

The resolution of conflict in families

PT Smiseth¹ & NJ Royle²

5 ¹Institute of Evolutionary Biology, School of Biological Sciences, University of
Edinburgh, Charlotte Auerbach Road, Edinburgh, EH9 3FL, U.K.

²Centre for Ecology and Conservation, College of Life and Environmental
Sciences, University of Exeter, Cornwall Campus, Penryn TR10 9EZ, U. K.

10 Word count: 1,996

Abstract

The emergence of family groups is associated with conflict over the allocation of
15 food or other limited resources. Understanding the mechanisms mediating the
resolution of such conflict is a major aim in behavioural ecology. Most empirical
work on the familial conflict has focused on birds. Here, we highlight how recent
work on insects provides new and exciting insights into how such conflict is
resolved. This work shows that conflict resolution can be more complex than
20 traditionally envisioned, often involving multiple mechanisms. For example, it
shows that the resolution of sexual conflict involves a combination of
behavioural negotiation, direct assessment of partner's state, and manipulation
using anti-aphrodisiacs or prenatal maternal effects. Furthermore, it highlights
that there is a shift from the traditional emphasis on conflict (and competition)
25 to a greater emphasis on the balance between conflict on the one hand and
cooperation on the other.

Highlights

- Evolution of family groups is associated with conflict over limited resources.
- 30 • Resolution of sexual conflict involves direct assessment of partner's state.
- Females control conflict resolution via anti-aphrodisiacs and egg production.
- Siblings compete, but there can also be competition among other family members.
- Siblings sometimes cooperate by sharing food.

Introduction

Group living is widespread among insects [1,2]. Familiar examples include the eusocial ants, bees and termites, which spent most or all of their life cycle in complex social groups comprising of reproductive individuals that are helped by sterile workers [1]. Less familiar examples include insects where parents remain with their offspring for some time after hatching or birth and enhance their offspring's fitness by provisioning them with resources and/or by protecting them from predators or other environmental hazards [2-4]. Group living is associated with conflict among individuals over access to limited resources, such as food, mates and space. Conflict among family members may seem paradoxical given that families usually are composed of close relatives that have overlapping interests with respect to each other's future survival and reproduction. Nevertheless, family members have diverging interests over the allocation of parental resources, such as food, due to a combination of asymmetries in relatedness between them and a limited supply of resources [5,6].

Families may be comprised of one or both parents caring for one or multiple offspring, giving rise to three social dimensions of conflict depending on the composition of the family [7]. Sexual conflict over much care each parent should provide occurs where both parents care for their joint offspring [8,9], parent-offspring conflict occurs where parents provision food or other limited resources for their young after hatching [5,10], and sibling conflict occurs where multiple offspring share access to limited resources [6,11]. Most empirical work on family conflict has focused on birds [6,12]. This taxonomic bias largely reflects the widespread prevalence of parental care in birds and the relative ease with

60 which it can be observed [3]. Until relatively recently, insects were largely
ignored, which is perhaps not surprising given that parental care is relatively
rare in insects, where most species are either solitary or eusocial [2, 13–15].
However, in a small number of insects, including burrower bugs (*Sehirus cinctus*),
European earwigs (*Forficula auricularia*) and burying beetles within the genus
65 *Nicrophorus*, parents provision food for their offspring after hatching, making
these species attractive model systems for the study of family conflict. In this
article, we show how recent work on insects provides new and exciting insights
into familial conflicts and their resolution.

70 **Sexual conflict and state-dependent cooperation**

Traditionally, the resolution of sexual conflict has been associated with
behavioural response rules, such as negotiation, whereby each parent adjusts its
own contribution based on information on its partner's workload [16].
Theoretical model of negotiation predicts that each parent responds to a
75 reduction in its partner's workload by increasing its contribution but not such
that it fully matches its partner's reduction ('incomplete compensation') [16].
Negotiation is thought to play a key role in the resolution of sexual conflict
because it provides each parent with information on its partner's ability to
provide care [16]. This idea assumes that a parent cannot directly assess its
80 partner's parental ability, but that it does so indirectly by monitoring its
workload. However, two recent studies on *N. vespilloides* showed that a focal
parent responded directly to two components of its partner's state that appears
likely to influence the partner's ability to provide care: its inbreeding status

[17•] and its body size [18•]. Both studies find evidence for negotiation, which
85 was detected as negative correlations between the amount of male and female
care. However, the studies also that focal parent responded to directly to its
partner's state by providing more care when the partner was inbred [17•] and
when the partner was larger [18•]. Crucially, there was no evidence that
behavioural response rules, such as negotiation, accounted for these responses
90 to the partner's state. Thus, these studies suggest that each parent assesses its
partner's parental ability independently of monitoring its workload and that the
resolution of sexual conflict may involve a combination of negotiation and direct
assessment of the partner's state.

95 **Sexual conflict and female control**

The traditional focus on behavioural response rules, including negotiation, as the
mechanism mediating the resolution of sexual conflict assumes that there is
symmetry between males and females with respect to how they influence the
resolution of sexual conflict. However, recent studies on *N. vespilloides* suggest
100 that females may hold the upper hand by influencing their partner's behaviour
through production of anti-aphrodisiacs and control over egg production. Engel
et al. [19••] showed that females of the burying beetle *Nicrophorus vespilloides*
produce an anti-aphrodisiac pheromone (methyl geranate) that suppresses male
sexual activity during the period where offspring require most parental care
105 (Figure 1), thereby directing the male's attention away from mating and towards
assisting in parental care. In situations where there is a risk of sperm
competition, it is beneficial to males to mate at a high frequency [20] because it

protects their paternity [21]. However, a high mating frequency is costly for females [22], which may help explain why females produce the anti-aphrodisiac to cool male ardour. Engel et al. [19••] also found that methyl geranate is chemically linked to Juvenile Hormone III, a hormone that temporarily suppresses female fertility while females care for their offspring. Under these circumstances, it may be in the male's best interest to suspend his sexual activity in response to the anti-aphrodisiac while the female is infertile. This in turn, may help shift the male's attention from mating to assistance in parental care [23]. Anti-aphrodisiacs that are physiologically linked to female fertility may play an important role in the resolution of sexual conflict and the co-evolution of male and female care [24], and there is therefore a need for further work to determine whether they play a similar role in other insects, as well as in other taxa, with biparental care.

Two recent studies on *N. vespilloides* highlight that female control over egg production may play an important role in the resolution of sexual conflict [25•,26••]. Ford and Smiseth [25•] found that females can manipulate male care by laying the eggs more asynchronously (i.e., over a longer period of time) because males provided more care for experimental broods that had a greater degree of asynchronous hatching. However, females paid a prohibitively high cost from doing so because asynchronous hatching had an adverse effect on offspring survival. Thus, although females in principle can manipulate male care through asynchronous laying of eggs, the benefit of doing so are outweighed by a cost to the offspring.

In a related study, Paquet and Smiseth [26••] examined whether females can manipulate the behaviour of caring males via prenatal maternal effects. In many species, females deposit hormones or other compounds into the eggs that may influence male involvement in care by altering the offspring's behaviour or development [27,28]. Paquet and Smiseth [26••] manipulated the presence or absence of the male during egg laying (a key prenatal environmental cue to females as to whether they can expect male assistance in parental care), performed a cross-fostering experiment where all broods (regardless of whether they were laid in presence or absence of a male) were cared for by both parents, and monitored the subsequent effects on offspring and parental performance. They found that offspring were smaller at hatching when females laid eggs in the presence of a male, suggesting that females invest less in eggs when expecting male assistance. Furthermore, broods laid in the presence of a male gained more weight during parental care. This increase in brood weight was associated with a reduction in male weight gain while breeding rather than an increase the male parental effort (Figure 2). Thus, this study showed that females can manipulate the behaviour of caring males through prenatal maternal effects, and that females suppressed the male's food consumption while breeding, thereby leaving more food for the offspring. However, the mechanism by which females manipulate male behaviour is still unclear.

Competition among other family members

There is ample evidence for intense competition among siblings for access to parental resources [6,11]. However, recent work on insects suggests there may

155 also be competition among other family members. In many insects, offspring
retain the ability to forage independently of their parents [29,30], which may
lead to competition between parents and offspring over shared resources [31••].
A recent study on European earwigs (*Forficula auricularia*) provided evidence
for resource competition between caring parent and their dependent offspring.
160 Kramer et al. [31••] found that females benefit from high weight gain as it allows
them to invest more in a subsequent clutch, but that high maternal weight gain is
costly to offspring as it reduces their survival prospects. Conversely, offspring
have higher survival when they have a higher weight gain. Thus, this study
shows that the presence of a caring female triggers parent-offspring competition
165 over shared resources. Parent-offspring competition may have important
implications for the early evolution of family group living. The reason for this is
that costs associated with such competition may counteract the benefits of
parental care, thereby impeding the evolution of family life in resource-poor
environments [31••].

170 In some insects with biparental care, both parents feed from the shared
resource used for breeding, leading to competition (or sexual conflict) between
the two parents over food. For example, burying beetles within the genus
Nicrophorus breed on carcasses of small vertebrates, which serve as a source of
food for the larvae as well as the two parents [32]. A recent study on *N.*
175 *vespilloides* suggests that the resolution of sexual conflict over food consumption
involved a combination of behavioural response rules and direct responses to
the partner's state [33•]. This study found that females adjusted their mass
change by matching their partner's mass change, gaining more mass when males

gained more mass. In contrast, males responded directly to their partner's state,
180 gaining more mass when paired to large females that on average consumed more
carriion than small females. This study shows that there is sexual conflict
between caring parents over how much care each parent should provide as well
as over how much food each parent should consume. There is now a need for
studies examining whether these two conflicts are related. For example, if a
185 parent is providing a disproportionate amount of care, its partner may be more
tolerant of that parent feeding more from the resource [33•].

Sibling cooperation

Traditionally, there has been an emphasis on competitive interactions among
190 siblings [6,11]. However, a recent study on European earwigs provides evidence
that siblings may cooperate [34••]. In this study, individual nymphs were fed
dyed food. The study found that dyed food eaten by a focal nymph was often
transferred to its siblings via active release of frass that was subsequently eaten
by other nymphs and via mouth-to-mouth contact and mouth-to-anus contact
195 between nymphs. The study also found that food sharing was more common
when nymphs had no contact with their mother, and that recipient nymphs
benefitted from food transfer by gaining more weight. Donor nymphs released
more frass when interacting with related nymphs, but recipients spent more
time at mouth-to anus contact when interacting with unrelated nymphs. The
200 study suggests that sibling cooperation may be an ancestral trait in species with
facultative parental care, and that it therefore may have played a key role in the

early evolution of post-hatching parental care by promoting females to stay with their nymphs after hatching [34••,35].

205 **Emerging perspective on family conflict**

Here, we have highlighted how recent work on insects provides new and exciting insights into the resolution of conflict within family groups. This work highlights that conflict resolution might be more complex than traditionally envisioned,

often involving multiple mechanisms. For example, the resolution of sexual
210 conflict may involve behavioural negotiation, direct assessment of partner's state, and manipulation using anti-aphrodisiacs or prenatal maternal effects.

Furthermore, it highlights that there is a shift from the traditional emphasis on conflict (and competition) to a greater emphasis on the balance between conflict (and competition) on the one hand and cooperation on the other. A potentially

215 fruitful direction for future research would be to explore how environmental conditions, such as availability of resources, shifts the balance from conflict to cooperation.

Conflicts of interest

220 None

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Figure legends

Figure 1

Methyl geranate emission by female *Nicrophorus vespilloides* in ng per individual
370 over 20 min (mean \pm SE). Females were either allowed to care for their larvae
(filled circles and solid lines; N = 170) or prevented from caring for their larvae
(open circles and dotted lines; N = 169). Redrawn from Engel et al. [19••]. This is
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BY license.

375

Figure 2

Weight change by breeding female (filled circles) and male (open circles)
Nicrophorus vespilloides parents in g (predicted mean \pm SE from final models).
Parents were caring for foster broods that hatched from eggs produced under
380 two different pre-hatching conditions: the absence or presence of a male.
Redrawn from Paquet and Smiseth [26••]. Used with permission from
Proceedings of the National Academy of the Sciences of the United States of
America.

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Figure 1

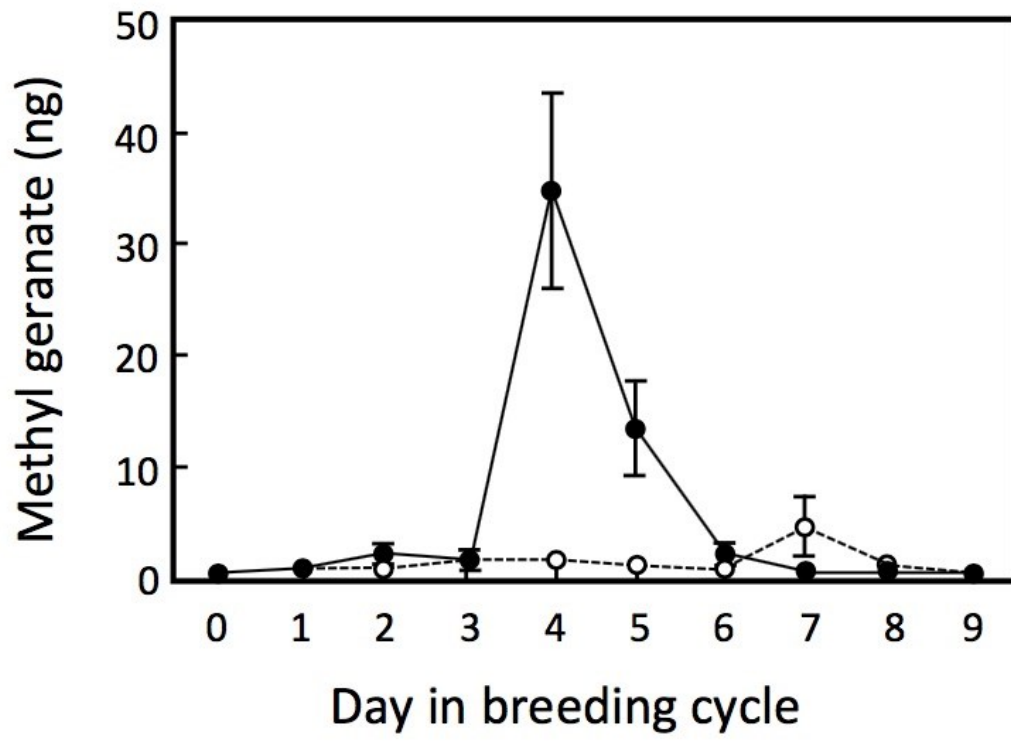


Figure 2

