) is placed in the role of a ‘second mover’ who must choose how much effort to invest after birth or hatching. Selection should favour mothers that adjust their investment in eggs according to the amount of help their offspring will receive later (Russell et al. 2007). Empirical tests of this idea present an interestingly mixed picture. In splendid fairy wrens (Malurus splendens; Russell et al. 2007), carrion crows (Corvus corone; Canestrari et al. 2011), and cooperative cichlids (Neolamprologus pucher; Taborsky et al. 2007), mothers reduce their investment in eggs when helpers are present, but in the wrens and crows this reduction is offset by the investment received from helpers post-hatching. By contrast, in acorn woodpeckers (Melanerpes formicivorus), mothers do not decrease investment per egg when helpers are present, but instead lay a greater number of eggs, so each offspring is worse off overall (Koenig et al. 2009). A recent model by Savage et al. (in press) suggests that these contrasting empirical patterns might be explained by variation in the personal fitness costs of increasing clutch size. Where clutch size is constrained by high costs of egg production, mothers are predicted to reduce their investment per egg, and helpers to compensate for this reduction so that...
each offspring receives greater resources overall. Where clutch size is more flexible, females should produce more eggs in the presence of helpers, to the detriment of each individual offspring (a situation similar to the results found in acorn woodpeckers). More work is needed to test the specific predictions of the model, and to determine the general conditions for which mothers might gain from 1) producing fragile offspring to attract compensatory care from helpers; versus 2) producing hardy clutches, or perhaps a mixture of hardy and fragile young, when helpers are present.

12.5 Reproductive conflict

Within cooperatively breeding groups there are usually strong asymmetries in fitness between breeders and helpers which leads to evolutionary conflict over reproduction, and often to intense competition among group members to monopolize reproduction (Cant and Johnstone 2009). Much research over the last 30 years has focused on understanding how this conflict is resolved, and the evolutionary causes of variation in the distribution of reproduction, or the degree of reproductive skew, between groups and between species. Many researchers were drawn to working on reproductive skew because there existed a simple candidate model which potentially applied very widely (the ‘concession’ model; Reeve 1991; Vehrencamp 1983). This model assumed that a single dominant individual controlled reproduction in the group, but that subordinates could use the threat of departure from the group to extract a reproductive concession or ‘staying incentive’ from dominant individuals, at least in cases where the presence of subordinates boosted the reproductive success of dominants. Thus in this model the level of skew in groups was determined by the inclusive fitness value of ‘outside options’ to subordinates, that is, their fitness pay-off should they choose to disperse to breed elsewhere. The model suggested that variation in skew both within and between species was explicable by variation in three parameters: relatedness, ecological constraints, and the productivity benefit of retaining subordinates.

Starting in the 1990s a number of other models appeared which relaxed the assumptions of the concession model, and produced quite different predictions. For example, ‘incomplete control’ models (Cant 1998; Reeve et al. 1998) assumed that no single individual had cost-free control over the allocation of reproduction, but rather that both dominants and subordinates could invest costly effort to increase their share of reproduction; while the ‘restraint’ model (Johnstone and Cant 1999) assumed that subordinate reproduction was limited only by the threat of eviction from the group. These and other models led to a confusing array of predictions and a tangled theoretical picture, at least initially. As Gardner and Foster (2008) put it:

From this simple beginning skew theory diversified into a comedy of additional models, each differing in their specific assumptions about the power of individuals, the information available, and whether and how individuals negotiate their reproductive share.

The problem with skew research, however, does not lie in the diversification of models: as a rule the development of different models represents a progression in the understanding of a natural system, since models can only be rejected by comparison with other models (Hilborn and Mangel 1997; Lakatos 1978). In the case of skew theory, the various models can be classified into those that assume the resolution of conflict is influenced by threats to exercise ‘outside options’ (such as leaving the group, or evicting a competitor), versus those that assume outside options are irrelevant. This distinction provides an opportunity to distinguish between and eliminate models, and to clear away some of the theoretical tangle.

The main problem with the research on reproductive skew has been a dearth of empirical tests of the models’ assumptions, particularly experimental tests. Two notable exceptions are the experimental studies of Langer et al. (2004) (on a social bee *Exoneura nigrescens*) and Heg et al. (2006) (on a cooperative cichlid *Neolamprologus pulcher*), both of which manipulated the value of outside options (i.e. breeding opportunities outside the group) to subordinates to test whether this influenced the outcome of reproductive conflict. In both cases varying outside options had no effect on skew, suggesting that threats of departure...
do not determine the pattern of reproduction in natural groups. In cooperatively breeding birds, experimental suppression of paternity share (by removing males during the female’s fertile period) has not been shown to lead to the departure of subordinates, as expected if the pattern of reproductive sharing among males reflects a subordinate’s threat of departure (Cant 2006). In banded mongooses (Mungos mungo), experimental suppression of dominant or subordinate breeders (using short-acting contraceptives) never leads to their departure from the group, or to the eviction of subordinates. Suppression does, however, trigger mass infanticide shortly after birth. In banded mongooses, therefore, it appears that low reproductive skew arises from a ‘Mexican standoff’—any female that attempts to monopolize reproduction is very likely to have her litter killed (see also Hodge et al. 2011; Fig. 12.3).

Current evidence, therefore, suggests that the value or availability of outside options does not determine the level of reproductive skew within groups, although more experiments are needed. This fits with recent theory which suggests that outside options will be least relevant in groups of relatives and where the productivity benefits of association are high—exactly the conditions that apply to most cooperative breeders (Cant and Johnstone 2009). Rather, the outcome of reproductive conflict within groups appears to depend on the ability of one party to suppress the reproductive attempts of other group members, and the costs of these attempts at suppression. Consequently, the hope that the simple framework offered by early skew models could provide a universal explanation for variation in skew both within and between species seems to have faded. The spotlight has shifted to understanding the evolution of conflict strategies within cooperative groups: how animals suppress each other’s breeding attempts, how conflicts are settled on a behavioural time scale, and why the outcome of reproductive conflict is so variable. The study of ‘reproductive skew’ has therefore given way to the study of ‘reproductive conflict’, which highlights conflict mechanisms that operate on a behavioural time scale as well as evolutionary outcomes, and the value of experiments over correlations (see also Chapters 7, 8, and 9).

In many cooperative species, reproductive conflict is resolved in a costly and wasteful manner, for example through egg destruction, nest destruction, infanticide, and aggression (Cant 2012). An important question is whether evolutionarily stable resolution of conflict always requires individuals to invest costly effort in conflict, or whether selection can favour less costly and more efficient resolutions mechanisms. Theory suggests two ways in which evolutionary conflicts need not be manifested in actual conflict: 1) through the use of an effective deterrent threat (Cant 2011; Cant et al. 2010); and 2) through mechanisms which make conflict investment unprofitable (Cant 2012). Threats can lead to efficient conflict resolution because they need only be carried out when the social rules they enforce are broken. For a threat (e.g. of departure, eviction, or attack) to be effective in this way requires effective communication and the ability to discriminate transgressors. Data from social hymenoptera, social fish, and mammals indicates that such effective communication exists in some systems, because threats of attack or infanticide do successfully deter subordinates from breeding or challenging the position of dominant (reviewed in Cant 2011). In fish size hierarchies, for example, dominant fish use the threat of eviction from the group to limit the growth and competitive ability of subordinates, but conflict is resolved without them having to carry out this threat (Cant 2011).

Second, evolutionary conflict (i.e. a disparity between the fitness optima of social partners; Chapter 9) may exist, but need not be manifested in costly or destructive acts. Outcomes featuring zero actual conflict are possible when biological conflict takes the form of ‘suppression competition’ (for example, infanticide, policing, mate guarding) in which success in competition depends on eliminating or nullifying the competitive acts of others. By contrast overt conflict is always expected in ‘production competition’ where success depends on maximizing proportional effort or competitive acts (as is the case, for example, in biological ‘scrambles’; Chapter 8). To illustrate the biological distinction between production and suppression competition, consider two female birds laying eggs in a shared nest. Where competition takes the form of a scramble between offspring after hatching, each female’s fitness pay-off will depend on her proportional representation in the communal clutch. A female who
invests nothing in competition (i.e. lays no eggs) is certain to get zero fitness pay-off. If, however, competition takes the form of infanticide after eggs are laid, females who invest nothing in infanticide may still achieve some reproductive success, particularly if egg discrimination is not perfect. A recent model explores this type of suppression competition and shows that asymmetry in strength and uncertainty about strength or conflict effort can promote peaceful resolution of evolutionary conflict, even among unrelated individuals (Cant 2012). The level of information in the contest has a strong effect on the costliness of behavioural conflict resolution, and can be expected to shape signalling.
strategies and dominance interactions (e.g. Chapters 7 and 8). Experiments to manipulate the status quo distribution of reproduction to reveal hidden threats, or to alter the level of uncertainty about relative strength, would help to test these models in the context of reproductive conflict and conflict over parental care.

12.6 Conclusion and future research

Cooperative breeding species are excellent subjects for research on the evolution of parental and allo-parental care; how cooperation evolves; and the behavioural mechanisms by which animals resolve conflicts and exercise control over each other’s behaviour. A recurring theme of this chapter is the need for more experimental tests of models of helping and reproductive conflict. Any proposed behavioural mechanism of social control (such as punishments or threats) can only be investigated rigorously through the use of manipulation experiments. Manipulations of this type are often challenging logistically, but without them there is a danger of developing a biased and inaccurate picture of the forces sustaining cooperation and resolving reproductive conflict in natural systems. For example, where threats of attack or infanticide are effective, observed acts of aggression may be just the tip of the iceberg of forces influencing behaviour in cooperative groups. Detecting hidden threats requires experiments to disturb the status quo.

There are many promising areas for future research; I mention four here. First, detailed longitudinal studies of cooperative animals in their natural environment provide an opportunity to investigate selection on aging in highly viscous populations. Field studies have an enormous advantage over laboratory studies to address these questions because key life-history trade-offs might only be manifested in an environment where individuals are exposed to their natural predators, parasites, and pathogens.

Longitudinal studies of cooperative breeders also offer unparalleled opportunities to examine transgenerational effects and epigenetic inheritance under natural conditions (see also Chapters 14 and 17). Studies of laboratory rodents have revealed mechanisms by which pre- and post-natal care can result in heritable changes in patterns of gene expression in adulthood, but much less is known about these mechanisms in wild populations and their ecological and evolutionary significance (Bossdorf et al. 2008). For example, the level of investment received in early life offers a strong candidate explanation for observed differences in later life-history and the consistency of contributions to helping in some cooperatively breeding species (e.g. English et al. 2010). Moreover, individuals that receive greater investment when young may be more or less likely to help themselves as adults, or more or less likely to disperse from the group, leading to positive or negative feedback in the quality of early versus late cooperative environments and potentially dramatic impacts on group stability and population dynamics over time.

Third, there is much scope for research on the behavioural processes by which animals resolve conflict over reproduction and helping. For example, low-level social aggression is a conspicuous feature of animal societies, but the function of aggressive interactions is often unclear. Are aggressive dominants advertising their strength to deter subordinates from challenging their status? Does submissive behaviour serve to conceal a subordinate’s true strength or motivation to challenge dominants? How frequently should dominants interact with subordinates to maintain their social status, and how often should subordinates probe dominant strength? Research on these questions would help to understand why some societies are peaceful while others are overtly fractious, and how social conflict influences the evolution of cognitive and neural processes such as individual recognition and social memory.

Fourth, current research is starting to reveal the neural and hormonal mechanisms controlling cooperative behaviour, and how these mechanisms are themselves shaped by natural selection. This is helping to break down the traditional barriers between studies of proximate mechanism and ultimate function. This barrier can be traced to an influential paper by Tinbergen (1963) which divided research questions into four categories (sometimes called the ‘four whys’): physiological causation, development, evolutionary history, and adaptive value. However, in that paper Tinbergen was at
pains to point out that these four research foci should be viewed as complementary and their protagonists united by a common aim, that is, to understand why animals behave in the way that they do. ‘Cooperation between all these workers is within reach’, he wrote, ‘and the main obstacle seems to be a lack of appreciation of the fact that there is a common aim’. In cooperative breeding species, research on physiological mechanisms would help to understand the proximate control of helping, punishment, winner–loser effects, and reproductive suppression (see also Chapter 3). All of these social responses have large impacts on inclusive fitness and hence the mechanisms controlling their development and expression are subject to selection and will be shaped by the social and ecological environment. Research programmes which blend evolutionary theory, life-history analysis, and investigation of physiological mechanism offer exciting possibilities to advance knowledge about cooperation and parental care. Much of this information may be relevant to ourselves: after all, our morphology, physiology, fertility, rate of senescence, and long period of offspring dependency all reflect an evolutionary history of cooperative breeding, not more recent technological developments.

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References


