

Chapter 4

The Ecology and Evolution of Helping in Hover Wasps (Hymenoptera: Stenogastrinae)

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Abstract In this chapter, I discuss the ecology and evolution of helping in hover wasps (Stenogastrinae), a tropical group that is uniquely suited for experimental studies in the field. I first outline the ecological benefits of helping that have been tested for in hover wasps, such as insurance advantages and direct fitness for helpers. I then discuss explanations for individual variation in helping decisions – why only some female offspring become helpers; and why some helpers work harder than others. Most of the chapter focuses on the hairy-faced hover wasp, whose behavioral ecology is best known, but I also discuss reproductive skew and task allocation in other species, and draw comparisons with other wasps where appropriate. The chapter ends with a comparison of the ecology of helping in hover wasps and that in cooperatively breeding vertebrates. The conclusion is that although helping can be understood using Hamilton's inclusive fitness framework in both of these major taxa, the critical ecological factors differ fundamentally between them.

4.1 Introduction

It is now 40 years since Hamilton (1964) provided what is still a generally accepted framework for viewing the evolution of altruism. In that time, wasps, together with cooperatively breeding vertebrates, have been the most popular models for studying the evolution of the particularly extreme form of altruism known as eusociality, in which some individuals forfeit their own reproduction to rear the offspring of a queen or breeding pair. Although much of the emphasis since Hamilton's paper has been on how variation in the coefficient of relatedness (r) could promote helping, the other two parameters in his famous inequality ($rb > c$), the costs (c) and benefits (b), are just as vital in determining whether helping is favored. It is therefore unsurprising that variation in relatedness alone has often proved to have limited power for explaining variation in critical features of social systems (e.g., Hughes et al. 1993;

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Cant and Field 2001; Clutton-Brock 2002; Griffin and West 2003; Hammond and Keller 2004; but see Wenseleers and Ratnieks 2006). Measuring costs and benefits and determining the importance of specific ecological factors in the decision to help, is challenging. It usually requires experimental manipulation, ideally under natural conditions where results will be most meaningful. Stenogastrine wasps (Hymenoptera: Stenogastrinae), also known as hover wasps, are probably better suited than any other group of wasps and bees for experimental and observational studies of helping in the field. Yet because hover wasps are restricted to tropical areas, they were little studied until the early 1980s. At that time, research programs initiated by M.P. Hansell and S. Turillazzi began to reveal the full details of their biology, so that today at least a little is known about the natural history of six of the seven genera. In this chapter, I will examine the behavioral ecology and evolution of helping in hover wasps, thus illustrating their utility as research systems. I will focus primarily on the species best-studied in this respect, the Hairy-Faced Hover Wasp *Liostenogaster flavolineata* (Cameron), while drawing comparisons with other hover wasps and polistines where appropriate. I will then briefly summarize related material on hover wasps other than *L. flavolineata*, and finally consider general similarities and differences between the social systems of hover wasps and cooperatively breeding vertebrates.

4.2 Distinguishing Features of Hover Wasp Biology

Hover wasps comprise approximately 50 described species in seven genera (Carpenter and Starr 2000). They are medium-sized (1–2 cm long) black or brown and yellow wasps found in rainforest ranging from India to Papua New Guinea (Turillazzi 1991). Carpenter's (1991) phylogeny, based on morphology and behavioral characters, placed them as the sister group of Polistinae+Vespinae, and subsequent molecular work casting doubt on that conclusion was controversial (Schmitz and Moritz 1998, 2000; Carpenter 2003). More recently, however, an independent molecular study based on four genes suggests that zethine potter wasps are the sister group of Polistinae+Vespinae, and that hover wasps are the sister group of all other vespids (Hines et al. 2007). This indicates that there have been two independent origins of eusociality among vespids, one in Polistinae+Vespinae and one in hover wasps. It also means that social traits shared between hover wasps and Polistinae+Vespinae represent convergence (Hines et al. 2007).

Hover wasps have several features unique among wasps, which I summarize here based mostly on Turillazzi (1991) and references therein. Most noteworthy is the 'abdominal substance', a gelatinous white material synthesized in Dufour's gland and produced from the tip of the adult female's abdomen. This substance, originally assumed to provide larval nutrition, is now thought to function as an oviposition tool and substrate on which small larvae rest, as well as a depository for food provisions. Instead of ovipositing directly into a cell, a female first produces a ball of abdominal substance. She then holds the ball in her mouth while she bends her abdomen under her thorax and lays an egg on it. The egg plus abdominal substance is then placed in the cell (see photographs in Turillazzi 1991). The abdominal

substance is also used to construct the ant guards that protect the nests of some hover wasps. Hover wasp larvae lie curled around the long axes of their cells, unlike the larvae of polistines and vespines, which lie longitudinally with their heads towards the cell entrances. Larvae are provisioned progressively like those of polistines and vespines, but instead of placing food directly onto the larval mouthparts, adults place it onto the abdominal substance in cells containing small larvae, or onto the middle of the bodies of larger larvae as they lie coiled in their cells.

Hover wasps nest typically in dark, hidden places near water: under overhanging earth banks, rocky overhangs, caves, etc. Nests lack the petiole of polistines and vespines, and are often highly camouflaged. Nest structure is incredibly diverse compared to most other groups of wasps, even within a single genus such as *Liostenogaster*, such that species are often easier to identify from their nests than from characteristics of the adults (see Turillazzi 1991 for examples). Hover wasps appear to have few specialized natural enemies, with major predators being generalists, notably ants and hornets. At least one specialized parasitic wasp is known, however (Coster-Longman et al. 2002; pers. observ.). Adult hover wasps are aggressive only towards conspecifics and enemies smaller than themselves: when confronted with a larger threat such as a hornet or human, they immediately flee.

The hover wasp's social groups are small; mean group sizes range between 1 and 4 females, with individual groups almost never exceeding ten females (Turillazzi 1996). Initially thought to vary in their level of sociality, all species are now thought to be eusocial in the sense that there is a clear reproductive and usually behavioral division of labor whenever group size is greater than one. No obligate socially parasitic species have been found. Further details of hover wasp biology, including what is known of male behavior, can be found in Turillazzi (1991).

4.3 The Hairy-Faced Hover Wasp *Liostenogaster Flavolineata* as a Model System

Research on *L. flavolineata* began with the monumental PhD thesis of Charlotte Samuel (1987). Her work included long-term monitoring of nests with individually marked wasps, and the first detailed description of the *L. flavolineata* social system, establishing a baseline on which later work has been built. *L. flavolineata* has primarily been studied near Gombak (bridge site and gazebo sites approximately 10 km apart) and near Fraser's Hill, a higher altitude area approximately 60 km from Gombak (1,000 m a.s.l.). All of these sites are in peninsular Malaysia.

4.3.1 Summary of Nesting Biology

L. flavolineata builds mud nests consisting of a single open comb of cells (Fig. 4.1), similar in basic form to the paper nest of *Polistes*. Nests are usually initiated by a single foundress, but a second female occasionally joins her before any offspring



Fig. 4.1 Mud nest of *L. flavolineata* with individually marked adults. Developing offspring are just visible in some of the inner cells. Photo: A Cronin

reach adulthood (Samuel 1987). Females are thought to be unusually specialized predators, feeding their larvae exclusively on winged ants and termites (Samuel 1987). Offspring development lasts approximately 100 days (Samuel 1987; J. Field unpubl. data), considerably longer than the 40–50 days typical of polistines and hover wasps of other genera (Hansell 1982, 1987b; Turillazzi 1985; Reeve 1991). Brood-rearing occurs throughout the year at the sites where *L. flavolineata* has been studied, but there still appears to be seasonal variation in parameters such as the frequency of nest-founding, mean group size, and the mean number of immature offspring being reared (Samuel 1987; Shreeves and Field 2002; J. Field and G. Shreeves, unpubl. data).

Many female offspring remain on their natal nests as helpers, which forage to feed the immature offspring. Females may, however, leave at any time. Many such females initially become nest-less floaters, but subsequently pursue alternative strategies (Samuel 1987; Field et al. 1999). These strategies include nest-founding, usurping a lone female or adopting a nest that has fallen vacant after its previous residents have disappeared, or occasionally joining a pre-existing group (Samuel 1987; Field et al. 1998a). Male offspring usually leave their natal nests soon after reaching adulthood, although some become nest-residents (J. Field, unpubl. data). There can be up to 90 cells and ten females resident on a nest, close to the maxima recorded for hover wasps (Turillazzi 1996). Brood-rearing cells are repeatedly re-used and nests are perennial, sometimes persisting for 10 years or more (J. Field, unpubl. data). The number of cells therefore reflects the largest number of offspring reared simultaneously during the history of the nest rather than the current number being

reared, and more than 50% of cells are typically empty at any one time (Field et al. 1998a). This suggests that the mechanism stimulating oviposition may not be the presence of empty cells as has been suggested for *Polistes* (Karsai et al. 1996).

4.3.2 Gerontocracy and Colony Genetic Structure

Observation of an *L. flavolineata* nest usually reveals a behaviorally dominant female that rarely leaves the nest, never forages for larval provisions and is more aggressive than other group-members (Samuel 1987; Field and Foster 1999). Sumner et al. (2002) used microsatellite markers to show that the dominant lays all or almost all of the eggs at any one time. Subordinates lay a small proportion (~10%) of the male eggs, perhaps because they tend to be more closely related to the dominant's daughters than to her sons. Genetic data suggest that females mate only once and that there is no inbreeding, consistent with mating not being observed on the nest (Sumner 1999; Sumner et al. 2002; Bridge 2005).

Samuel's (1987) long-term monitoring of a single nest suggested that the dominant tended to be the oldest female in the group, replaced on her death by the next-oldest female, a system termed 'gerontocracy' by Strassmann and Meyer (1983). Bridge and Field (in press) have recently confirmed the generality of this pattern in *L. flavolineata* by experimentally removing successive dominants from nests with residents of known age. After 87% of 69 removals, the next-oldest female indeed inherited the dominant position. The gerontocracy in *L. flavolineata* appears to contradict a recent model which predicts that in tropical taxa, where colonies outlive individuals, replacement dominants should be younger rather than older individuals (Tsuji and Tsuji 2005). It is possible that age represents an arbitrary convention for deciding dominance, although this begs the question of why the same convention is used in multiple taxa (Tsuji and Tsuji 2005). The immatures from eight out of the 13 nests genotyped in detail by Sumner et al. (2002) comprised two different sibships, indicating that at least some of a previous dominant's offspring are reared through after she dies. The remaining five nests contained only a single sibship.

The first genetic study of *L. flavolineata* was allozyme-based and estimated mean within-nest adult female relatedness as 0.22 ± 0.10 , the lowest then known for a primitively eusocial insect (Strassmann et al. 1994). Sumner et al. (2002) took wasps from under the same bridge sampled by Strassmann et al. 5 years earlier, and obtained a considerably higher estimate of 0.52 ± 0.05 using hypervariable microsatellite loci. Sumner (1999) obtained a similar estimate of 0.45 ± 0.1 using a smaller sample from the nearby Gazebo site, and Bridge (2005; Field et al. 2006) obtained an estimate of 0.46 ± 0.08 from Fraser's Hill. Overall, these data suggest that mean relatedness is normally 0.4–0.5, within the range typical for other primitively eusocial wasps (Ross and Carpenter 1991). Female nest-mates are probably a mixture of mainly sisters, aunt-niece, mother-daughter or cousins, primarily reflecting the gerontocratic inheritance system (Field et al. 2006). The relatedness estimates that have been obtained for three other hover wasps are also fairly high: 0.46 ± 0.054 and

0.56 ± 0.19 in *Parischnogaster alternata*; 0.33 ± 0.05 in *P. mellyi*; and 0.43 ± 0.13 in *Eustenogaster fraterna* (Strassmann et al. 1994; Landi et al. 2003; Fanelli et al. 2005; Bolton et al. 2006).

4.3.3 Advantages of *L. flavolineata* for Experimental Work

L. flavolineata has most of the same advantages as *Polistes* as a model system, including behavioral flexibility and an open comb of cells upon which all adult behavior can be observed (Fig. 4.1), but *L. flavolineata* has three additional advantages not typical of *Polistes*, whose practical value cannot be over-emphasized. It is one of three hover wasp species in which nests are often clustered together in groups of sometimes 100 or more (Fig. 4.2). Large clusters occur naturally under rocky overhangs but are also found on man-made structures such as under bridges and on the ceilings of culverts that carry streams under roads (Samuel 1987; Coster-Longman et al. 2002; J. Field, pers. obs.). Much smaller clusters and isolated nests are also common, and nests additionally occur attached to plant roots that hang exposed beneath overhanging soil banks. Large clusters of nests associated with accessible man-made structures are ideal for research purposes. They allow many social groups to be studied under the same environmental conditions, and this is facilitated by the lack of aggression towards humans. The individually marked wasps on a group of 100 nests can be censused in less than an hour, a considerable



Fig. 4.2 Part of a cluster of *L. flavolineata* nests under a bridge. Each of the pale, roughly circular structures is a separate nest. Photo: J. Field

advantage compared to the more spatially separate nests typical of polistines. A second major practical advantage provided by hover wasps is the low rate of nest predation. This is especially true of *L. flavolineata*, whose robust mud nests are rarely damaged by hornets (Samuel 1987; Coster-Longman et al. 2002). If a group of 100 *L. flavolineata* nests is experimentally manipulated then monitored for 3 months, more than 95 will typically still be present at the end of the experiment. A third advantage is that hover wasp groups remain continuously small, allowing all group members to be kept individually marked over long periods of time: there is not the sudden increase in group size that occurs after worker emergence in temperate wasps such as *Polistes*. One disadvantage for some purposes is that offspring development lasts approximately twice as long as *Polistes*.

4.4 Ecological Benefits of Helping

A fundamental question in *L. flavolineata*, as in other primitively eusocial animals, is why some individuals choose to become helpers on their natal nests instead of leaving to reproduce independently. *L. flavolineata* helpers are less closely related to both female and male brood than they would be to their own offspring (Sumner et al. 2002). This suggests that there must be ecological advantages to becoming a helper. In the following three sections, I will review studies that have tested for such advantages in *L. flavolineata*.

4.4.1 Costs of Nest Initiation

Independent nesting involves paying two costs associated with nest initiation: the cost of finding a suitable nest site and the cost of building a new nest. Potentially, this could explain why females opt to become helpers. In many wasps and bees, a helper avoids only some of the nest-building costs, such as those involved in producing a nest petiole or a protective nest envelope. If her decision to help leads to the group rearing more offspring, then new cells may have to be built to house those offspring, just as an independent nester will have to build new cells. In *L. flavolineata*, however, a female that chooses to help may avoid more of the costs of nest initiation than in most wasps and bees. Because more than half of the cells in a typical nest are empty at any given time, any extra offspring that a helper rears may be placed in these pre-existing cells (Field et al. 1998a). Furthermore, the mud nest of *L. flavolineata* may be unusually costly to build: nest weight per cell is roughly 50 times that of a *Polistes* nest, although costs of processing mud versus wood pulp are unknown (Field et al. 1998a).

L. flavolineata nests occasionally fall vacant when their owners disappear (Samuel 1987; pers. obs.). If independent nesting is constrained primarily by the costs of nest initiation, helpers should adopt vacant nests, as has sometimes been

observed (Samuel 1987; Field et al. 1999). Aggregated clusters of *L. flavolineata* nests provide an ideal opportunity to test this hypothesis (Fig. 4.2). In two experiments, helpers were provided with easily accessible vacant nests, either by removing the residents from one-third of the nests in the cluster, or by adding nests taken from a different site. In each experiment, less than 5% of the vacancies were filled by helpers from unmanipulated nests, even though the ratio of helpers:vacant nests was >8:1 (Field et al. 1998a). Helpers did visit vacant nests, but chose not to adopt them. Thus, although the costs of nest initiation may contribute towards the decision to become a helper, they do not seem to provide a complete explanation (see also Bull and Schwarz 1996 in an allodapine bee). These results are opposite to those of analogous experiments on cooperatively breeding birds, in which helpers immediately left their groups to adopt experimentally provided territorial vacancies (Komdeur 1992; Pruett-Jones and Lewis 1990; Walters et al. 1992). Together, these findings suggest that a territory is a more valuable resource for a vertebrate than is a nest for a wasp (Field et al. 1998a).

4.4.2 Insurance-Based Advantages of Helping

Insurance-based advantages depend on what happens to a female's investment after she dies. In hover wasps and other eusocial vespids, offspring require continuous adult care during their development. This is partly because larvae are fed gradually as they grow: the death of its carers will mean starvation for a partially fed larva. Even fully grown larvae and pupae remain vulnerable, however. Without the second component of adult care, protection, they often fall prey to generalist predators such as ants. It is therefore a paradoxical feature of social wasp life-histories that adult carers are short-lived compared to the development period of their dependent offspring. Lifespans may be short because foraging is a risky activity. As in polistines, fewer than 50% of independent-nesting *L. flavolineata* females can expect to survive long enough to bring any offspring through to adulthood, the remainder will have zero reproductive success (Samuel 1987; Queller 1996; Field et al. 1998a, 2000). This may explain why so few of the vacant nests were adopted in the experiment of Field et al. (1998a): a vacant nest is of little value if there is only a small chance of rearing independent offspring in it.

Nesting independently is clearly a risky option for a female wasp, but will a helper fare any better? A helper also has to forage, and in *L. flavolineata* has the same life expectancy as an independent nester (Field et al. 2000). The critical difference is that even if a helper dies young, her investment may be preserved through various forms of insurance that are unavailable to independent nesters. The first form occurs because when she reaches adulthood, a helper is usually on a nest that already contains partially reared offspring. Unlike an independent nester, she does not have to start rearing offspring from the egg stage (Queller 1989). It is therefore more likely that some of the offspring she helps to rear will have reached adulthood before the group fails. The second reason that an early death need not mean total

failure for a helper is that while she was present as a forager, her dominant relative did not have to carry out risky foraging herself, and other high-ranking helpers were able to decrease their foraging effort partially (Cant and Field 2001; Field et al. 2006). Through prolonging her relatives' lifespans, the helper also reduces the risk that the whole group will fail (see Reeve 1991; Queller 1996). This advantage, known as 'survivorship insurance', will be largest for the first helper (Nonacs 1991). Consistent with survivorship insurance, groups that are made smaller experimentally do take longer to fail in *L. flavolineata* (Shreeves and Field 2002).

The third potential insurance advantage for helpers, and the one best investigated in *L. flavolineata*, is known as 'Assured Fitness Returns' (Gadagkar 1990). The idea is straightforward: after an independent nester dies, her part-reared offspring are doomed. In contrast, after a helper dies, the offspring she contributed to may be brought to maturity by surviving nest-mates (Strassmann and Queller 1989; Gadagkar 1990). As in most primitively eusocial insects, each additional *L. flavolineata* helper allows the group to rear a few more offspring (Field et al. 2000; Shreeves and Field 2002). When a helper dies, therefore, the reduced group is left with extra offspring compared to the number that such a group would normally rear (Fig. 4.3). Experimental removal of helpers to mimic natural deaths showed that these extra offspring are indeed almost entirely reared through to maturity, effectively preserving the dead helper's investment (Field et al. 2000). In contrast, experimental removal of independent nesters not surprisingly led to the almost complete failure of their part-reared offspring. Even allowing for the fact that independent nesters are more

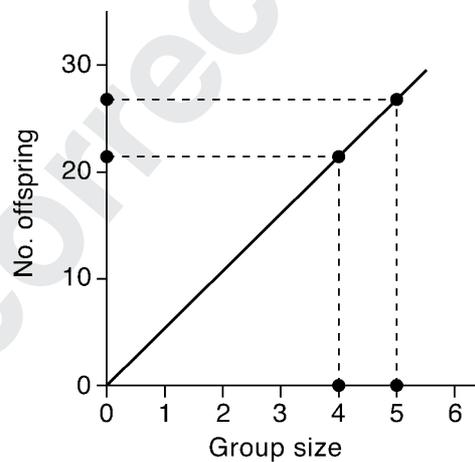


Fig. 4.3 Illustration of assured fitness returns. The *solid line* shows the observed positive relationship between group size and the total number of offspring being reared in *L. flavolineata*. *Dashed lines* show numbers of offspring reared by groups of 4 and 5 females, the difference on the y-axis representing the investment of the fifth individual. If that individual dies, the reduced group of four will be left with extra offspring on top of the number that a group of four would normally rear. In *L. flavolineata*, the extra offspring are almost all reared through, so that helpers do indeed have assured fitness returns (Field et al. 2000)

closely related than helpers to the offspring being reared, they would have to be approximately 1.7 times as productive as helpers to compensate for failure of their offspring when they die (Field et al. 2000). To put this in context, Hamilton's (1964) famous 'haplodiploidy' hypothesis gave helpers a 1.5 times productivity advantage. How a reduced group manages to rear the extra offspring left after a helper dies is uncertain: remaining adults do not seem to increase their foraging rates, and offspring development time is the same as on control nests (Field et al. 2000). Some of the extra offspring will be fully fed larvae or pupae that require only protection to complete their development: remaining adults can provide this through their presence alone. The extra pupae should themselves increase the short-term rate of helper recruitment to a reduced group, making it easier to rear extra smaller offspring through to adulthood. A third mechanism is suggested by finding that the very smallest extra offspring (eggs and tiny larvae) are not reared through after a helper's death. These may be sacrificed to feed the larger offspring. Effectively, when left with a package of extra offspring that it cannot afford to rear, a reduced group may rear the larger, more valuable offspring by feeding them with the smaller, less valuable offspring (Field et al. 2000). Even if some larvae receive less than the normal amount of food, investment is preserved so long as resulting adults suffer a decrease in fitness that is no more than proportionate with the reduction in food.

4.4.3 *Direct Fitness for Helpers Through Inheritance*

Although the dominant lays almost all of the eggs on an *L. flavolineata* nest, helpers have a chance of eventually inheriting the dominant position themselves. Helpers are in an age-based queue, each waiting until she is the oldest living female and becomes the dominant (Samuel 1987; Bridge and Field 2007). Age-based queuing is common in primitively eusocial animals, and queue dynamics are predictable (Fig. 4.4): Kokko and Sutherland 1998; Field et al. 1999; Shreeves and Field 2002). In particular, the further a female is from the front of the queue, the smaller her chance of surviving to inherit.

The obvious alternative to remaining in the queue is for a female to leave her natal nest and nest independently. She can then immediately become an egg-layer, but will have no helpers herself unless she is joined by other females or survives to produce adult offspring. In contrast, a queuing female stands to inherit not just the egg-laying position but also a group of younger females that will rear her offspring and provide insurance if she dies (Shreeves and Field 2002). Since offspring production increases linearly with group size in *L. flavolineata*, this is a significant advantage. The relatively small group sizes found in hover wasps mean that the chance of inheritance may be unusually high (Fig. 4.4). Furthermore, unlike temperate wasps, waiting times for hover wasp helpers are not constrained by the arrival of winter. Overall, direct fitness may be a relatively large component of total fitness for hover wasp helpers, although this has yet to be quantified. One question this

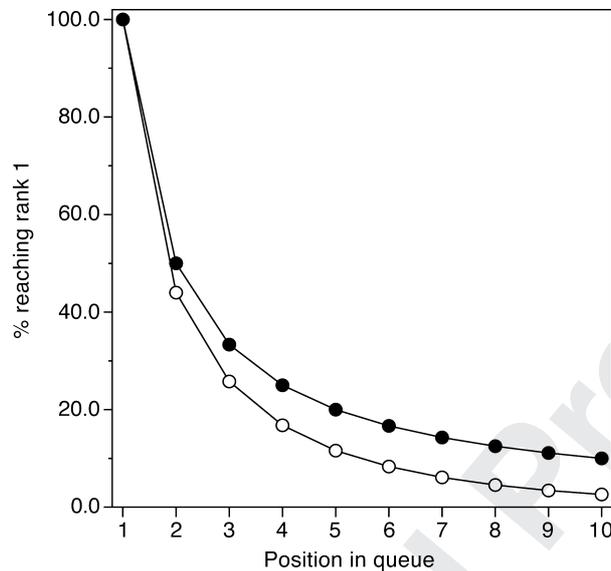


Fig. 4.4 Estimated relationship between position in the queue and chance of surviving to inherit the dominant (rank 1) position. The *filled circles* assume that all individuals have equal expected lifespans and constant mortality rates, so that the probability of inheritance is simply $1/n$, where n = group size. The *open circles* are based on the observed relationship between mortality rate and queue position in *L. flavolineata*, in which higher-ranked individuals live longer than lower-ranked individuals (re-drawn from Field et al. 1999)

leads to is whether a female would do best to remain in the group but not forage, thus minimizing her mortality risk while maximizing her chance of surviving to inherit. It is possible that other group members would punish such cheats or expel them from the group (see Mulder and Langmore 1993; Balshine-Earn et al. 1998). In addition, although foraging probably has significant personal costs, it has indirect fitness benefits through increased production of related offspring, and perhaps also direct benefits (Kokko et al. 2001). The interplay between the various costs and benefits of actively helping is an interesting area for future research that will be discussed further below, when considering individual variation in helping effort (Sect. 4.5.3).

4.5 Individual Variation in Helping Decisions

Insurance advantages, indirect benefits through rearing relatives, and resource inheritance through queuing are factors that could help to explain why females choose to become helpers. A further question, however, is why there is variation. First, why do some females choose to help while others leave their natal nests and

pursue other strategies? One possibility is that this represents a parental bet-hedging strategy. Another, not mutually exclusive explanation is that different decisions are adaptive for the individual offspring concerned. A second, related question is why do some helpers appear to work harder than others? Before discussing whether decision-making is adaptive, I will briefly outline the evidence that some female offspring do indeed leave.

The proportion of female offspring that choose to leave their natal nests is hard to quantify in *L. flavolineata* because of the difficulty of distinguishing between leaving and death. Samuel (1987) implies that around 70% of 230 newly emerged females disappeared from their natal nests, the other 30% becoming helpers. Of those that disappeared, 22% were seen subsequently, so that 15% is a minimum estimate of the true proportion leaving. Two-thirds of the definite 'leavers' initially became nest-less floaters, while others immediately built new nests, adopted vacant nests, or joined lone foundresses. Samuel (1987) does not give the timescale over which females disappeared, and it is not clear whether she took possible effects of marking into account. Field et al. (1999) examined the fates of 126 newly emerged females whose decisions were unlikely to have been affected by marking. They found that on average, 2.5% of females disappeared per day. There was no indication that this rate changed during the first month of life, but older females disappeared at the significantly lower rate of 1.2% per day. One explanation for this difference is that there is a 'leaving window' early in life, while another is simply that younger females have higher mortality rates, although this did not agree with the fact that they spent more time on the nest than older subordinates (Field et al. 1999). Only 13% of females that disappeared were seen again. Coster-Longman and Turillazzi (1998) could distinguish between leaving and death in their captive population of another hover wasp, *Parischnogaster mellyi*. They found that 75% of newly emerged females left their natal nests, supporting the idea that many of the disappearances seen in the wild truly represent leaving.

4.5.1 Queue Length and Leaving Decisions

A female's decision to stay or leave might depend on her phenotype or genotype as well as environmental conditions including the social environment on her natal nest. One key variable could be queue length, the number of older females already on the nest. A newly emerged female will start at the end of the queue, and her chance of inheriting the dominant position will decline exponentially with decreasing rank (Fig. 4.4). The positive relationship between group size and both productivity and insurance benefits in *L. flavolineata* will tend to counteract this effect: females that do inherit will enjoy greater reproductive success in larger groups (Field et al. 1999; Cant and Field 2001; Shreeves and Field 2002). Nevertheless, the net effect might be a threshold queue length above which females would do better to leave (Shreeves and Field 2002). To test this idea, Field et al. (1999) experimentally reduced the queue lengths on half of the nests

in two clusters, but found that newly emerged females were no less likely to disappear from manipulated nests than controls. This suggests that the disadvantage of starting from the end of a longer queue may be approximately balanced by advantages that are positively correlated with group size (Shreeves and Field 2002). However, a threshold queue length above which newly emerged females leave their natal nests might be revealed by experimentally lengthening (rather than shortening) natural queues.

4.5.2 *The Subfertility Hypothesis*

The subfertility hypothesis is another potential explanation for variation in leaving decisions. It suggests that females of relatively low quality choose to become helpers because they would achieve little reproductive success if they attempted independent reproduction (West-Eberhard 1975; Craig 1983). Effectively, the cost of helping, in terms of own reproduction lost, is low for such females. A general problem for the subfertility hypothesis is that low-quality females may also make poor helpers (Craig 1983; Queller 1996): helpers must carry out the same tasks as independent-nesting females, including nest-building and foraging. An exception, however, is egg-laying. Females with a reduced ability to lay eggs but with normal capabilities otherwise, might choose to become helpers. Field and Foster (1999) tested the ability of *L. flavolineata* helpers to lay eggs by removing the dominant and all but one focal helper from 22 nests. The focal helpers thus forced to nest alone soon mated and developed ovaries characteristic of dominants. While far from a quantitative comparison of helpers and independent nesters, this experiment shows that helpers are generally not unconditionally physiologically constrained.

Also arguing against subfertility as an explanation for helping in *L. flavolineata* and many other primitively eusocial insects is the gerontocratic system of inheritance: today's 'subfertile' helpers are tomorrow's dominant egg-layers. One way around this might be if low-quality helpers have higher mortality rates, and are therefore less likely to ever become dominants. To the extent that size reflects quality, there is no evidence for this in *L. flavolineata*: rates of disappearance are independent of size, and dominants are not systematically larger than subordinates (Field et al. 1999; Sumner et al. 2002). In a study of *Polistes fuscatus*, smaller females were actually more likely than larger females to disappear from their natal nests (Reeve et al. 1998b). This is opposite to the predictions of the subfertility hypothesis because disappearing females are thought to be those that overwinter and found new nests in spring. In contrast, Yanega (1989) found that larger female offspring were more likely to leave and overwinter in the sweat bee *Halictus rubicundus*, but he suggested that the underlying cause could be a seasonal increase in offspring size rather than size-based decision-making. Whereas Yanega re-sighted a large proportion of leavers the following spring, interpreting the data for *Polistes* and *Liostenogaster* is complicated by the problem of not being able to distinguish whether most disappearing females had truly left or had simply died. This could

make it harder to detect adaptive patterns, and observed patterns could even reflect size-related mortality rather than individual decision-making. Further progress in this area awaits the development of tracking devices suitable for individual wasps, or might involve captive populations such as those studied by Coster-Longman and Turillazzi (1998). The subfertility hypothesis seems worthy of further investigation in primitively eusocial insects. There is a dearth of experimental tests to date, perhaps because of the difficulty of measuring quality or fertility.

4.5.3 Individual Variation in Helping Effort

Helping is not an all-or-nothing decision. In eusocial and cooperatively breeding societies there is substantial variation in how hard individual helpers work (Clutton-Brock et al. 2000; Cant and Field 2001). Initial attempts to understand this variation focused on the prediction that more help should be given to closer relatives, but with mixed results (e.g., Clutton-Brock et al. 2000; Queller et al. 2000; Griffin and West 2003). In *L. flavolineata*, for example, helping effort is not correlated with relatedness, even after controlling for other variables (Field et al. 2006). In insects, the lack of support for kinship-based nepotism in general may reflect informational constraints, or prohibitive costs to the group (Keller 1997; Hannonen and Sundström 2003). The failure to explain much of the variation in helping effort using relatedness has led some to question whether kin selection truly provides a general explanation for helping (Clutton-Brock 2002; Griffin and West 2002).

Cant and Field (2001, 2005) developed models in which variation in helping effort primarily reflects variation in the costs of helping. Helpers face a fundamental trade-off: by working harder to rear the offspring of a relative, they simultaneously decrease their own future survival and reproductive success through inheriting breeding positions. Because individuals with greater expected future fitness have more to lose, they should work less hard (Cant and Field 2001). Social queues, where individuals inherit breeding positions in a predictable order, are ideal for testing this hypothesis because they lead to systematic differences in expected future fitness. In particular: (1) individuals nearer the front of the queue are more likely to inherit (Fig. 4.4), and (2) if larger groups are more productive, an individual waiting in a longer queue can expect greater reproductive success should she succeed in inheriting. Consistent with these differences, Cant and Field (2001) found that subordinate co-foundresses in *Polistes dominulus* allocated a smaller proportion of their time to risky foraging if they were nearer to the front of the queue, or if they were in a larger group. In both cases, individuals with more to lose were prepared to work less hard. These effects were only correlative, however. Position in the queue cannot be deduced *a priori* in *P. dominulus*, so that it cannot easily be manipulated. The strict age-based queue in *L. flavolineata* allows a more convincing test: by knowing their relative ages, it is possible to order females precisely in the queue. Recent experiments in which queue position and group size were experimentally manipulated show that *L. flavolineata* helpers adjust their foraging effort just as predicted from the life-history perspective of Cant and Field. Helpers

worked less hard after being promoted in the queue, but worked harder if their groups were made smaller (Field et al. 2006).

The absence of any correlation between helping effort and relatedness might primarily reflect the inability of helpers to distinguish variation in relatedness at the individual level (Keller 1997). In contrast, group size and position in the queue may provide easily discernible indications of the future fitness that a helper stands to lose. Helpers may thus respond to variation in individual future fitness, while being forced to respond only to the average relatedness. How females determine their position in the queue is unknown. In small groups, one possible mechanism might be for a female to learn the identities of the other females that were already present when she first reached adulthood (see Tibbetts 2002). The fewer of these that remain alive, the nearer to the front of the queue she must be if queuing is age-based. A second possibility is that cues such as cuticular hydrocarbon composition are correlated with age, and therefore with queue position (see Sledge et al. 2001; Cuvillier-Hot et al. 2004; Turillazzi et al. 2004). Females might compare their own cues with those of nest-mates.

4.5.4 Individual Variation in Aggression

Position in the queue should affect a female's willingness to perform any act that might jeopardize her future fitness, not just foraging. A possible example is aggression towards nest-mates. Like foraging, aggression may be risky, if it can lead to the aggressor's death or injury, but unlike foraging, aggression could also increase the actor's future direct fitness through queue-jumping. Cant et al. (2006) showed theoretically that if aggression functions to test or challenge individuals ahead in the queue, or to deter challenges from individuals further back, high-ranking subordinates should be more aggressive. Most interactions on unmanipulated *L. flavolineata* nests are apparently mild antennations of one female by another, but this can escalate into chasing and biting (A. Cronin and J. Field, submitted). Cronin and Field (submitted) obtained results consistent with Cant et al.'s model in that high-ranking subordinates tended to both initiate and receive more interactions, although this was partly because high rankers spent more time on the nest. Most interactions were between wasps of adjacent rank, suggesting that interactions might indeed function in maintaining or contesting queue position. Cronin and Field (2007) found a similar pattern in defensive behavior: higher-ranked individuals were the most likely to defend the nest against foreign conspecifics.

4.6 Helping in Hover Wasps Other than *L. flavolineata*

Although *L. flavolineata* is the only hover wasp in which experimental manipulations have been used to study costs and benefits of helping, the social biology of other species has been examined in more or less detail (see summary and references in

Turillazzi 1991). Here, I will briefly summarize just two aspects of these studies: first, reproductive skew; and second, the reduced behavioral division of labor that seems to occur in *Eustenogaster fraterna*.

4.6.1 *Reproductive Skew in Hover Wasps*

Whenever there is genetic heterogeneity among the individuals in an animal society, relatedness asymmetries between group members and potential offspring may lead to conflicts of interest as different individuals simultaneously attempt to maximize their genetic profit (Ratnieks and Reeve 1992). Reproductive skew, the degree to which reproduction is shared among the members of a society, is one such conflict that has recently attracted particular attention. The distribution of reproduction among group members may range from complete equality (low skew) to monopolization by a single breeder or dominant (high skew). Over the past decade, several models have been formulated to examine how skew may be affected by genetic, ecological, and behavioral factors: for reviews, see Johnstone (2000), Magrath and Heinsohn (2000), Reeve and Keller (2001). Concessions models are built on the assumption that groups contain a single dominant breeder that has complete control over subordinate reproduction (Vehrencamp 1983; Reeve and Ratnieks 1993; Kokko and Johnstone 1999; Ragsdale 1999). This dominant individual has the option of yielding a reproductive concession to a subordinate in exchange for its cooperation. In contrast, tug-of-war models assume that dominants have incomplete control of subordinates, and group-members channel resources into intra-group competition over reproduction (Reeve et al. 1998a).

All female hover wasps are potential reproductives, but the small groups and small physical nest structures suggest that dominants could have complete control over reproduction, as in the 'concessions' framework. Hover wasps therefore represent potentially useful model systems, and genetic markers have been used to estimate skew in *L. flavolineata*, *Parischnogaster mellyi* and *P. alternata* (Sumner et al. 2002; Fanelli et al. 2005; Bolton et al. 2006). Despite intraspecific variation in some of the parameters predicted theoretically to influence skew, however, and despite the somewhat lower average relatedness in *P. mellyi*, skew in all three species is consistently extremely high, close to complete monopolization of reproduction by the dominant. Individual groups with lower relatedness do occur, but generally still maintain high skew. These results are contrary to initial speculation that hover wasps might have relatively low skew (Sherman et al. 1995). Within the framework of the concessions models, at least two factors could account for consistently high skew. The first is strong ecological constraints on independent nesting: a lone *L. flavolineata* female has at most a 50% chance of surviving to produce adult offspring (Samuel 1987; Field et al. 2000). The concessions models predict that strong constraints will induce helpers to accept a high skew (Reeve and Ratnieks 1993). The second factor is the

relatively good chance that helpers have of eventually inheriting dominance themselves: effectively, skew is lower when considered over a helper's entire lifespan (Fig. 4.4; Sumner et al. 2002). Life-history-based models of skew predict that such delayed benefits can stabilize a high skew (Kokko and Johnstone 1999; Ragsdale 1999). Although somewhat unsatisfying because of their qualitative nature, these conclusions are mirrored by studies of reproductive skew in *Polistes* (Field et al. 1998b; Queller et al. 2000; Seppa et al. 2002; but see Reeve et al. 2000; reviewed by Field and Cant, 2007). Further progress in this area will require experimental manipulation of key parameters such as ecological constraints and relatedness (e.g., Langer et al. 2004), together with interspecific comparative analyses.

4.6.2 Task Allocation in *Eustenogaster Fraterna*

Some hover wasps, such as species of *Stenogaster* and *Anischnogaster*, have considerably smaller average group sizes than *L. flavolineata*, with most nests having just a single female resident at any one time (e.g., Spradbery 1975; Turillazzi and Hansell 1991). This might reflect weak constraints on independent nesting so that most offspring leave their natal nests, or environmental conditions that lead to high adult mortality rates relative to the birth rate. Peculiarities of nest structure that limit maximum nest size might also contribute (Hansell 1987a; Turillazzi 1990). Nevertheless, in the minority of groups that have multiple female residents, there is still a clear behavioral division of labor in these species, comprising one or more foragers and a dominant female that rarely leaves the nest (Turillazzi and Hansell 1991). Recently, however, an apparent exception to this pattern has been described in *E. fraterna* (Francescato et al. 2002). In *E. fraterna*, relatedness is fairly high and group size not as small as in *Stenogaster* and *Anischnogaster* (Landi et al. 2003). There seems to be only a single egg-layer as in other hover wasps, but unusually, the egg-layer carries out much of the risky foraging. This contrasts with most other primitively eusocial wasps, including other hover wasps such as the congeneric *E. calyptodoma*, in which the egg-layer rarely leaves the nest and never forages for larval provisions (Hansell 1987b). Other exceptions to this rule appear to be very small groups of some *Polistes*, where dominants carry out some of the foraging, and xylocopine bees in which an older egg-layer does most or all of the foraging while a non-egg-layer guards the nest entrance (e.g., Lorenzi and Turillazzi 1986; Field et al. 1998b; Hogendoorn and Velthuis 1999). The situation in *E. fraterna* superficially resembles that in some co-operatively breeding vertebrates, in which breeders continue to forage in the presence of helpers. By working less hard and thereby forcing the dominant to work harder, helpers may increase their chance of inheriting the dominant position (Francescato et al. 2002). Francescato et al.'s data suggest that the behavioral division of labor may even vary between nests of *E. fraterna*, and more work on this system could be of great interest.

4.7 Conclusions: Helping in Stenogastrine and Vertebrate Social Systems—Similarities and Differences

In eusocial wasps and bees, helping takes a form similar to that in many cooperatively breeding vertebrates, particularly birds: by foraging to feed the breeder's offspring, helpers increase the number of offspring successfully reared. In most wasps, such as *L. flavolineata*, however, the increase results partly from increased clutch size, whereas in vertebrates it typically results from a larger proportion of offspring reaching maturity from a fixed initial clutch (e.g., Field et al. 2000 and Shreeves et al. 2003 in wasps; Heinsohn and Cockburn 1994 and Wright 1997 in vertebrates). In part, this may reflect a limitation on clutch size in vertebrates that produce relatively large offspring, compared to the smaller, less costly offspring of insects. In wasps, breeders completely cease foraging in the presence of helpers, almost certainly increasing their own and often the group's survivorship, paralleling the 'load-lightening' that occurs in many cooperatively breeding birds (e.g., Reeve and Nonacs 1997; Shreeves and Field 2002; Shreeves et al. 2003; Hatchwell 1999). In wasps, the continuous presence of the breeder on the nest also reduces the chance that the nest will be usurped by nest-less conspecific 'floaters'.

The primary ecological pressures that favor helping in stenogastrines appear to differ qualitatively from those in vertebrates. In many vertebrates, a major ecological constraint on independent reproduction is a shortage of suitable breeding territories ('habitat saturation': Komdeur 1992; Pruett-Jones and Lewis 1990; Walters et al. 1992). In contrast, wasps and bees are not territorial. A potentially analogous factor, the cost of nest initiation, while important in at least one extreme environment (McCorquodale 1989), is not enough to alone favor helping in *L. flavolineata* or an allodapine bee (Bull and Schwarz 1996; Field et al. 1998a). Insurance advantages appear to be a major factor that does favor helping in both stenogastrines and polistines (Reeve and Nonacs 1997; Field et al. 2000; Shreeves et al. 2003). Insurance advantages have not been seriously investigated in vertebrates, but may be less important (but see Langen 2000). One reason is that carer mortality rates in vertebrates are probably lower in relation to the period of offspring dependency than they are in wasps (Queller 1996). For example, Davies (1992) reports that only 13–20% of dunnock breeders die during the breeding season itself. A second reason is that while wasps can potentially recycle excess offspring at minimal cost after the death of a carer, this may not be an option for non-carnivorous vertebrates such as many birds, in which previous investment may be lost after a carer dies (Shreeves et al. 2003).

One similarity between cooperatively breeding vertebrates and stenogastrines in particular among wasps may be that resource inheritance is a significant benefit of remaining on the natal nest (as also in termites: Korb, this volume). Two features of stenogastrines underlie this. First, stenogastrine groups are always small, so that helpers may always have a reasonable chance of outliving individuals ahead of them in the queue to inherit (Field et al. 1999; Shreeves and Field 2002). Second, stenogastrine helpers can potentially wait indefinitely for their chance to inherit. This is a consequence of their relatively aseasonal tropical environment, in which

there is no absolute winter to truncate the lives of individuals waiting in the queue. Whether the chance of inheritance in stenogastrines is quantitatively similar to that in vertebrates remains to be seen, however, particularly given the significantly higher survivorship of the dominant egg-layer compared to her helpers in *L. flavolineata* (Field et al. 1999; Shreeves and Field 2002).

While resource inheritance has long been viewed as a significant benefit for vertebrate helpers, the possible importance of other direct benefits has been emphasized only recently (reviewed by Clutton-Brock 2002). One of these, that by helping an individual may improve its chances of eventually mating with the opposite-sex breeder, does not apply to wasps and bees, where mating occurs outside the group. A second direct benefit, demonstrated in some vertebrates, is that by remaining in its natal group an individual may increase its expected survivorship, perhaps because larger groups are better defended against predators. *L. flavolineata* is one of the few wasps for which reasonably comprehensive demographic data exist from natural populations. These data suggest that helpers do not have lower mortality rates than independent-nesting females (Field et al. 2000). It would, however, be interesting to compare their mortality rates with those of nest-less floaters, but reliable survivorship data do not currently exist for floaters.

Another direct benefit of helping that has recently been highlighted is group augmentation (Kokko et al. 2001). An example is when an individual can boost (augment) group size by helping, so that she will later have more helpers herself if she survives to inherit. By helping, *L. flavolineata* females do increase the number of offspring reared by the group, and the age-based queuing system ensures that such offspring are indeed potential future helpers themselves. This indicates that group augmentation benefits do exist, but their importance in driving patterns of helping behavior is less clear. Group augmentation effects alone should cause females nearer the front of the queue to work hardest: they have the greatest chance of inheriting and therefore of receiving help from any offspring that they contribute to rearing. That high-ranking helpers in fact work less hard than low rankers suggests that potential group augmentation benefits are outweighed by the negative effect that working harder would have on the chance of inheritance itself (Field et al. 2006). The relative importance of direct versus indirect benefits in driving helping remains an interesting area for future research in *L. flavolineata* and other insect and vertebrate taxa.

In conclusion, although the evolution of helping in both wasps and vertebrates can potentially be understood using the framework provided by Hamilton (1964), the critical ecological factors seem to be fundamentally different in these two major taxa (see also Chap. 7, for a comparison with lower termites). Simply measuring genetic relatedness cannot provide a clear understanding of why helping evolved, or explain individual variation in helping decisions. Costs and benefits are just as important, and the natural history of hover wasps makes them an ideal system for investigating these costs and benefits.

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References

- Balshine-Earn S, Neat FC, Reid H, Taborsky M (1998) Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. *Behav Ecol* 9:432–438
- Bolton A, Sumner S, Shreeves G, Casiraghi M, Field J (2006) Colony genetic structure in a facultatively eusocial hover wasp. *Behav Ecol* 17:873–880
- Bridge CAL (2005) Rank and inheritance in a facultatively eusocial hover wasp. PhD Thesis, University College London, London
- Bridge CAL, Field J (2007) Queuing for dominance: gerontocracy and queue-jumping in the hover wasp *Liostenogaster flavolineata*. *Behav Ecol Sociobiol* (in press)
- Bull NJ, Schwarz MP (1996) The habitat saturation hypothesis and sociality in an allodapine bee: cooperative nesting is not “making the best of a bad situation”. *Behav Ecol Sociobiol* 39:267–274
- Cant MA, Field J (2001) Helping effort and future fitness in cooperative animal societies. *Proc R Soc Lond B* 268:1959–1964
- Cant MA, Field J (2005) Helping effort in a dominance hierarchy. *Behav Ecol* 16:708–715
- Cant MA, Llop JB, Field J (2006) Individual variation in social aggression and the probability of inheritance: theory and a field test. *Am Nat* 167:837–852
- Carpenter JM (1991) Phylogenetic relationships and the origin of social behavior in the Vespidae. In: Ross KG, Matthews RW (eds) *The social biology of wasps*. Cornell University Press, New York, pp 7–32
- Carpenter JM (2003) On “Molecular phylogeny of Vespidae (Hymenoptera) and the evolution of sociality in wasps”. *Am Museum Novitates* 3389:1–20
- Carpenter JM, Starr CK (2000) A new genus of hover wasps from Southeast Asia (Hymenoptera: Vespidae; Stenogastrinae) *Am Museum Novitates* 3291:1–12
- Clutton-Brock TH (2002) Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72
- Clutton-Brock TH, Brotherton PNM, O’Riain MJ, Griffin AS (2000) Individual contributions to babysitting in a cooperative mongoose *Suricata suricatta*. *Proc R Soc Lond B* 267:301–305
- Coster-Longman C, Turillazzi S (1998) Leaving the nest and related behavioural strategies in a captive population of *Parischnogaster mellyi* (Stenogastrinae, Vespidae, Hymenoptera) *Insect Social Life* 2:37–44
- Coster-Longman C, Landi M, Turillazzi S (2002) The role of passive defence (selfish herd and dilution effect) in the gregarious nesting of *Liostenogaster* wasps (Vespidae, Hymenoptera, Stenogastrinae). *J Insect Behav* 15:331–350
- Craig R (1983) Subfertility and the evolution of social behaviour by kin selection. *J Theoret Biol* 100:379–397
- Cronin A, Field J (2007) Rank and colony defence in the facultatively eusocial hover wasp *Liostenogaster flavolineata*. *Behav Ecol* 18:331–336
- Cuvillier-Hot V, Lenoir A, Crewe R, Malosse C, Peeters C (2004) Fertility signalling and reproductive skew in queenless ants. *Anim Behav* 68:1209–1219
- Davies NB (1992) *Dunnock behaviour and social evolution*. Oxford University Press, Oxford
- Fanelli D, Boomsma JJ, Turillazzi S (2005) Multiple reproductive strategies in a tropical hover wasp. *Behav Ecol Sociobiol* 58:190–199

- Field J, Cant MA (2007) Reproductive skew in primitively eusocial wasps: how useful are current models? In: Hager R, Jones CB (eds) Reproductive skew in vertebrates. Cambridge University Press, Cambridge (in press)
- Field J, Foster W (1999) Helping behaviour in facultatively eusocial hover wasps: an experimental test of the subfertility hypothesis. *Anim Behav* 57:633–636
- Field J, Foster W, Shreeves G, Sumner S (1998a) Ecological constraints on independent nesting in facultatively eusocial hover wasps. *Proc R Soc Lond B* 265:973–977
- Field J, Solis CR, Queller DC, Strassmann JE (1998b) Social and genetic structure of paper wasp cofoundress associations: tests of reproductive skew models. *Am Nat* 151:545–563
- Field J, Shreeves G, Sumner S (1999) Group size, queuing and helping decisions in facultatively eusocial hover wasps. *Behav Ecol Sociobiol* 45:378–385
- Field J, Shreeves G, Sumner S, Casiraghi M (2000) Insurance-based advantage to helpers in a tropical hover wasp. *Nature* 404:869–871
- Field J, Cronin A, Bridge C (2006) Future fitness and helping in social queues. *Nature* 441:214–217
- Francescato E, Massolo A, Landi M, Gerace L, Hashim R, Turillazzi S (2002) Colony membership, division of labour, and genetic relatedness among females of colonies of *Eustenogaster fraterna* (Hymenoptera, Vespidae, Stenogastrinae). *J Insect Behav* 15:153–170
- Gadagkar R (1990) Evolution of eusociality: the advantage of assured fitness returns. *Phil Trans R Soc Lond B* 329:17–25
- Griffin AS, West SA (2002) Kin selection: fact and fiction. *Trends Ecol Evol* 17:15–21
- Griffin AS, West SA (2003) Kin discrimination and the benefits of helping in cooperatively breeding vertebrates. *Science* 302:634–636
- Hamilton WD (1964) The genetical evolution of social behaviour. I and II. *J Theoret Biol* 7:1–52
- Hammond RL, Keller L (2004) Conflict over male parentage in social insects. *PLoS Biol* 2:e248
- Hannonen M, Sundström L (2003) Worker nepotism among polygynous ants. *Nature* 421:910
- Hansell M (1982) Brood development in the subsocial wasp *Parischnogaster mellyi* (Saussure), (Stenogastrinae, Hymenoptera) *Insectes Soc* 29:3–14
- Hansell M (1987a) Nest building as a facilitating and limiting factor in the evolution of eusociality in the Hymenoptera. *Oxf Surv Evol Biol* 4:155–181
- Hansell M (1987b) Elements of eusociality in colonies of *Eustenogaster calyptodoma* (Sakagami & Yoshikawa) (Stenogastrinae, Vespidae). *Anim Behav* 35:131–141
- Hatchwell B (1999) Investment strategies of breeders in avian cooperative breeding systems. *Am Nat* 154:205–219
- Heinsohn R, Cockburn A (1994) Helping is costly to young birds in cooperatively breeding white-winged choughs. *Proc R Soc Lond B* 256:293–298
- Hines HM, Hunt JH, O'Connor TK, Gillespie JJ, Cameron SA (2007) Multigene phylogeny reveals eusociality evolved twice in vespid wasps. *Proc Natl Acad Sci USA* 104:3295–3299
- Hogendoorn K, Velthuis HHW (1999) Task allocation and reproductive skew in social mass provisioning carpenter bees in relation to age and size. *Insectes Soc* 46:198–207
- Hughes CR, Queller DC, Strassmann JE, Davis SK (1993) Relatedness and altruism in *Polistes* wasps. *Behav Ecol* 4:128–137
- Johnstone RA (2000) Models of reproductive skew: a review and synthesis. *Ethology* 106:5–26
- Karsai I, Penzes Z, Wenzel JW (1996) Dynamics of colony development in *Polistes dominulus*: a modeling approach. *Behav Ecol Sociobiol* 39:97–105
- Keller L (1997) Indiscriminate altruism: unduly nice parents and siblings. *Trends Ecol Evol* 12:99–103
- Kokko H, Johnstone RA (1999) Social queuing in animal societies: a dynamic model of reproductive skew. *Proc R Soc Lond B* 266:571–578
- Kokko H, Sutherland WJ (1998) Optimal floating and queuing strategies: consequences for density dependence and habitat loss. *Am Nat* 152:354–366
- Kokko H, Johnstone RA, Clutton-Brock TH (2001) The evolution of cooperative breeding through group augmentation. *Proc R Soc Lond B* 268:187–196
- Komdeur J (1992) Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* 358:493–495

- Landi M, Queller DC, Turillazzi S, Strassmann JE (2003) Low relatedness and frequent queen turnover in the stenogastrine wasp *Eustenogaster fraterna* favour the life insurance over the haplodiploid hypothesis for the origin of eusociality. *Insectes Soc* 50:262–267
- Langen TA (2000) Prolonged offspring dependence and cooperative breeding in birds. *Behav Ecol* 11:367–377
- Langer P, Hogendoorn K, Keller L (2004) Tug-of-war over reproduction in a social bee. *Nature* 428:844–847
- Lorenzi MC, Turillazzi S (1986) Behavioural and ecological adaptations to the high mountain environment of *Polistes biglumis bimaculatus*. *Ecol Entomol* 11:199–204
- Magrath RD, Heinsohn RG (2000) Reproductive skew in birds: models, problems and prospects. *J Avian Biol* 31:247–258
- McCorquodale DB (1989) Soil softness, nest initiation and nest sharing in the wasp, *Cerceris antipodes* (Hymenoptera: Sphecidae). *Ecol Entomol* 14:191–196
- Mulder R, Langmore NE (1993) Dominant males punish helpers for temporary defection in superb fairy-wrens. *Anim Behav* 45:830–833
- Nonacs P (1991) Alloparental care and eusocial evolution: the limits of Queller's head start advantage. *Oikos* 61:122–125
- Pruett-Jones SG, Lewis MJ (1990) Sex-ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature* 348:541–542
- Queller DC (1989) The evolution of eusociality: reproductive head starts of workers. *Proc Natl Acad Sci USA* 86:3224–3226
- Queller DC (1996) The origin and maintenance of eusociality: the advantage of extended parental care. In: Turillazzi S, West-Eberhard MJ (eds) *Natural history and evolution of paper-wasps*. Oxford University Press, Oxford, pp 218–234
- Queller DC, Zacchi F, Cervo R, Turillazzi S, Henshaw MT, Santorelli LA, Strassmann JE (2000) Unrelated helpers in a social insect. *Nature* 405:784–787
- Ragsdale JE (1999) Reproductive skew theory extended: the effect of resource inheritance on social organisation. *Evol Ecol Res* 1:859–874
- Ratnieks FLW, Reeve HK (1992) Conflict in single-queen hymenopteran societies: the structure of conflict and processes that reduce conflict in advanced eusocial species. *J Theoret Biol* 158:33–65
- Reeve HK (1991) *Polistes*. In: Ross KG, Matthews RW (eds) *The social biology of wasps*. Cornell University Press, New York, pp 99–148
- Reeve HK, Keller L (2001) Tests of reproductive skew models in social insects. *Annu Rev Entomol* 46:347–85
- Reeve HK, Nonacs P (1997) Within-group aggression and the value of group members: theory and a field test with social wasps. *Behav Ecol* 8:75–82
- Reeve HK, Ratnieks LW (1993) Queen-queen conflicts in polygynous societies: mutual tolerance and reproductive skew. In: Keller L (ed) *Queen number and sociality in insects*. Oxford University Press, Oxford, pp 45–85
- Reeve HK, Emlen ST, Keller L (1998a) Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behav Ecol* 9:267–278
- Reeve HK, Peters JM, Nonacs P, Starks PT (1998b) Dispersal of first “workers” in social wasps: causes and implications of an alternative reproductive strategy. *Proc Natl Acad Sci USA* 95:13737–13742
- Reeve HK, Starks PT, Peters JM, Nonacs P (2000) Genetic support for the evolutionary theory of reproductive transactions in social wasps. *Proc R Soc Lond B* 267:75–79
- Ross K, Carpenter JM (1991) Population genetic structure, relatedness, and breeding systems. In: Ross KG, Matthews RW (eds) *The social biology of wasps*. Cornell University Press, New York, pp 451–479
- Samuel CT (1987) Factors affecting colony size in the stenogastrine wasp *Liostenogaster flavolineata* (PhD dissertation). University of Malaya, Kuala Lumpur
- Schmitz J, Moritz RFA (1998) Molecular phylogeny of Vespidae (Hymenoptera) and the evolution of sociality in wasps. *Molec Phylogenet Evol* 9:183–191

- Schmitz J, Moritz RFA (2000) Molecular evolution in social wasps. In: Austin AD, Downton M (eds) Hymenoptera: evolution, biodiversity and biological control, VIC: CSIRO Publishing, pp 84–89
- Seppa P, Queller DC, Strassmann JE (2002) Reproduction in foundress associations of the social wasp, *Polistes carolina*, conventions, competition, and skew. *Behav Ecol* 13:531–542
- Sherman PW, Lacey EA, Reeve HK, Keller L (1995) The eusociality continuum. *Behav Ecol* 6:102–108
- Shreeves G, Field J (2002) Group size and direct fitness in social queues. *Am Nat* 159:81–95
- Shreeves G, Cant MA, Bolton A, Field J (2003) Insurance-based advantages for subordinate co-foundresses in a temperate paper wasp *Proc R Soc Lond B* 270:617–1622
- Sledge MF, Boscaro F, Turillazzi S (2001) Cuticular hydrocarbons and reproductive status in the social wasp *Polistes dominulus* *Behav Ecol Sociobiol* 49:401–409
- Strassmann JE, Meyer DC (1983) Gerontocracy in the social wasp, *Polistes exclamans*. *Anim Behav* 31:431–438
- Strassmann JE, Queller DC (1989) In: Breed MD, Page RE (eds) The genetics of social evolution. Westview Press, Boulder, pp 81–101
- Strassmann JE, Hughes CR, Turillazzi S, Solis CR, Queller DC (1994) Genetic relatedness and incipient eusociality in stenogastrine wasps. *Anim Behav* 48:813–821
- Sumner S (1999) Conflicts over reproduction in facultatively eusocial hover wasps. PhD Thesis, University College London, London
- Sumner S, Casiraghi M, Foster W, Field J (2002) High reproductive skew in tropical hover wasps. *Proc R Soc Lond B* 269:179–186
- Tibbetts EA (2002) Visual signs of individual identity in the wasp *Polistes fuscatus*. *Proc R Soc Lond B* 269:1423–1428
- Tsuji K, Tsuji N (2005) Why is dominance hierarchy age-related in social insects? The relative longevity hypothesis. *Behav Ecol Sociobiol* 58:517–526
- Turillazzi S (1985) Brood rearing behaviour and larval development in *Parischnogaster nigricans serrei* (du Buysson) (Hymenoptera Stenogastrinae). *Ins Soc* 32:117–127
- Turillazzi S (1990) Notes on the biology, social behaviour and nest architecture of *Metischnogaster drewseni* (Saussure) (Hymenoptera, Stenogastrinae). *Boll Zool* 57:331–339
- Turillazzi S (1991) The Stenogastrinae. In: Ross KG, Matthews RW (eds) The social biology of wasps. Cornell University Press, New York, pp 74–98
- Turillazzi S (1996) *Polistes* in perspective: comparative social biology and evolution in *Belonogaster* and Stenogastrinae. In: Turillazzi S, West-Eberhard MJ (eds) Natural history and evolution of paper-wasps. Oxford University Press, Oxford, pp 235–247
- Turillazzi S, Hansell MH (1991) Biology and social behaviour of three species of *Anischnogaster* (Vespidae, Stenogastrinae) in Papua New Guinea. *Insectes Soc* 38:423–437
- Turillazzi S, Sledge MF, Dapporto L, Landi M, Fanelli D, Fondeli L, Zanetti P, Dani FR (2004) Epicuticular lipids and fertility in primitively social wasps (Hymenoptera Stenogastrinae). *Physiol Entomol* 29:464–471
- Vehrencamp SL (1983) A model for the evolution of despotic versus egalitarian species. *Anim Behav* 31:667–682
- Walters JR, Copeyon CK, Carter JH (1992) Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. *Auk* 109:90–97
- Wenseleers T, Ratnieks FLW (2006) Comparative analysis supports worker policing theory. *Am Nat* 168:E163–E179
- West-Eberhard MJ (1975) The evolution of social behaviour by kin selection. *Q Rev Biol* 50:1–33
- Wright J (1997) Helping-at-the-nest in Arabian babblers: signalling social status or sensible investment in chicks? *Anim Behav* 54:1439–1448
- Yanega D (1989) Caste determination and differential diapause within the first brood of *Halictus rubicundus* in New York (Hymenoptera: Halictidae). *Behav Ecol Sociobiol* 24:97–107

Uncorrected Proof