

potential for reciprocal parent–offspring interactions provides opportunity for parent–offspring conflict to arise and drive the evolution of offspring begging signals. This parent–offspring conflict over parental investment arises because each offspring is twice as related to itself as it is to a sibling, whereas parents are equally related to each of their offspring. It generates selection favouring traits that allow offspring to increase their share of the parental resources. Trivers (1974) postulated the evolution of behavioural means by which offspring can manipulate parents into providing more than they should. A large number of explicit evolutionary game-theoretical models subsequently confirmed that the conflict can indeed lead to the evolution of conspicuous and costly offspring begging (Parker & Macnair 1979; Godfray 1991, 1995; reviewed in Parker et al. 2002; Royle et al. 2004). In these models, two major scenarios for conflict resolution have been considered: scramble models assumed that sibling rivalry drives the evolution of competitive begging to which parents respond passively (Parker & Macnair 1979) and honest-signalling models assumed that parents actively select for offspring begging signals that ‘honestly’ reflect their true need for parental resources (Godfray 1991, 1995).

Considerable empirical research has been done to test predictions of these models and distinguishing between the two scenarios experimentally has turned out to be a major challenge since both models qualitatively predict the same outcomes (reviewed in Kilner & Johnstone 1997; Royle et al. 2004; Smiseth et al. 2008). The strong experimental focus on bird systems has resulted in a taxonomic bias in our understanding of the evolution of begging signals (Smiseth et al. 2003). Altricial young birds are completely dependent on parents to get food, and they produce highly specialized and conspicuous multicomponent begging displays (Kilner & Johnstone 1997; Budden & Wright 2001). Thus, albeit excellent for studying conflict resolution, birds may represent an evolutionary state that is too derived to test parent–offspring conflict theory fully, in particular with regard to the ancestral conditions under which begging originated (Smiseth et al. 2003). A difficulty of such evolutionarily derived systems is that the scope for experimentally testing the fitness consequences of variation in offspring begging and parental provisioning is limited; in addition, the measured fitness consequences reflect the dependence of offspring development on parental provisioning. Social insects as experimental systems may here be critical complements to current research in parent–offspring conflict.

In most social insects, posthatching parental care is provided by females (Tallamy 1984) and is not prerequisite for offspring to survive. They may therefore represent a less derived state of parent–offspring interactions. For instance, in earwigs and burying beetles, offspring can either self-forage or obtain food from parents (Vancassel 1984; Smiseth & Moore 2004). Thus, social insects are potentially powerful experimental systems for better understanding the ancestral conditions for the evolution of begging signals from a nonsignalling state and their influence in the regulation of parental care (Smiseth et al. 2003). Except for eusocial insects where offspring are

sealed in cells and are completely dependent on worker care, the other social insects have been relatively little studied (Costa 2006) and mechanisms of provisioning and begging are still not sufficiently well documented. Nevertheless, there is increasing indirect and direct evidence for offspring influencing maternal care, and begging behaviours have now been described in a number of species, for instance in burying beetles (Rauter & Moore 1999).

Chemical signalling is the most important mode of communication between individuals in insects and it has been widely studied in several orders, mainly in the contexts of sexual selection, social recognition and regulation (Wyatt 2003). However, the study of chemical communication in the context of parent–offspring interactions in social insects has remained fairly unexplored and could reveal important new mechanisms of maternal care regulation. For instance, recent experiments have shown that condition-dependent offspring chemical cues influence caregiver food provisioning in burrower bugs, *S. cinctus* (Kölliker et al. 2005b, 2006) and bumblebees, *Bombus terrestris* (den Boer & Duchateau 2006). Also, honeybee, *Apis mellifera*, larvae produce a brood pheromone that influences care behaviours of workers, suggesting a possible role of the brood pheromone as a begging signal. The brood pheromone not only influences worker behaviour but also has lasting consequences for their physiology (Le Conte et al. 1995, 2001).

Maternal care in other social insects has been mainly studied in the context of female reproductive physiology and the hormones maintaining maternal care behaviours (reviewed in Nijhout 1994; Trumbo 2002). Specific hormones in females, notably juvenile hormone (JH), regulate the trade-off between care for current offspring and the production of new eggs/clutches (Vancassel et al. 1984; Rankin et al. 1995a; Scott et al. 2001; Scott & Panaitov 2004). Since the evolutionary resolution of parent–offspring conflict implies, on a behavioural level, coevolution of offspring begging signals and maternal responses, and, on a physiological level, coevolution of maternal reproductive physiology and offspring developmental physiology, considerations of how behaviours and physiology interact to generate the observed patterns of parent–offspring interactions may be particularly revealing to understand better the evolutionary resolution of parent–offspring conflict (see also Wright & Leonard 2002; Lessells 2008).

Our aims in this review on maternal care and offspring begging in social insects are to (1) provide a comprehensive summary of mother–offspring interactions, (2) review the evidence for offspring begging behaviours that influence the level of maternal care, and (3) discuss the evolutionary implications of offspring signals, and in particular chemical signals, in the behavioural regulation and physiological maintenance of maternal care in social insects. Our review highlights the need for further research on mechanisms of maternal care and offspring begging in social insects, and especially on offspring chemical signals and female reproductive physiology.

MOTHER–OFFSPRING INTERACTIONS

Care by females (i.e. maternal care) is the most frequent form of parental care in insects (Tallamy & Brown 1999). Thus we focus here on insect mother–offspring interactions, although our arguments would be valid for father–offspring interactions in species with paternal or biparental care. Table 1 provides an overview of different forms of posthatching maternal care behaviours observed in various insect orders and which we classified into two main categories: protection (which can be behavioural, chemical or physical) and food provisioning to offspring (specifying whether the resource is provided to the brood as a whole or allocated to individual offspring). We also list the evidence for offspring influences on these maternal behaviours, including offspring begging signals. For comprehensive reviews of parental care in insects, see Zeh & Smith (1985) and Tallamy & Wood (1986).

As mentioned before, the most frequent form of posthatching maternal care in social insects is protection against predators (Tallamy & Wood 1986). For instance, females of shield bugs *Elasmucha* spp. (Hemiptera) stay in the vicinity of their offspring and, when threatened, sit on top of their offspring and fan their wings to deter predators (Kaitala & Mappes 1997). The benefit of maternal protection to offspring has been tested in several species by removing tending mothers and measuring offspring survival. For instance, when thornbug treehopper, *Umbonia crassicornis*, mothers were experimentally removed, wasp attacks were successful in 94% of cases, compared to an attack success rate of only 23% when offspring were attended by mothers (Cocroft 2002). Other social insects lay their eggs in a safe place such as a nest, a burrow, a gallery, a tunnel or a ball. When the eggs hatch, the females (sometimes with a contribution of their male mate) stay to defend the entrance of the burrow by behavioural displays and, also, with defensive secretions released from specialized glands as, for example, in some beetles (Table 1). Keeping offspring in a protected area may have contributed to the evolution of food provisioning (Trumbo 1996) owing to the associated reduction in the cost of provisioning (i.e. in order to provision, parents have to leave their offspring temporarily unprotected which is less risky if they are in a burrow). Depending on the predator species, predators may also pose a direct threat to the tending female, making offspring protection a costly investment. Hence, according to parent–offspring conflict theory, offspring protection may be considered a form of parental investment where offspring may be selected to influence and maintain the protective tendency of the mother beyond her own optimum (Cocroft 2002). Offspring begging signals have rarely been studied in the context of protection against predation, and conflict resolution models may need to be adjusted to incorporate this functional aspect of care.

The other form of maternal care, food provisioning, is observed in fewer insect species but represents the typical form of care considered in conflict resolution models and has been mainly addressed in bird studies. By providing food to their offspring, mothers may suffer not only from

higher risks of predation while foraging but also increased energy expenditure. In addition, food provisioning may decrease the female's own energy intake because, by sharing food with her offspring, she might accumulate fewer resources required for future reproduction. The benefit of enhancing offspring development and survival must have exerted strong selection favouring the evolution of mechanisms that ensure adequate food provisioning to offspring. In some species, females progressively provision food to the entire brood (Field 2005). For instance, the mother brings food back to the brood, as in burrower bugs (Kight 1997), or leads offspring to the food source and facilitates access to the food by pre-processing it as in stink bugs and treehoppers (reviewed in Tallamy & Wood 1986). In these cases, the benefit of maternal food provisioning is simultaneously shared among all offspring (Lazarus & Inglis 1986). Individual offspring of a given brood may compete among each other for access to the provided food, but this competition is not directed at the mother and cannot lead to competitive begging signals. Nevertheless, begging signals may also evolve because of between–brood competition, selecting for cooperative begging signals that allow offspring of the same brood collectively to influence the rate of maternal food provisioning to the brood (Johnstone 2004).

In other species, females directly allocate food to individual offspring, mostly through direct regurgitation by mouth-to-mouth contact. In these species, an individual offspring can directly influence the likelihood of obtaining food from the mother by begging and competing with siblings. For instance, earwig females have been observed in nature to make several foraging trips between the food sources and their burrow to provision food to their offspring (Lamb 1976a, b). Direct mouth-to-mouth transfer of food (i.e. regurgitation) between mother and offspring as a mechanism of maternal food provisioning was suspected for a long time (Fulton 1924; Lamb 1976a) and recently experimentally confirmed in the European earwig (Staerke & Kölliker, in press). In burying beetles, one of the rare cases of biparental care (Fetherston et al. 1990; Eggert & Müller 1997), larvae can either feed on the preprocessed carcass or obtain food directly from either the female or the male by regurgitation (Smiseth & Moore 2002).

All these forms represent different mechanisms of maternal care which can have differential implications for the resolution of parent–offspring conflict (Johnstone 2004; Smiseth et al. 2008). Comparisons among them are valuable because they may shed light on how the dynamics of mother–offspring interactions evolved and influenced the evolution of begging signals. The diversity of these mechanisms observed among social insects may provide a promising arena to explore the relation between mechanisms of parent–offspring interactions and the evolution of begging signals also from a phylogenetic perspective (Smiseth et al. 2008). Yet, behavioural mother–offspring interactions have not been broadly studied in social insects and correspondingly few begging behaviours have been documented (Table 1). Clearly, more experimental research is needed to understand insect mother–offspring interactions better.

Table 1. Forms of posthatching maternal care and offspring cues and behaviours in social insects (blank cells represent unstudied areas)

| Insect order | Species | Posthatching maternal care | | Offspring cues and behaviours | Source | |
|---|--|--|--------------------|--|--|--|
| | | Protection* | Food provisioning† | | | |
| Blatodea | German cockroach, <i>Blatella germanica</i> | B | Brood | Aggregation pheromone | Brossut 1983; Nalepa & Bell 1997 Nalepa 1984, 1990 | |
| | Wood roach, <i>Cryptocercus punctulatus</i> | P | Individual | | | |
| | Pacific beetle cockroach, <i>Diploptera punctata</i> | P, C | Individual | Alarm pheromone | Roth & Stay 1958 | |
| Coleoptera | Bessbug, <i>Odontotaenius disjunctus</i> | P | Brood | Stridulation | Schuster & Schuster 1997 | |
| | Dung beetle, <i>Oniticellus cinctus</i> | P | Brood | Chemical cues deposited on the ball | Halffter 1997 | |
| | <i>Cephalodesmius</i> spp. | P | Brood | Swaying behaviour and tactile stimuli | Monteith & Storey 1981 | |
| | Coprini, <i>Copris</i> spp. | P | Brood | | Klemperer 1982, 1983a, b | |
| | Burying beetle, <i>Nicrophorus vespilloides</i> | B | Individual | | Fetherston et al. 1990; Eggert & Müller 1992, 1997; Rauter & Moore 1999; Smiseth & Moore 2002; Trumbo 2007 | |
| | Dermaptera | Bark beetle, <i>Monarthrum</i> spp. | P | Brood | Aggregation pheromone | Kirkendall et al. 1997 |
| | | Engraver beetle, <i>Ips pini</i> | C | Brood | | Reid & Roitberg 1994 |
| | | Ambrosia beetle, <i>Xyleborus</i> spp. | P | | | Kirkendall et al. 1997 |
| | | Desert beetle, <i>Parastizopus armaticeps</i> | P | Brood | | Rasa 1998, 1999 |
| | | Common European earwig, <i>Forficula auricularia</i> | P, B, C | Individual | Antennal contact | Lamb 1976b; Vancassel & Foraste 1980; Vancassel 1984; Eisner et al. 2000 |
| <i>Doru taeniatum</i> | | P, B, C | Individual | | Rankin et al. 1996; Eisner et al. 2000 | |
| Hump earwig, <i>Anechura bipunctata</i> | | P, B, C | Individual | | Vancassel & Foraste 1980; Vancassel 1984 | |
| <i>Anechura harmandi</i> | | P, B, C | Individual | | Kohn 1997 | |
| Striped earwig, <i>Labidura riparia</i> | | P, B, C | Individual | | Vancassel 1977; Caussanel et al. 1986; Rankin et al. 1995b | |
| Embioptera | | Ring-legged earwig, <i>Eurobellia annulipes</i> | P, B, C | Individual | | Klostermeyer 1942; Rankin et al. 1996 |
| | Web spinner, <i>Antipaluria urichi</i> | P | Brood | | Edgerly 1997 | |
| Hemiptera | <i>Embia ramburi</i> | P | Brood | | Ledoux 1958 | |
| | Burrower bug, <i>Sehirus cinctus</i> | P, B, C | Brood | Solicitation pheromone (?) | Sites & McPherson 1982; Kight 1997; Kölliker et al. 2005b 2006 | |
| | <i>Sehirus bicolor</i> | P, B, C | Brood | | Costa 2006 | |
| | Grey or parent bug, <i>Elasmucha</i> spp. | B | Brood | Alarm pheromone | Melber et al. 1980; Kudô 1990, 2000 | |
| | Stink bug, <i>Antiteuchus triperus</i> | B | Brood | Defence pheromone | Borges & Aldrich 1992 | |
| | Southern green stink-bug, <i>Nezara viridula</i> | B | Brood | Aggregation pheromone | Lockwood & Story 1985, 1986, 1987 | |
| | Treehopper, <i>Membracidae</i> spp. | B | Brood | Alarm pheromone, secrete honey dew | Nault et al. 1974 | |
| | <i>Publilia reticulata</i> | B | Brood | | Bristow 1983 | |
| | Thornbug treehopper, <i>Umbonia crassicornis</i> | B | Brood | Substrate-borne vibrational signals, alarm pheromone | Nault et al. 1974; Wood 1976; Cocroft 1996, 1999, 2001, 2002; | |
| | Lace bug, <i>Gargaphia solani</i> | B | Brood | Defence & alarm pheromone | Tallamy & Denno 1981; Tallamy 1985; Parr et al. 2002; | |
| Orthoptera | Ground weta, <i>Hemiandrus</i> spp. | P, B | Brood | | Gwynne 2004 | |
| | Short-tailed cricket, <i>Anurogryllus muticus</i> | P | Brood | | West & Alexander 1963 | |

*Protection: P=physical (nest, burrow, gallery tunnel, brood ball, etc.); B=behavioural (i.e. defence display, guarding); C=chemical (defensive pheromone, aggregation pheromone, alarm pheromone).

†Food provisioning directed to the brood (i.e. bring food back to the nest, facilitation of feeding by guiding offspring to food source, processing the food) or to an individual (regurgitation through mouth-to-mouth contact, body secretions).

Finally, behavioural interactions are embedded in the physiological state of the interacting individuals (West-Eberhard 2003). For instance, maternal food provisioning is expected only when females are in a physiological state that maintains their tendency to care as opposed to a physiological state that triggers egg production for the subsequent clutch (Vancassel 1984; Rankin et al. 1995c, 1997; Trumbo 1997; Scott et al. 2001). Thus, the evolution of parent–offspring interactions also requires the evolution of the relevant underlying reproductive and developmental physiology. In insects, JH is well known to play a role in the physiological maintenance of maternal care tendencies (see above) as well as vitellogenin synthesis and ovarian development (Nijhout 1994), and to be involved in the regulation of juvenile development (i.e. by repressing moult). A recent study also showed that JH may affect begging signals in burying beetles, albeit indirectly through an influence on larval growth (Crook et al. 2008). Thus, the critical role of JH in the reproductive and developmental physiology of most social insects makes it a good candidate for a proximate factor regulating mother–offspring interactions in social insects, although the exact physiological details of JH action still remain to be elucidated.

Exceptionally well-studied systems in the context of insect caregiver–offspring interactions, both on a behavioural and a physiological level, are eusocial insects (the honeybee in particular). In most eusocial insects, larvae are sealed in brood cells and are completely dependent on nurses for food, as are bird chicks in their nest. Whether a larva becomes a reproductive queen or a worker is usually determined by the quantity and quality of food it receives from the nurses (Wilson 1971; Wheeler 1986). Therefore, if larvae are able to influence their food provisioning, they may, in part, be able to determine their own development to become a worker or a queen (Bourke & Ratnieks 1999; Kaptein et al. 2005; den Boer & Duchateau 2006). Although workers and larvae are usually more genetically related (owing to the haplodiploid reproductive system) than parents and offspring, conflict between larvae and worker over food provisioning akin to parent–offspring conflict may also have driven the evolution of worker food-provisioning mechanisms and larval begging signals.

OFFSPRING BEGGING BEHAVIOURS

Begging for Protection

In several hemipteran species, nymphs have specialized dorsoabdominal glands to store chemical cues which are released by nymphs when in danger. These chemical cues elicit a defensive response from the mother and are defined as alarm pheromones (Roth & Stay 1958; Nault et al. 1974; Tallamy & Denno 1981; Kudó 1990, 2000). In the subsocial thornbug treehopper, offspring produce a substrate-borne vibrational signal in addition to chemical signals, both of which trigger maternal defensive behaviours (Cocroft 1996, 1999, 2001). In the case of the vibrational signal, the activity of several offspring is required to trigger the defensive response from the mother

(Cocroft 1996, 1999). Protection is a shared maternal investment so not only the signalling individual but also all the other siblings located in the vicinity benefit from the maternal protection. Therefore, competition between siblings to signal more than the others is not expected to evolve as it will benefit everyone. Instead, begging for protection is expected to be an honest signal of risk of predation. However, Cocroft (2002) showed that individuals close to the mother have a better chance of survival than individuals at the edge. Thus, differential survival may promote selection in offspring for manipulative signals potentially allowing individual nymphs to monopolize more protective positions close to the mother, but this hypothesis remains to be tested. The high cost of predation must have exerted a strong selection for efficient communication that can be expressed in a flexible way, highly conditional on predator, shaping the evolution of chemical signals (e.g. offspring alarm pheromones).

Begging for Food

In contrast to the need for protection, the need for food is the typical proximate context in which parent–offspring conflict has been studied. The typical experimental design usually consists of a manipulation of offspring nutritional state by food deprivation or satiation, and the measurement of the level of offspring begging (reviewed in Kilner & Johnstone 1997; Budden & Wright 2001; Wright & Leonard 2002; Royle et al. 2002). The currently best studied insect system where offspring begging behaviour reflecting hunger has been explored in some detail is the burying beetle. Larvae of the genus *Nicrophorus* raise their head and wave their legs in the direction of the parents and, when in contact, tactile stimuli from their legs on the parent's mouthparts trigger food regurgitation (Rauter & Moore 1999; Smiseth & Moore 2002). Smiseth & Moore (2004) counted the times larvae were seen raising their head while waving their legs or touching the parent under different food treatments and they showed that food-deprived larvae spend more time raising their head than control larvae, clearly showing condition-dependent expression of this behaviour as would be required for a begging signal.

In addition to begging behaviours, a different sensory modality for the evolution of insect parent–offspring interactions has been proposed, and evidence supporting this hypothesis reported, in the burrower bug, *S. cinctus*. Kölliker et al. (2005b, 2006) experimentally varied the nutritional conditions of nymphs and later measured food provisioning of mothers when exposed to crude cuticular extracts (Kölliker et al. 2005b) and volatile chemical cues (Kölliker et al. 2006) emitted by these nymphs. Females exposed to chemical cues (both extracts and volatiles) obtained from nymphs in poor nutritional conditions provided significantly more food than females exposed to chemical cues obtained from nymphs that had access to ad libitum food. Chemical analysis of the nymphal volatiles showed a significant quantitative difference in the blend of monoterpenes emitted by nymphs raised on the two food treatments. Thus, as predicted for the

postulated solicitation pheromone (i.e. a chemical begging signal; Kölliker et al. 2006), offspring chemical cues were condition dependent and females responded correspondingly by adjusting their food provisioning. This example supports the hypothesis that social insect offspring can produce chemical cues that elicit maternal provisioning, providing information on offspring nutritional condition. Given the chemosensory predisposition of insects in general, parent–offspring conflict may have often led to the evolution of condition-dependent chemical begging signals in offspring. Solicitation pheromones may therefore be generally expected among the social insects (see also below for eusocial insects). However, it is still unclear whether cuticular chemicals are passive cues directly transferred from food processing to the cuticle or active signals that have evolved for their signalling function and which offspring can strategically adjust to influence maternal food provisioning (Kölliker et al. 2006). As expected for burrower bugs where females provide food to the whole brood, these results show that the overall signal produced by the brood can influence the rate of maternal food provisioning. Yet in other species with direct food provisioning to individual offspring (e.g. through regurgitation), individual chemical begging signals may be expected as well. More studies exploring offsprings' chemical signals to caring parents are needed.

Among eusocial insects, several larval begging signals have been documented. For instance, in Vespidae wasps, larvae use acoustic signals by scraping their mandibles on the wall of their cells, and the scraping intensity seems to be related to larval hunger level (Ishay & Landau 1972; Ishay & Schwartz 1973; reviewed in Matsuura & Yamane 1984). Hölldobler et al. (1978) observed that in ants, such as *Formica sanguinea* and *Solenopsis invicta*, larvae appear to solicit food from workers by swaying their head and mandibles, similar to the begging display of burying beetle larvae. Kaptein et al. (2005) experimentally showed that the intensity of this swaying behaviour in larvae of the ponerine ant *Gnamptogenys striatula* is related to nutritional condition. Hungry larvae sway significantly more than well-fed larvae, confirming its function as a hunger signal. In honey bees, Huang & Otis (1991) experimentally deprived larvae for 2–6 h and measured the amount of food provisioned by nurse bees. They found that deprived larvae receive more food than well-fed larvae, suggesting a correlation between level of hunger and allocation of food through some unknown larval cue or behaviour. Finally, there is also evidence for chemical signalling between larvae and workers in bee colonies, although this evidence has, to our knowledge, not been interpreted functionally as chemical begging signals. Le Conte et al. (1990, 1995) showed that extract of cuticular chemicals from bee larvae is correlated with larval age, and that it induces different quantity and quality of food provisioning by the nurses. This blend of chemical compounds (i.e. a blend of 10 aliphatic esters, Le Conte et al. 1995) on the larva's cuticle was accordingly termed the 'brood pheromone'. After experimental bioassay with different synthetic chemicals similar to the ones present in the blend, one specific compound, the methyl linoleate, applied on the cell of larvae increased the amount of royal

jelly deposited by workers (Le Conte et al. 2001). The brood pheromone in general, and this specific chemical compound in particular, thus represents a prime candidate for a solicitation pheromone. Further research on the functional significance of the brood pheromone, including experimental tests of condition-dependent emission (i.e. whether compound quantity depends on larval hunger), is required, however. A recent experimental study in bumblebees showed that larval cuticular chemical cues are in fact condition dependent and thus support the hypothesis of chemical hunger signals produced by larvae that influence food provisioning of workers (den Boer & Duchateau 2006).

EVOLUTION OF A CHEMICAL BEGGING SIGNAL

Chemical cues represent particularly interesting potential begging signals in the study of the resolution of parent–offspring conflict in social insects for several reasons: (1) they represent signals of the evolutionarily most ancient sensory modality (Wyatt 2003); (2) they are involved in communication for several insect species in a broad range of functional contexts (Vander Meer et al. 1998); and (3) pheromones (external signals) and hormones (internal signals) may often use similar or related molecular pathways (Tillman et al. 1999; Bellés et al. 2005) facilitating both their evolution and maybe our capacity to understand the details of their expression. Because the expression of both maternal behaviour and offspring begging is likely to be regulated by both physiological mechanisms with an underlying genetic basis and environmental influences, the investigation of chemically mediated mother–offspring interactions may turn out to be particularly fruitful. Thus, in the following discussion, we focus on chemical signals, but vocal or other signals may have analogous implications.

From a Cue to a Signal

The possibility of a begging signal evolving from a pre-existing condition-dependent nonsignalling cue raises several important questions with respect to the definition of signals and the evolutionary process resolving parent–offspring conflict. Maynard Smith & Harper (2003, page 3) defined a signal as 'any act or structure that alters the behaviour of other organisms, which evolved owing to that effect, and which is effective because the receiver's response has also evolved'. Hence a signal implies a coevolutionary history between the signaller's behaviour and the receiver's response (as in 'honest-signalling' models). Experimental data showing an effect of offspring chemical cues on mother's food provisioning are now available, but there is as yet no evidence that the offspring condition-dependent chemical cues evolved for the function of soliciting food (Kölliker et al. 2006). Exposure of mothers to the compounds identified and confirmation that both the offspring cues and the female response are confined to the functional context of caring would be required to demonstrate that the cue evolved for the specific effects. Alternatively, the begging signal may have evolved

for the purpose of influencing maternal provisioning, but the mother's response did not evolve (i.e. as in scramble models), and may rather represent a sensory bias (Ryan 1990; Endler & Basolo 1998). In this case, the offspring signal may have manipulative potential. The following examples stress the need for careful consideration of these alternative scenarios in parent–offspring interactions. Experiments in earwigs and burying beetles showed that continuous replacement of older offspring by younger offspring maintains care by mothers and delays future reproduction, suggesting an effect of age-dependent offspring stimuli on the mother's reproductive state and future reproduction (Vancassel et al. 1987; Scott & Panaitof 2004). Females may thereby adaptively respond to offspring age-specific stimuli by maintaining their tendency to care (i.e. maternal control scenario; Godfray 1991). Alternatively, these results could also be interpreted as evidence that offspring produce a cue that has at least the potential to manipulate the mother's reproductive physiology (i.e. offspring control; Parker & Macnair 1979). Some chemical cues have been shown to have a primer effect on the physiology of the receiver (see below) which, owing to their lasting effects, may manipulate the receiver's behaviour against its own interests (Wyatt 2003). A good example is the previously mentioned brood pheromone of honeybee larvae which acts as a releaser pheromone with transient effects on worker foraging and food provisioning (Le Conte et al. 1990, 1995; Pankiw 2007), but also as a primer pheromone with a lasting effect on worker physiology, delaying their behavioural and physiological, transition from nurses to foragers (Le Conte et al. 2001). Le Conte et al. (2001) also showed that the brood pheromone may in part influence worker JH titre, which contributes to this behavioural transition in eusocial hymenoptera (Robinson & Vargo 1997).

Hypothetical Mechanism of Maternal Care Regulation

In analogy to the chemical control of worker behaviour in honeybees, we propose the hypothesis that offspring of social insects produce a 'solicitation pheromone' that may act as a releaser pheromone inducing mothers to provide food as first suggested by Kölliker et al. (2005b). Since JH mediates the amount and duration of maternal care, any influence by the offspring on the mother's JH titre through a solicitation pheromone raises questions about the resolution of parent–offspring conflict in insects in terms of the interplay of behavioural interactions and physiological mechanisms (Fig. 1). If offspring can directly influence the mother's JH titre, they may gain substantial control over maternal care, potentially influencing her trade-off between current and future reproduction. Therefore, experimental research on begging signals should not only look at transient behavioural responses by parents, but also monitor physiological changes with potential lasting consequences for maternal reproduction. One problem in studying insect hormones for now remains the lack of a powerful and reliable methodology to measure and quantify JH (Schooley et al. 2005).

Despite the increasing evidence for condition-dependent offspring cues to which insect mothers respond, the causal compounds remain to be chemically identified and experimentally tested in social insects (Kölliker et al. 2006). The finding of such chemical signals will allow direct manipulation of offspring begging by exposing mothers continuously to the offspring signal to test the critical and previously untested prediction that offspring, by producing a begging signal, can affect maternal reproductive physiology and reproductive output. Owing at least partly to the difficulty of experimentally manipulating behavioural begging displays, current evidence of the effects of begging on parents is fully based on short-term behavioural responses with transient effects on maternal physiology and reproduction (Scott & Panaitof 2004). Thus, important predictions from parent–offspring conflict theory remain to be tested, and social insects and solicitation pheromones may provide a promising system once more research has been done in this area.

The evolution of an honest versus manipulative signal is at the core of parent–offspring conflict theory (Trivers 1974; Godfray 1995; Kilner & Johnstone 1997; Royle et al. 2004). One may argue that a begging signal with a priming effect on maternal physiology would be mostly in the interests of the offspring by maintaining parental investment in the present brood at the expense of future broods for the parents. Meanwhile, the evolutionary interests of mothers may be best served if the effect of offspring signals has transient (i.e. releaser-type) effects on their behaviour, allowing the mother to respond flexibly to variation in offspring conditions. Therefore, the integrative approach of studying begging signals and female reproductive physiology deserves further research which could provide a direct test of the power of offspring begging to control maternal care. Physiological studies focusing particularly on the endocrine regulation of maternal care

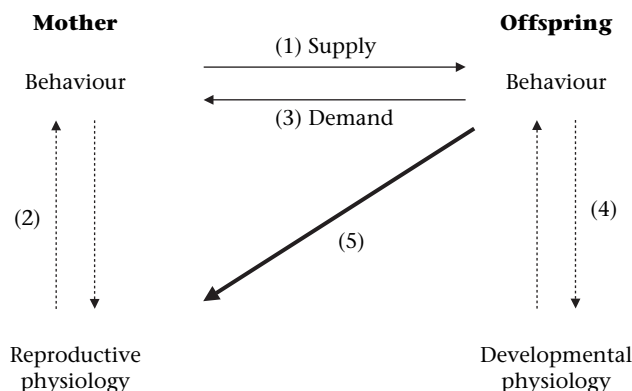


Figure 1. Schematic illustration of the regulation of maternal care in social insects. Mothers provide care to offspring (resources supply, arrow 1) that is influenced by the mothers' reproductive physiology (in part regulated by the juvenile hormone; arrows 2). Similarly, the effect of offspring begging signals (resources demand) on maternal provisioning (arrow 3) is modulated by offspring developmental physiology (varying with age, nutritional state, juvenile hormone; arrows 4). Arrow 5 describes a hypothetical direct priming effect of offspring signals on the physiology of mothers.

and offspring begging in social insects (Scott & Panaitof 2004; Crook et al. 2008) as well as in birds (Groothuis & Ros 2005; Quillfeldt et al. 2006) already provide promising results. Here, and beyond the current focus of deposition of maternal hormones in the eggs affecting offspring development (e.g. Müller et al. 2007), we suggest the physiological approach should be expanded to incorporate indirect effects of offspring solicitation on maternal physiology.

CONCLUSION

Social insect species show a wide range of forms of posthatching parental care, usually provided by females, including protection and/or food provisioning directed to the whole brood and/or to individual offspring. Thus, they offer the potential to study the differential effects of parent–offspring interactions on the evolution of begging signals and the maintenance of maternal care. Offspring stimuli that signal need for protection have been described in several insect species (offspring alarm pheromones being the most common ones), but hardly studied from the perspective of parent–offspring conflict. Conversely, begging behaviours for food are less well known in social insects and only the tactile begging display of burying beetle larvae has been well investigated experimentally (Smiseth & Moore 2004). Yet, the difficulty of directly manipulating behavioural displays has prevented experimental tests of certain predictions of parent–offspring conflict theory with regard to lasting influences of offspring begging on maternal reproductive physiology and reproductive output. An in depth study of chemical mother–offspring interactions and the identification of solicitation pheromones in insects (Kölliker et al. 2005b, 2006; den Boer & Duchateau 2006) might be a promising way to find systems where these predictions of parent–offspring conflict theory could be tested. The usually rather short and discrete generations of these insects thereby facilitate the quantification of variation in lifetime reproductive success.

Furthermore the tendencies of both mothers to care and offspring to beg seem to be at least partly regulated by JH (Crook et al. 2008). Such a common hormonal mechanism of offspring and parental trait is consistent with predictions of evolutionary models of supply–demand coadaptation that predict a common inherited basis to (i.e. a genetic correlation between) parental provisioning and offspring begging (Wolf & Brodie 1998; Agrawal et al. 2001; Lock et al. 2004; Kölliker et al. 2005a). The focus on chemical communication in the context of mother–offspring interaction may offer a new perspective of research to test proximate mechanisms of maternal care regulation and the evolutionary function of offspring begging signals with regard to scramble and honest–signalling models. Further research in chemical signalling and hormonal regulation of offspring begging and maternal provisioning is now needed to substantiate the currently scarce, but promising, data on parental care and offspring begging in social insects.

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