



Maternal care and offspring begging in social insects: chemical signalling, hormonal regulation and evolution

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(Received 17 December 2007; initial acceptance 22 January 2008;
final acceptance 5 June 2008; published online 3 August 2008; MS. number: D-07-20039R)

Posthatching maternal care such as food provisioning and protection has evolved several times in insects, allowing offspring (larvae, nymphs) to interact with their mothers and potentially influence their investment. The evolutionary conflict over the duration and amount of parental care is thought to promote the evolution of offspring begging behaviours either as honest signals of need or as competitive signals with the potential to manipulate parents into investing more. In most social insects, parental care is not obligatory and may represent a less derived state than in vertebrate systems making them more appropriate to test ancestral conditions for the evolution of begging signals. Here, we review forms of maternal care in insects ranging from protection to food provisioning and evidence of offspring begging behaviours influencing maternal care, including condition-dependent chemical cues produced by offspring that may turn out to be solicitation pheromones. Since behavioural parent–offspring interactions are embedded in the reproductive and developmental physiology of mother and offspring, we stress the need for behavioural studies to be complemented by physiological measurements which will allow us to understand better the nature of conflict resolution. We propose a hypothetical mechanism of maternal care regulation by direct internal chemical signals (i.e. hormones) and indirect external chemical signals (i.e. solicitation pheromones) influencing maternal reproductive physiology and future reproduction. Social insect species and the integrated study of behavioural interactions and physiological/reproductive consequences may represent promising new experimental systems for direct tests of the evolution of begging signals, complementing current research on parent–offspring conflict.

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Keywords: begging behaviour; chemical cue; juvenile hormone; maternal care; parent–offspring conflict; pheromone; signal; social insect

In insects, posthatching parental care has evolved independently in at least 10 orders (Zeh & Smith 1985). The most common form of posthatching parental care is the protection of young against predators, but active parental food provisioning to offspring also occurs in a number of species (Tallamy & Wood 1986). The benefit of posthatching care for offspring survival has been experimentally shown, for instance, in the burrower bug, *Sehirus cinctus* (Heteroptera: Cydnidae; Kight 1997), burying beetles, *Nicrophorus* spp. (Coleoptera; Eggert et al. 1998; Smiseth et al. 2003) and in the

European earwig, *Forficula auricularia* (Dermaptera; Kölliker 2007). For parental care to evolve and be maintained, however, this benefit has to outweigh the cost of care because by providing care parents forego the opportunity to produce additional offspring (Trivers 1974; Clutton-Brock 1991). Consistent evidence for such a cost of care has been experimentally demonstrated in several insect species where females caring for offspring delay and/or reduce their future reproductive output relative to noncaring females (Tallamy & Denno 1982; Vancassel 1984; Hunt & Simmons 2004; Agrawal et al. 2005; Kölliker 2007).

When parents care after hatching, offspring have the potential to interact behaviourally with them and influence the duration and amount of costly care. This potential for reciprocal parent–offspring interactions

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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 & Panaitof 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, *Umberia 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	
	Copriini, <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		Kohno 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	Alarm pheromone	Costa 2006	
	Grey or parent bug, <i>Elasmucha</i> spp.	B	Brood		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	Substrate-borne vibrational signals, alarm pheromone	Bristow 1983	
	Thornbug treehopper, <i>Umbonia crassicornis</i>	B	Brood		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

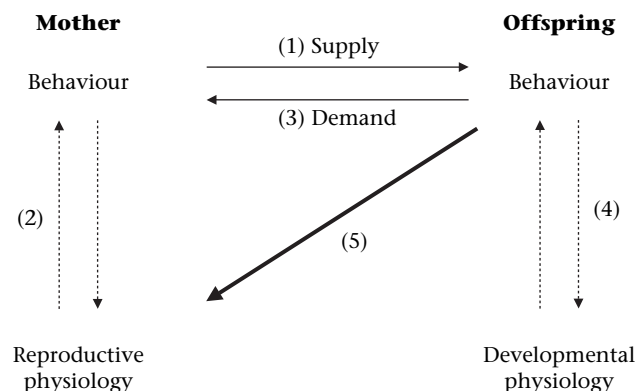


Figure 1. Schematic illustration of the regulation of maternal care in social insects. Mothers provide care to offspring (resources supply, arrow 1) that is influenced by the mothers' reproductive physiology (in part regulated by the juvenile hormone; arrows 2). Similarly, the effect of offspring begging 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.

Acknowledgments

We thank two anonymous referees for their valuable and insightful comments. This research was supported financially by the Swiss National Science Foundation, grant no. 3100A0-11969 (to M.K.).

References

- Agrawal, A. F., Brodie, E. D. & Brown, J. 2001. Parent–offspring coadaptation and the dual genetic control of maternal care. *Science*, **292**, 1710–1712.
- Agrawal, A. F., Combs, N. & Brodie, E. D. 2005. Insights into the costs of complex maternal care behavior in the burrower bug (*Sehirus cinctus*). *Behavioral Ecology and Sociobiology*, **57**, 566–574.
- Bellés, X., Martin, D. & Piulachs, M. D. 2005. The mevalonate pathway and the synthesis of juvenile hormone in insects. *Annual Review of Entomology*, **50**, 181–199.
- den Boer, S. & Duchateau, M. 2006. A larval hunger signal in the bumblebee *Bombus terrestris*. *Insectes Sociaux*, **53**, 369–373.
- Borges, M. & Aldrich, J. R. 1992. Instar-specific defensive secretions of stink bugs (Heteroptera, Pentatomidae). *Experientia*, **48**, 893–896.
- Bourke, A. F. G. & Ratnieks, F. L. W. 1999. Kin conflict over caste determination in social Hymenoptera. *Behavioral Ecology and Sociobiology*, **46**, 287–297.
- Bristow, C. M. 1983. Treehoppers transfer parental care to ants: a new benefit of mutualism. *Science*, **220**, 532–533.
- Brossut, R. 1983. Allomonal secretions in cockroaches. *Journal of Chemical Ecology*, **9**, 143–158.
- Budden, A. E. & Wright, J. 2001. Begging in nestling birds. *Current Ornithology*, **16**, 83–118.
- Caussanel, C., Olivier, A., Arnault, C., Breuzet, M. & Karlinsky, A. 1986. Mechanisms and control of egg-laying of the earwig *Labidura riparia* (Dermaptera, Labiduridae). *Annales de la Société Entomologique de France*, **22**, 119–128.
- Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.
- Cocroft, R. B. 1996. Insect vibrational defence signals. *Nature*, **382**, 679–680.
- Cocroft, R. B. 1999. Offspring–parent communication in a subsocial treehopper (Hemiptera: Membracidae: *Umberonia crassicornis*). *Behaviour*, **136**, 1–21.
- Cocroft, R. B. 2001. Vibrational communication and the ecology of group-living, herbivorous insects. *American Zoologist*, **41**, 1215–1221.
- Cocroft, R. B. 2002. Antipredator defense as a limited resource: unequal predation risk in broods of an insect with maternal care. *Behavioral Ecology*, **13**, 125–133.
- Costa, J. T. 2006. *The Other Insect Society*. Cambridge, Massachusetts: Harvard University Press.
- Crook, T. C., Flatt, T. & Smiseth, P. T. 2008. Hormonal modulation of larval begging and growth in the burying beetle *Nicrophorus vespilloides*. *Animal Behaviour*, **75**, 71–77.
- Edgerly, J. S. 1997. Life beneath silk walls: a review of the primitively social Embiidina. In: *The Evolution of Social Behavior in Insects and Arachnids* (Ed. by J. C. Choe & B. J. Crespi), pp. 14–25. Cambridge: Cambridge University Press.
- Eggert, A. K. & Müller, J. K. 1992. Joint breeding in female burying beetles. *Behavioral Ecology and Sociobiology*, **31**, 237–242.
- Eggert, A.-K. & Müller, J. K. 1997. Biparental care and social evolution in burying beetles: lessons from the larder. In: *The Evolution of Social Behavior in Insects and Arachnids* (Ed. by J. C. Choe & B. J. Crespi), pp. 216–236. Cambridge: Cambridge University Press.

- Eggert, A. K., Reinking, M. & Müller, J. K. 1998. Parental care improves offspring survival and growth in burying beetles. *Animal Behaviour*, **55**, 97–107.
- Eisner, T., Rossini, C. & Eisner, M. 2000. Chemical defense of an earwig (*Doru taeniatum*). *Chemoecology*, **10**, 81.
- Endler, J. A. & Basolo, A. L. 1998. Sensory ecology, receiver biases and sexual selection. *Trends in Ecology & Evolution*, **13**, 415–420.
- Fetherston, I. A., Scott, M. P. & Traniello, J. F. A. 1990. Parental care in burying beetles: the organization of male and female brood-care behavior. *Ethology*, **85**, 177–190.
- Field, J. 2005. The evolution of progressive provisioning. *Behavioral Ecology*, **16**, 770–778.
- Fulton, B. B. 1924. Some habits of earwigs. *Annals of the Entomological Society of America*, **17**, 357–367.
- Godfray, H. C. J. 1991. Signaling of need by offspring to their parents. *Nature*, **352**, 328–330.
- Godfray, H. C. J. 1995. Signalling of need between parents and young: parent–offspring conflict and sibling rivalry. *American Naturalist*, **146**, 1–24.
- Groothuis, T. G. G. & Ros, A. F. H. 2005. The hormonal control of begging and early aggressive behavior: experiments in black-headed gull chicks. *Hormones & Behavior*, **48**, 207–215.
- Gwynne, D. T. 2004. Reproductive behavior of ground weta (Orthoptera: Anostomatidae): drumming behavior, nuptial feeding, post-copulatory guarding and maternal care. *Journal of the Kansas Entomological Society*, **77**, 414–428.
- Halffter, G. 1997. Subsocial behavior in Scarabeinae beetles. In: *The Evolution of Social Behavior in Insects and Arachnids* (Ed. by J. C. Choe & B. J. Crespi), pp. 237–259. Cambridge: Cambridge University Press.
- Hölldobler, B., Stanton, R. C. & Markl, H. 1978. Recruitment and food-retrieving behavior in *Novomessor* (Formicidae, Hymenoptera). 1. Chemical Signals. *Behavioral Ecology and Sociobiology*, **4**, 163–181.
- Huang, Z. Y. & Otis, G. W. 1991. Inspection and feeding of larvae by worker honey-bees (Hymenoptera, Apidae): effect of starvation and food quantity. *Journal of Insect Behavior*, **4**, 305–317.
- Hunt, J. & Simmons, L. W. 2004. Optimal maternal investment in the dung beetle *Onthophagus taurus*? *Behavioral Ecology and Sociobiology*, **55**, 302–312.
- Ishay, J. & Landau, E. M. 1972. *Vespa* larvae send out rhythmic hunger signals. *Nature*, **237**, 286–287.
- Ishay, J. & Schwartz, A. 1973. Acoustical communication between members of an oriental hornet (*Vespa orientalis*) colony. *Journal of the Acoustical Society of America*, **53**, 640–649.
- Johnstone, R. A. 2004. Begging and sibling competition: how should offspring respond to their rivals? *American Naturalist*, **163**, 388–406.
- Kaitala, A. & Mappes, J. 1997. Parental care and reproductive investment in shield bugs (Acanthosomatidae, Heteroptera). *Oikos*, **80**, 3–7.
- Kaptein, N., Billen, J. & Gobin, B. 2005. Larval begging for food enhances reproductive options in the ponerine ant *Gnamptogenys striatula*. *Animal Behaviour*, **69**, 293–299.
- Right, S. L. 1997. Factors influencing maternal behaviour in a burrower bug, *Sehirus cinctus* (Heteroptera: Cydnidae). *Animal Behaviour*, **53**, 105–112.
- Kilner, R. & Johnstone, R. A. 1997. Begging the question: are offspring solicitation behaviours signals of needs. *Trends in Ecology & Evolution*, **12**, 11–15.
- Kirkendall, L. R., Kent, D. S. & Raffa, K. A. 1997. Interactions among males, females and offspring in bark and ambrosia beetles: the significance of living in tunnels for the evolution of social behavior. In: *The Evolution of Social Behavior in Insects and Arachnids* (Ed. by J. C. Choe & B. J. Crespi), pp. 181–215. Cambridge: Cambridge University Press.
- Klemperer, H. G. 1982. Parental behavior in *Copris lunaris* (Coleoptera, Scarabaeidae): care and defense of brood balls and nest. *Ecological Entomology*, **7**, 155–167.
- Klemperer, H. G. 1983a. The evolution of parental behavior in scarabaeinae (Coleoptera, Scarabaeidae): an experimental approach. *Ecological Entomology*, **8**, 49–59.
- Klemperer, H. G. 1983b. Subsocial behavior in *Oniticellus cinctus* (Coleoptera, Scarabaeidae): effect of the brood on parental care and oviposition. *Physiological Entomology*, **8**, 393–402.
- Klostermeyer, E. C. 1942. The life history and habits of the ring-legged earwig, *Eurobellia annulipes* (Lucus [sic]) (Order Dermaptera). *Journal of the Kansas Entomological Society*, **15**, 13–18.
- Kohno, K. 1997. Possible influences of habitat characteristics on the evolution of semelparity and cannibalism in the hump earwig *Anechura harmandi*. *Researches on Population Ecology*, **39**, 11–16.
- Kölliker, M. 2007. Benefits and costs of earwig (*Forficula auricularia*) family life. *Behavioral Ecology and Sociobiology*, **61**, 1489–1497.
- Kölliker, M., Brodie, E. D., III & Moore, A. J. 2005a. The coadaptation of parental supply and offspring demand. *American Naturalist*, **166**, 505–516.
- Kölliker, M., Chuckalovcak, J. P. & Brodie, E. D., III 2005b. Offspring chemical cues affect maternal provisioning in burrower bugs (*Sehirus cinctus*). *Animal Behaviour*, **69**, 959–966.
- Kölliker, M., Chuckalovcak, J. P., Haynes, K. F. & Brodie, E. D. 2006. Maternal food provisioning in relation to condition-dependent offspring odours in burrower bugs (*Sehirus cinctus*). *Proceedings of the Royal Society of London, Series B*, **273**, 1523–1528.
- Kudô, S. 1990. Brooding behavior in *Elasmucha putoni* (Heteroptera, Acanthosomatidae), and a possible nymphal alarm substance triggering guarding responses. *Applied Entomology and Zoology*, **25**, 431–437.
- Kudô, S. I. 2000. The guarding posture of females in the subsocial bug *Elasmucha dorsalis* (Heteroptera: Acanthosomatidae). *European Journal of Entomology*, **97**, 137–139.
- Lamb, R. J. 1976a. Dispersal by nesting earwigs, *Forficula auricularia* (Dermaptera, Forficulidae). *Canadian Entomologist*, **108**, 213–216.
- Lamb, R. J. 1976b. Parental behavior in Dermaptera with special reference to *Forficula auricularia* (Dermaptera, Forficulidae). *Canadian Entomologist*, **108**, 609–619.
- Lazarus, J. & Inglis, I. R. 1986. Shared and unshared parental investment, parent offspring conflict and brood size. *Animal Behaviour*, **34**, 1791–1804.
- Le Conte, Y., Arnold, G., Trouiller, J. & Masson, C. 1990. Identification of a brood pheromone in honeybees. *Naturwissenschaften*, **77**, 334–336.
- Le Conte, Y., Sreng, L. & Poitout, S. H. 1995. Brood pheromone can modulate the feeding behavior of *Apis mellifera* workers (Hymenoptera, Apidae). *Journal of Economic Entomology*, **88**, 798–804.
- Le Conte, Y., Mohammedi, A. & Robinson, G. E. 2001. Primer effects of a brood pheromone on honeybee behavioural development. *Proceedings of the Royal Society of London, Series B*, **268**, 163–168.
- Ledoux, A. 1958. Biologie et comportement de l'Embioptère *Monotylota ramburi*. *Annales des Sciences Naturelles, Zoologie*, **20**, 515–523.
- Lessells, C. M. 2008. Neuroendocrine control of life histories: what do we need to know to understand the evolution of phenotypic plasticity? *Philosophical Transactions of the Royal Society of London, Series B*, **363**, 1589–1598.

- Lock, J. E., Smiseth, P. T. & Moore, A. J. 2004. Selection, inheritance, and the evolution of parent-offspring interactions. *American Naturalist*, **164**, 13–24.
- Lockwood, J. A. & Story, R. N. 1985. Bifunctional pheromone in the 1st instar of the southern green stink bug, *Nezara viridula* (L) (Hemiptera, Pentatomidae): its characterization and interaction with other stimuli. *Annals of the Entomological Society of America*, **78**, 474–479.
- Lockwood, J. A. & Story, R. N. 1986. Adaptive functions of nymphal aggregation in the southern green stink bug, *Nezara viridula* (L) (Hemiptera, Pentatomidae). *Environmental Entomology*, **15**, 739–749.
- Lockwood, J. A. & Story, R. N. 1987. Defensive secretion of the southern green stink bug (Hemiptera, Pentatomidae) as an alarm pheromone. *Annals of the Entomological Society of America*, **80**, 686–691.
- Matsuura, M. & Yamane, S. 1984. *Biology of the Vespine Wasps*. Berlin: Springer.
- Maynard Smith, J. & Harper, D. 2003. *Animal Signals*. New York: Oxford University Press.
- Melber, A., Holscher, L. & Schmidt, G. H. 1980. Further studies on the social behavior and its ecological significance in *Elasmucha grisea* L (Hem-Het, Acanthosomatidae). *Zoologischer Anzeiger*, **205**, 27–38.
- Montheit, G. B. & Storey, R. I. 1981. The biology of *Cephalodesmus*, a genus of dung beetles which synthesizes 'dung' from plant material (Coleoptera: Scarabaeidae: Scarabaeinae). *Memoires of Queensland Museum*, **20**, 253–277.
- Müller, W., Lessells, C. M., Korsten, P. & von Engelhardt, N. 2007. Manipulative signals in family conflict? On the function of maternal yolk hormones in birds. *American Naturalist*, **169**, E84–E96.
- Nalepa, C. A. 1984. Colony composition, protozoan transfer and some life-history characteristics of the woodroach *Cryptocercus punctulatus scudder* (Dictyoptera, Cryptocercidae). *Behavioral Ecology and Sociobiology*, **14**, 273–279.
- Nalepa, C. A. 1990. Early development of nymphs and establishment of hindgut symbiosis in *Cryptocercus punctulatus* (Dictyoptera, Cryptocercidae). *Annals of the Entomological Society of America*, **83**, 786–789.
- Nalepa, C. A. & Bell, W. J. 1997. Postovulation parental investment and parental care in cockroaches. In: *The Evolution of Social Behavior in Insects and Arachnids* (Ed. by J. C. Choe & B. J. Crespi), pp. 26–51. Cambridge: Cambridge University Press.
- Nault, L. R., Wood, T. K. & Goff, A. M. 1974. Treehopper (Membracidae) alarm pheromones. *Nature*, **249**, 387–388.
- Nijhout, H. F. 1994. *Insect Hormones*. Princeton, New Jersey: Princeton University Press.
- Pankiw, T. 2007. Brood pheromone modulation of pollen forager turnaround time in the honey bee (*Apis mellifera* L.). *Journal of Insect Behavior*, **20**, 173–180.
- Parker, G. A. & Macnair, M. R. 1979. Models of parent-offspring conflict. 4. Suppression: evolutionary retaliation by the parent. *Animal Behaviour*, **27**, 1210–1235.
- Parker, G. A., Royle, N. J. & Hartley, I. R. 2002. Intrafamilial conflict and parental investment: a synthesis. *Philosophical Transactions of the Royal Society of London, Series B*, **357**, 295–307.
- Parr, A., Tallamy, D. W., Monaco, E. L. & Pesek, J. D. 2002. Proximate factors regulating maternal options in the eggplant lace bug, *Gargaphia solani* (Heteroptera: Tingidae). *Journal of Insect Behavior*, **15**, 495–511.
- Quillfeldt, P., Masello, J. F., Strange, I. J. & Buchanan, K. L. 2006. Begging and provisioning of thin-billed prions, *Pachyptila belcheri*, are related to testosterone and corticosterone. *Animal Behaviour*, **71**, 1359–1369.
- Rankin, S. M., Fox, K. M. & Stotsky, C. E. 1995a. Physiological correlates to courtship, mating, ovarian development and maternal behavior in the ring-legged earwig. *Physiological Entomology*, **20**, 257–265.
- Rankin, S. M., Palmer, J. O., Larocque, L. & Risser, A. L. 1995b. Life history characteristics of ringlegged earwig (Dermaptera: Labiduridae): emphasis on ovarian development. *Annals of the Entomological Society of America*, **88**, 887–893.
- Rankin, S. M., Palmer, J. O., Yagi, K. J., Scott, G. L. & Tobe, S. S. 1995c. Biosynthesis and release of juvenile hormone during the reproductive cycle of the ring-legged earwig. *Comparative Biochemistry and Physiology C*, **110**, 241–251.
- Rankin, S. M., Storm, S. K., Piecto, D. L. & Risser, A. L. 1996. Maternal behavior and clutch manipulation in the ring-legged earwig (Dermaptera: Carcinophoridae). *Journal of Insect Behavior*, **9**, 85–103.
- Rankin, S. M., Chambers, J. & Edwards, J. P. 1997. Juvenile hormone in earwigs: roles in oogenesis, mating, and maternal behaviors. *Archives of Insect Biochemistry and Physiology*, **35**, 427–442.
- Rasa, O. A. E. 1998. Biparental investment and reproductive success in a subsocial desert beetle: the role of maternal effort. *Behavioral Ecology and Sociobiology*, **43**, 105–113.
- Rasa, O. A. E. 1999. Division of labour and extended parenting in a desert tenebrionid beetle. *Ethology*, **105**, 37–56.
- Rauter, C. M. & Moore, A. J. 1999. Do honest signalling models of offspring solicitation apply to insects? *Proceedings of the Royal Society of London, Series B*, **266**, 1691–1696.
- Reid, M. L. & Roitberg, B. D. 1994. Benefits of prolonged male residence with mates and brood in pine engravers (Coleoptera, Scolytidae). *Oikos*, **70**, 140–148.
- Robinson, G. E. & Vargo, E. L. 1997. Juvenile hormone in adult eusocial hymenoptera: gonadotropin and behavioral pacemaker. *Archives of Insect Biochemistry and Physiology*, **35**, 559–583.
- Roth, L. M. & Stay, B. 1958. The occurrence of para-quinones in some arthropods, with emphasis on the quinone-secreting tracheal glands of *Diploptera punctata* (Blattaria). *Journal of Insect Physiology*, **1**, 305–310.
- Royle, N. J., Hartley, I. R. & Parker, G. A. 2002. Begging for control: when are offspring solicitation behaviours honest? *Trends in Ecology & Evolution*, **17**, 434–440.
- Royle, N. J., Hartley, I. R. & Parker, G. A. 2004. Parental investment and family dynamics: interactions between theory and empirical tests. *Population Ecology*, **46**, 231–241.
- Ryan, M. J. 1990. Sexual selection, sensory systems, and sensory exploitation. *Oxford Surveys in Evolutionary Biology*, **7**, 157–195.
- Schooley, D. A., Tobe, S. S. & Yagi, K. J. 2005. JH8: recent progress in juvenile hormone research. *Journal of Insect Physiology*, **51**, 343.
- Schuster, J. C. & Schuster, L. B. 1997. The evolution of social behavior in Passalidae (Coleoptera). In: *The Evolution of Social Behavior in Insects and Arachnids* (Ed. by J. C. Choe & B. J. Crespi), pp. 260–269. Cambridge: Cambridge University Press.
- Scott, M. P. & Panaitof, S. C. 2004. Social stimuli affect juvenile hormone during breeding in biparental burying beetles (Silphidae: *Nicrophorus*). *Hormones & Behavior*, **45**, 159–167.
- Scott, M. P., Trumbo, S. T., Neese, P. A., Bailey, W. D. & Roe, R. M. 2001. Changes in biosynthesis and degradation of juvenile hormone during breeding by burying beetles: a reproductive or social role? *Journal of Insect Physiology*, **47**, 295–302.
- Sites, R. W. & McPherson, J. E. 1982. Life-history and laboratory rearing of *Sehirus cinctus cinctus* (Hemiptera, Cydnidae), with descriptions of immature stages. *Annals of the Entomological Society of America*, **75**, 210–215.
- Smiseth, P. T. & Moore, A. J. 2002. Does resource availability affect offspring begging and parental provisioning in a partially begging species? *Animal Behaviour*, **63**, 577–585.
- Smiseth, P. T. & Moore, A. J. 2004. Signalling of hunger when offspring forage by both begging and self-feeding. *Animal Behaviour*, **67**, 1083–1088.

- Smiseth, P. T., Darwell, C. T. & Moore, A. J. 2003. Partial begging: an empirical model for the early evolution of offspring signalling. *Proceedings of the Royal Society of London, Series B*, **270**, 1773–1777.
- Smiseth, P. T., Wright, J. & Kölliker, M. 2008. Parent-offspring conflict and co-adaptation: behavioural ecology meets quantitative genetics. *Proceedings of the Royal Society of London, Series B*, **275**, 1823–1830.
- Staerke, M. & Kölliker, M. In press. Maternal food regurgitation to nymphs in earwigs (*Forficula auricularia*). *Ethology*.
- Tallamy, D. W. 1984. Insect parental care. *Bioscience*, **34**, 20–24.
- Tallamy, D. W. 1985. Egg dumping in Lace bugs (*Gargaphia solani*, Hemiptera, Tingidae). *Behavioral Ecology and Sociobiology*, **17**, 357–362.
- Tallamy, D. W. & Brown, W. P. 1999. Semelparity and the evolution of maternal care in insects. *Animal Behaviour*, **57**, 727–730.
- Tallamy, D. W. & Denno, R. F. 1981. Maternal care in *Gargaphia solani* (Hemiptera, Tingidae). *Animal Behaviour*, **29**, 771–778.
- Tallamy, D. W. & Denno, R. F. 1982. Life-history trade-offs in *Gargaphia solani* (Hemiptera, Tingidae): the cost of reproduction. *Ecology*, **63**, 616–620.
- Tallamy, D. W. & Wood, T. K. 1986. Convergence patterns in sub-social insects. *Annual Review of Entomology*, **31**, 369–390.
- Tillman, J. A., Seybold, S. J., Jurenka, R. A. & Blomquist, G. J. 1999. Insect pheromones: an overview of biosynthesis and endocrine regulation. *Insect Biochemistry and Molecular Biology*, **29**, 481–514.
- Trivers, R. L. 1974. Parent-offspring conflict. *American Zoologist*, **14**, 249–264.
- Trumbo, S. T. 1996. Parental care in invertebrates. *Advances in the Study of Behavior*, **25**, 3–51.
- Trumbo, S. T. 1997. Juvenile hormone-mediated reproduction in burying beetles: from behavior to physiology. *Archives of Insect Biochemistry and Physiology*, **35**, 479–490.
- Trumbo, S. T. 2002. Hormonal regulation of parental behavior in insects. In: *Hormones, Brain and Behavior*. Vol. 3 (Ed. by D. W. Pfaff, A. P. Arnold, A. M. Etgen, S. E. Fahrbach, R. L. Moss & R. R. Rubin), pp. 115–139. New York: Academic Press.
- Trumbo, S. T. 2007. Defending young biparentally: female risk-taking with and without a male in the burying beetle, *Nicrophorus pustulatus*. *Behavioral Ecology and Sociobiology*, **61**, 1717–1723.
- Vancassel, M. 1977. Le développement du cycle parental de *Labidura riparia*. *Biology of Behaviour*, **2**, 51–64.
- Vancassel, M. 1984. Plasticity and adaptive radiation of dermapteran parental behavior: results and perspectives. *Advances in the Study of Behavior*, **14**, 51–80.
- Vancassel, M. & Foraste, M. 1980. Importance of contacts between female and larvae in some Dermaptera. *Biology of Behaviour*, **5**, 269–280.
- Vancassel, M., Foraste, M., Strambi, A. & Strambi, C. 1984. Normal and experimentally induced changes in hormonal hemolymph titers during parental behavior of the earwig *Labidura riparia*. *General and Comparative Endocrinology*, **56**, 444–456.
- Vancassel, M., Foraste, M., Quris, R., Strambi, A. & Strambi, C. 1987. The parental response of females *Labidura riparia* to young and its control. *Comparative Endocrinology*, **6**, 169–173.
- Vander Meer, R. K., Breed, M. D., Espelic, K. E. & Winston, M. L. 1998. *Pheromone Communication in Social Insects*. Boulder, Colorado: West View Press.
- West-Eberhard, M. J. 2003. *Developmental Plasticity and Evolution*. Oxford: Oxford University Press.
- West, M. J. & Alexander, R. D. 1963. Sub-social behavior in a burrowing cricket *Anurogryllus muticus* (De Geer). *Ohio Journal of Science*, **63**, 19–24.
- Wheeler, D. E. 1986. Developmental and physiological determinants of caste in social Hymenoptera: evolutionary implications. *American Naturalist*, **128**, 13–34.
- Wilson, E. O. 1971. *Insect Societies*. Cambridge, Massachusetts: Harvard University Press.
- Wolf, J. B. & Brodie, E. D., III 1998. The coadaptation of parental and offspring characters. *Evolution*, **52**, 299–308.
- Wood, T. K. 1976. Alarm behavior of brooding female *Umbonia crassicornis* (Homoptera Membracidae). *Annals of the Entomological Society of America*, **69**, 340–344.
- Wright, J. & Leonard, M. L. 2002. *The Evolution of Begging, Competition, Cooperation & Communication*. Dordrecht: Kluwer Academic.
- Wyatt, T. D. 2003. *Pheromones and Animal Behaviour*. Cambridge: Cambridge University Press.
- Zeh, D. W. & Smith, R. L. 1985. Paternal investment by terrestrial arthropods. *American Zoologist*, **25**, 785–805.