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Proc. R. Soc. B 2009 **276**, 2847-2853 first published online 13 May 2009
doi: 10.1098/rspb.2009.0498

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A chemical signal of offspring quality affects maternal care in a social insect

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Begging signals of offspring are condition-dependent cues that are usually predicted to display information about the short-term need (i.e. hunger) to which parents respond by allocating more food. However, recent models and experiments have revealed that parents, depending on the species and context, may respond to signals of quality (i.e. offspring reproductive value) rather than need. Despite the critical importance of this distinction for life history and conflict resolution theory, there is still limited knowledge of alternative functions of offspring signals. In this study, we investigated the communication between offspring and caring females of the common earwig, *Forficula auricularia*, hypothesizing that offspring chemical cues display information about nutritional condition to which females respond in terms of maternal food provisioning. Consistent with the prediction for a signal of quality we found that mothers exposed to chemical cues from well-fed nymphs foraged significantly more and allocated food to more nymphs compared with females exposed to solvent (control) or chemical cues from poorly fed nymphs. Chemical analysis revealed significant differences in the relative quantities of specific cuticular hydrocarbon compounds between treatments. To our knowledge, this study demonstrates for the first time that an offspring chemical signal reflects nutritional quality and influences maternal care.

Keywords: begging signal; chemical communication; parent–offspring conflict; signal of quality; cuticular hydrocarbons; *Forficula auricularia*

1. INTRODUCTION

Food provisioning is usually an essential form of post-hatching parental care enhancing offspring development and survival (see Clutton-Brock 1991). The amount and duration of parental investment is influenced by a conflict between parents and offspring (Trivers 1974), and the evolution of offspring begging signals is predicted based on an evolutionary resolution of this conflict (Parker *et al.* 2002b). Begging signals are supposed to reflect a cryptic short-term need (i.e. hunger) of offspring that parents use to adjust their food allocation (Godfray 1991). Despite a large number of experimental studies confirming the general function of offspring begging as a signal of short-term need (Kilner & Johnstone 1997; Budden & Wright 2001), recent studies also demonstrate that begging signals vary also with the social environment (brood size), physiological condition (age and size) and past experience (learning) of offspring (for e.g. Price *et al.* 1996; Lotem 1998; Cotton *et al.* 1999; Parker *et al.* 2002a; Grodzinski *et al.* 2008). Furthermore, the focus on vocal and postural signals of bird chicks that were clearly shown to signal a short-term need may have resulted in an underestimation of other forms of cues signalling an offspring quality and influencing parental care.

Godfray (1991, 1995) modelled ‘need’ as the marginal fitness gain for the parent from investment of extra resources in individual offspring. It is usually assumed that this definition of need is equivalent to variation in short-term nutritional condition, because one unit of food

would have a higher value for a hungry than for a satiated offspring. But the theoretical definition of need can also be interpreted as the amount of food required to reach independency, hence reflecting long-term physiological state (Price *et al.* 1996). Offspring in better physiological condition (quality) represent higher reproductive value for parents because the expected investment required to successfully raise offspring to independence is lower (Haig 1990; Davis *et al.* 1999; Jeon 2008). Experimental studies trying to disentangle short-term and long-term needs and their effects on begging signals have often manipulated offspring hunger and the composition of broods in terms of offspring age (for e.g. Lotem 1998; Cotton *et al.* 1999; Smiseth & Moore 2007). Because age is often confounded with competitive ability, it is not clear from these studies if parental food allocation is the result of parental choices or scramble competition (Royle *et al.* 2002). Nevertheless, a few recent studies in birds have revealed the presence of offspring cues that signal quality such as beak coloration (Saino *et al.* 2000), plumage coloration (Lyon *et al.* 1994) or UV reflectance (Jourdie *et al.* 2004; Bize *et al.* 2006; Tanner & Richner 2008).

Some social insect species display facultative parental care and offspring are not completely dependent on parental food (see Mas & Kölliker 2008). Such species provide a unique opportunity to study behaviours or cues that may reflect more ancestral conditions for the function of evolved begging signals (Smiseth *et al.* 2003; Smiseth & Moore 2004). In the present study, we tested the currently still insufficiently explored hypothesis that social insect offspring produce condition-dependent chemical cues that

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carers use to allocate their investment (Kölliker *et al.* 2005; den Boer & Duchateau 2006; Kölliker *et al.* 2006; Mas & Kölliker 2008) using the common earwig, *Forficula auricularia* (Dermaptera) as our experimental system. Female earwigs regurgitate food individually to nymphs (Staerkle & Kölliker 2008) and nymphs can survive without maternal care, albeit at a lower rate (Kölliker 2007; Kölliker & Vancassel 2007). Under the hypothesis of a signal of need, earwig females were predicted to provide more food after exposure to chemical cues of food-deprived nymphs. Conversely, under the hypothesis of a signal of quality, they were predicted to provide more food after exposure to chemical cues of well-fed nymphs. No *a priori* prediction could be made with regard to the effect of nymph condition on the chemical cue profiles because these were unknown and explored here for the first time.

2. MATERIAL AND METHODS

(a) *Earwig husbandry*

We collected adult common earwigs from a natural population located in Gommiswald, Switzerland (see Kölliker 2007) in early summer (June–July) 2007. We set-up groups of approximately 30 males and 30 females for mating in glass aquaria (20×30×20 cm) with humid sand as substrate and *ad libitum* food consisting of either vegetables and fruits (carrots and apples), or flower pollen (Swiss Extract, Bonadoz, CH) and bird food (Beo, Vitakraft) provided twice a week in alternating order. The aquaria were kept in a climate chamber at a constant temperature of 20 : 15°C and 50 per cent humidity with controlled photoperiod of 14 : 10 hours (day : night). In early August, 100 females were individually set-up in small Petri-dishes (10×2 cm) with humid sand and offered a piece of a half-cut plastic tube as shelter and kept under a new photoperiod of 8 : 16 hours to accelerate egg-laying. When egg-laying was observed, females were transferred with their clutch at 5°C and 50 per cent humidity in a dark chamber to terminate diapause of the eggs.

(b) *Experimental design*

When eggs hatched, between 9 and 12 weeks later, females with their brood were transferred in new Petri-dishes (10×2 cm) with humid sand and a shelter to a 16 : 8 hours and 20 : 15°C photoperiod-temperature regime for the experiment. Females and their brood were randomly assigned to be used as either biosource or bioassay broods. Biosource broods were used for chemical extraction of the chemical cues of nymphs, whereas bioassay broods were used for the behavioural tests.

Biosource broods were standardized to 25 nymphs and set-up without a mother. In six cases out of 33, nymphs of different broods were combined to generate a biosource brood in order to maximize the use of hatching clutches per day. Whether extracts came from a single- or mixed-origin broods had no significant influence on the results (all $p > 0.28$). All biosource broods received *ad libitum* food (pollen pellets; Kölliker 2007) from days 1 to 3 and were assigned randomly to two food treatments: the low-food (LF) treatment broods did not get any food from day 4 to 5, the high-food (HF) treatment broods were provided with food during this time. Thus, 2 days of food deprivation differentiated the LF and HF biosource broods. On the morning of day 6, LF and HF biosource broods were frozen at −20°C.

After thawing, 20 nymphs randomly selected from each biosource brood were immersed together in 1 ml of solvent (*n*-heptane, Rotisolv 99 per cent pure; Carl-Roth AG, Reinach, Switzerland) for 10 min. From this total cuticular extraction, three times 300 µl were transferred in three cleaned glass vials (2 ml, Sigma-Aldrich, Buchs, Switzerland). Two samples of 300 µl (each one equivalent to 6 nymphs) were concentrated down to 100 µl under a light nitrogen stream for their later use during the behavioural experiments. The third sample was stored at −80°C for later chemical analysis using a gas-chromatograph coupled to a mass-spectrometer (GC/MS). We used 100 µl of pure solvent (*n*-heptane) for controls (C). To avoid pseudo-replication, each extract was used only once in the behavioural assays.

Bioassay broods were set-up with a standardized 20 nymphs per brood and their mother. They were provided with food daily from day 1 to 4. To standardize the nutritional condition of the bioassay nymphs, the food was removed on day 5, 24 hours before the behavioural test.

(c) *Exposure and behavioural experiments*

On day 6, females from bioassay broods were removed from their brood and set-up in an exposure chamber. Exposure chambers consisted of a small Petri-dish (3.5×1 cm) painted in black with openings cut on the side that could be opened or closed. This exposure chamber was placed as an artificial nest burrow inside a medium-sized Petri-dish (10×2 cm) with humid sand. To reduce the effect of handling and habituate the females to the experimental procedure, females were transferred to the exposure chamber and back to their brood on the previous day 2 and 4. Prior to the start of the experiment, one extract (100 µl of either LF, HF or solvent) was applied to a filter paper disc (diameter 55 cm). After complete evaporation of the solvent, the impregnated filter paper was inserted in the exposure chamber. At the start of the experiment, bioassay females were enclosed for 30 min in the exposure chamber to expose them to the experimental treatment (volatile and non-volatile chemical cues of the extracts). The origin of the extracts (LF, HF or C) was selected from a randomization list and not known by the experimenter during the test.

After 30 min of exposure, the exposure chamber was opened and the females were allowed to forage on pollen pellets coloured with blue food-dye (synthetic E-131; patent blue V; Werner Schweizer AG, Switzerland) used as colour marker of female provisioning (Staerkle & Kölliker 2008). After one hour of access to the food, females were returned to their brood and allowed to interact with their nymphs for an hour. This procedure (30 min exposure + 1 hour foraging) was repeated a second time for each female using a second sample (100 µl) from the same total extract used in the first exposure and a new blue-dyed food pellet. This second session simulated a second foraging trip between the nest and the food source. This procedure differed from previous studies (Kölliker *et al.* 2005; den Boer & Duchateau 2006; Kölliker *et al.* 2006) in that it experimentally separated female exposure from her provisioning. Thus, it ensured that only mothers, and not the provisioned nymphs, were exposed to extracts, preventing a possible confounding exposure effect on nymph behaviour. After the second exposure session, females were returned to their brood, and they were left to interact overnight. On the subsequent morning (approx. 15 hours after the second exposure), we scored the total number of nymphs and the number of nymphs with green gut

content (mix of blue dye and the yellow pollen). The pollen pellets females could feed on were weighed on a Mettler Toledo AT261 balance before and after each of the two experimental sessions. To standardize the food weight measurements, the food pellets were dried overnight at 70°C after use in the experiments and cleaned of sand grains (repeatability of measurements: 99.9%; $F_{9,49}=7e5$, $p<0.0001$). The difference of weight of the same pellet before and after the exposure session provided us with a measurement of total food consumed by mothers after being exposed to extract of nymphs (Kölliker 2007). All behavioural experiments took place between 1500 and 1800 hours from 16 November 2007 to 12 February 2008 in a dark room at room temperature. Two red lights were used during short handling periods. Earwigs were not disturbed by the red lights and their nocturnal activity started as soon as the room was darkened (F. Mas 2008, personal observation).

(d) Chemical analysis

The third sample from each total extraction of biosource broods was used for GC/MS analysis. We added 200 ng of an internal standard (*n*-octadecane, $C_{18}H_{34}$; Sigma-Aldrich, St Louis, MO) to each sample and concentrated down to 50 μ l with a light stream of nitrogen. We injected 2 μ l of each concentrated extract in a GC/MS (Hewlett-Packard 6890 coupled to a Hewlett-Packard 5793). The extract was carried through a DB-5 capillary column (30 \times 0.25 mm ID and 0.25 μ m film-thickness, J&W Scientific, Folsom, CA) with a helium flow rate of 1 ml min⁻¹. The injector temperature was 250°C and was operated in split/splitless mode. The temperature program started at 70°C for 2 min and reached a maximum of 320°C at a rate of 5°C min⁻¹ where it was held for 5 min. Chromatograms were analysed using ChemStation software (Hewlett-Packard, Agilent Technologies). The identity of peaks was determined based on their retention time and mass-spectrum using the NIST 98 compound library as a reference, and guided by the preliminary identification of nymph cuticular compounds by (Liu 1991). Two peaks (C23.2 and 9-C23.1) were not well separated on the column, so we integrated both peaks together. We used the letters 'x' and 'y' to indicate different albeit unidentifiable positions of double-bonds or methyl-group. We estimated the absolute quantity of each compound by dividing the peak area by the area of the internal standard, and multiplying by 200 ng.

(e) Statistical analysis

One bioassay family was discarded because of high offspring mortality in the brood (50% died). We carried out the statistical analysis using R v. 2.7.0 (R Development Core Team 2008) and SAS (SAS 1999). Sample sizes varied slightly between models due to technical problems for two measurements of food weight. Measures of maternal provisioning (food quantity foraged and proportion of nymphs fed) were analysed using generalized linear models with the extract treatment (LF=18, HF=15, C=17) entered as factor. The normality and homoscedascity of the residuals were verified for each model and planned contrasts were defined in the models.

For the statistical analysis of the chemical compounds, we used the absolute quantities calculated from the internal standard. Several compounds were not normally distributed, even after transformation, thus we conducted a Wilcoxon rank test to compare chemical quantities between the two

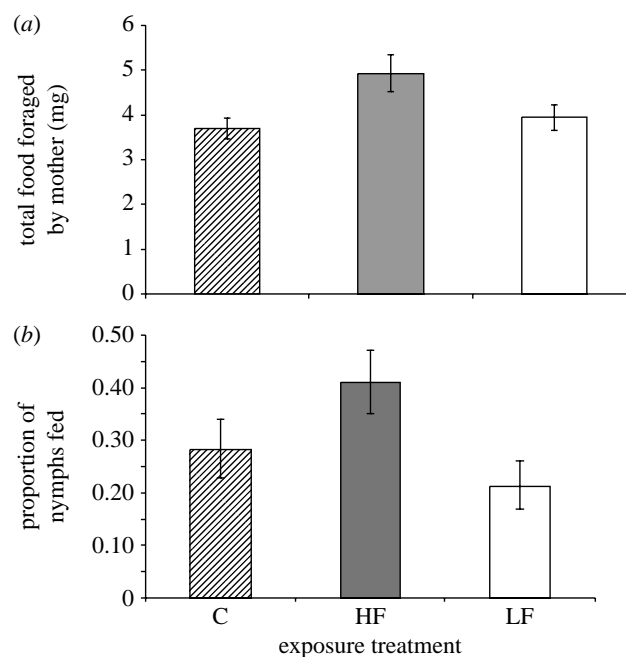


Figure 1. Effect of exposure treatment on maternal behaviours (C=solvent, HF=high-food nymph extract or LF=low-food nymph extract): (a) Mean total food foraged by mothers (in mg). (b) Mean proportions of nymphs fed by mothers. Error bars represent standard errors.

food treatments (LF versus HF). To control for multiple testing, we provide the standardized effect size as well as *p*-values obtained with the false discovery rate correction (Nakagawa 2004). The chemical compounds were further analysed in a multivariate analysis of variance (MANOVA) with compound quantity as the dependent variable, the brood as the subject, peak identity as the within-subject factor, and treatment as between-subject factor. All *p*-values are two-tailed.

3. RESULTS

(a) Effect of exposure to nymphs' extracts on maternal care behaviours

As predicted if condition-dependent chemical cues affect maternal food provisioning, the exposure treatment had a significant effect on the total quantity of food eaten by mothers during the two sessions (figure 1a; one-way ANOVA, $r^2=0.15$, $F_{2,45}=3.98$, $p=0.025$). Mothers exposed to HF-extracts consumed significantly more food than mothers exposed to LF-extracts (contrast 'HF-LF' $t=2.21$, $p=0.032$) or just the solvent (contrast 'HF-C' $t=2.65$, $p=0.011$).

The exposure treatment also significantly affected the proportion of nymphs with green guts (figure 1b; GLM with binomial error distribution, a logit link function and Williams correction for overdispersion: $F_{2,47}=6.812$, $p=0.033$), demonstrating an effect of the exposure treatment on how females allocated food among the nymphs. Mothers exposed to HF-extracts provided food to significantly more nymphs than mothers exposed to LF-extracts (contrast HF-LF $z=2.552$, $p=0.011$) but not compared to solvent (contrast HF-C $z=1.581$, $p=0.11$).

(b) Effect of food treatment on offspring cuticular hydrocarbons

From the total cuticular extractions of the biosource broods, we identified 21 peaks that each represented at

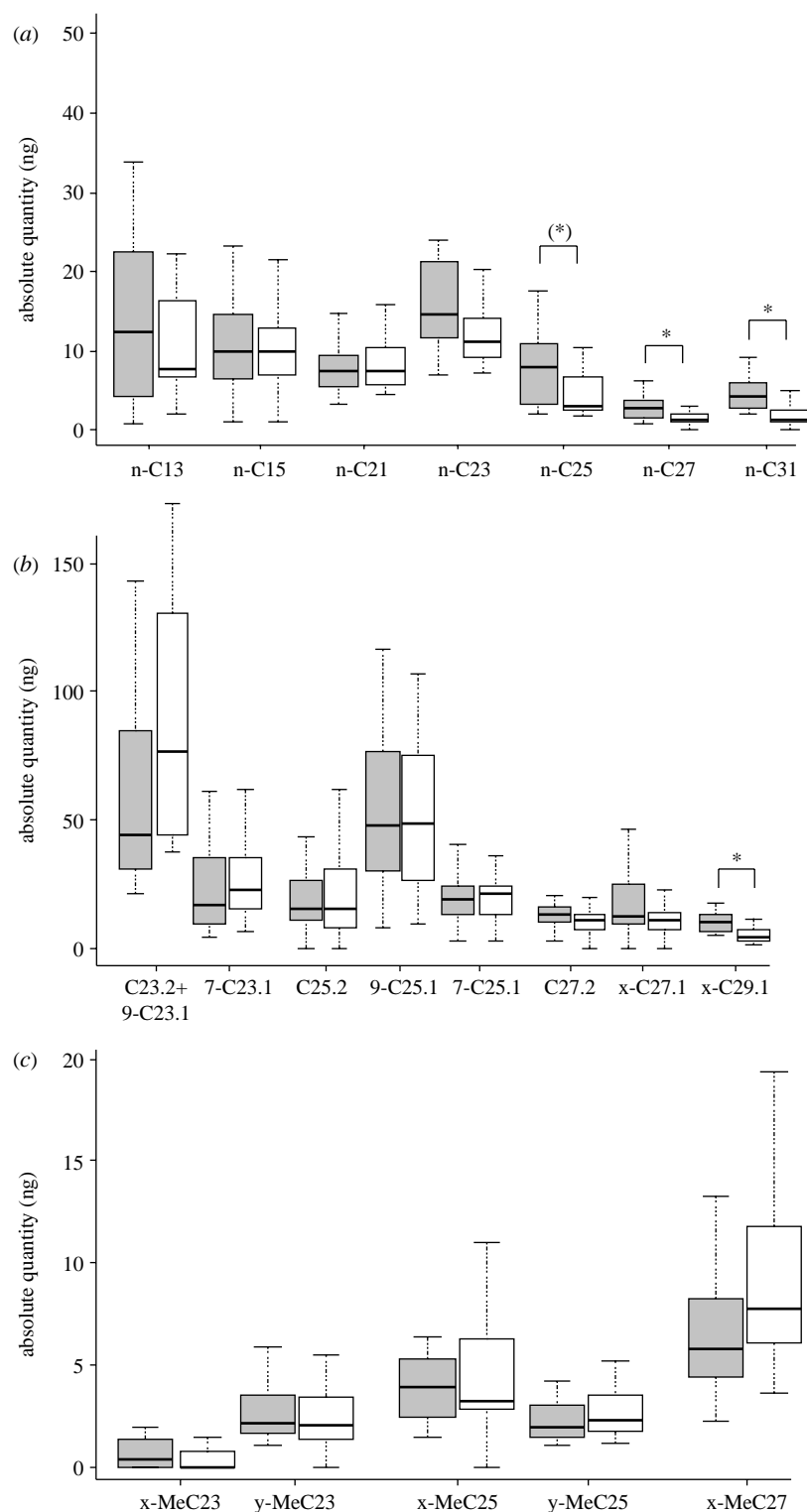


Figure 2. Box-plots of the absolute quantities (in ng) of hydrocarbons found on nymph's cuticle between the two food treatments: in grey HF, in white LF. The line represents the median of the sample, the box provides the upper and lower quartiles and the whiskers show 1.5 times the interquartile range. The scale of each graph was adjusted to the highest peak present in each class. (a) alkanes, (b) alkenes and (c) methyl-branched hydrocarbons. Asterisks show significant differences ($p < 0.05$) between HF and LF based on a Wilcoxon signed-rank test after adjustment for multiple testing. Asterisks in bracket indicate significant raw p -values but non-significant adjusted p -values.

least 1 per cent of the total abundance found on the cuticle. The chemical compounds were all hydrocarbons ranging from 13 to 31 carbons. Nymphs from LF and HF treatment had a qualitatively similar chemical profile with hydrocarbons from the alkene class being the most abundant compounds independent from the treatment effect ($74.4 \pm 0.9\%$) and alkanes as the second most

prevalent class ($19.3 \pm 0.9\%$) before methyl-branched hydrocarbons ($6.2 \pm 0.45\%$; see figure 2*a-c*). There was no significant difference between treatments in the overall absolute quantities of all cuticular hydrocarbons (CHCs) but there was a significant interaction of treatment and peaks (repeated MANOVA, between treatment effect: $F_{1,33} = 0.0358$, $p = 0.85$, treatment*peak interaction:

$F_{19,15}=2.53$, $p=0.037$). Three peaks in particular (two alkanes and one alkene) were strongly affected by the food treatment in terms of standardized effect size (r^2) and statistical significance (adjusted p -value): heptacosane (n -C27: $r^2=0.22$, $W=238$, $p=0.003$), nonacosene (x -C29.1: $r^2=0.30$, $W=259$, $p=0.003$) and hentriacontane (n -C31: $r^2=0.35$, $W=267$, $p=0.001$). Pentacosane (n -C25) also showed a notable effect size with a significant raw (but not adjusted) p -value ($r^2=0.12$, $W=221$, raw- $p=0.024$, adjusted- $p=0.12$). These four compounds were all found in higher amounts in HF extracts as compared to LF nymphs extracts, resulting in an overall larger proportions of alkanes among the CHCs profile of HF nymphs (% alkanes: HF = 21.4 ± 1.2 , LF = 17.2 ± 1.2 , $W=217$, $p=0.035$).

4. DISCUSSION

Our experiment confirmed the presence of chemical communication between earwig mothers and their offspring in the context of maternal care as previously hypothesized (Mas & Kölliker 2008). Our results demonstrate that offspring secrete a blend of hydrocarbons on their cuticle that vary with their nutritional condition and that mothers respond by adjusting their food provisioning. Mothers foraged for significantly more food and regurgitated to more nymphs after being exposed to chemical cues from HF nymphs as compared to LF nymphs. The positive maternal response to chemical cues from well-fed offspring supports the prediction for a signal of quality rather than a signal of need. While signals of quality have recently been described for visual cues in birds, this is to our knowledge the first demonstration of a chemical signal of quality expressed by offspring in a social insect.

The few studies that also explored chemical communication between carers and offspring (larvae or nymphs) in social insects have reported variable responses to condition-dependent offspring signals that, in contrast to our study, support the evolution of a signal of need. For instance in burrower bugs (*Sehirus cinctus*), Kölliker *et al.* (2005, 2006) showed that caring mothers increased their rate of food provisioning when exposed to volatiles from LF nymphs compared to HF nymphs or a solvent control. The major difference that may explained their contrasting results is that burrower bug mothers do not regurgitate food directly to an individual offspring but provide seeds to the entire brood (Sites & McPherson 1982). Thus, conflict between parent and offspring is expected to happen between different broods only and not among sibs of the same brood (Kölliker *et al.* 2005) which may shape differently the evolution of an offspring begging signal (Trivers 1974; Parker & Macnair 1978). In several species of eusocial insects, the foraging activity of the colony was also shown to be affected by chemical stimuli produced by the brood. For instance, in bumble-bees (*Bombus terrestris*), workers fed significantly more to larvae experimentally sprayed with extracts from food-deprived larvae compared to control larvae or larvae sprayed with extract from fed larvae (den Boer & Duchateau 2006). In honeybees (*Apis mellifera*), whole hexane extracts of the brood was also shown to affect the foraging activity of workers (Pankiw *et al.* 1998; Pankiw 2007). It was suggested that bee foragers used this brood pheromone

to estimate the level of need of the brood (Pankiw *et al.* 1998; Pankiw 2007). However, Dreller & Tarpay (2000) demonstrated that volatile cues from hungry young brood were not sufficient to stimulate foraging, but their results suggested that maybe non-volatile chemical cues communicated by direct contact may play a role. Workers of eusocial insects are generally reproductively inactive so the cost of food provisioning is expected to be low compared with the social benefit of raising larvae that will become future workers. This could explain why eusocial insect workers respond to a signal of need rather than quality. Only in the context of larvae with the potential to become queens, we may expect selection from workers for an offspring signal of quality. These examples highlight the importance of the social organization and the ecology of the species in the evolution of an offspring begging signals and the resolution of carer offspring conflicts.

The chemical analyses in our study show that the CHC profiles of earwig nymphs carry information about their nutritional state. Higher relative amounts of alkanes characterized well-fed nymphs (HF) compared to poorly fed nymphs (LF). Hydrocarbons are the most commonly found compounds on insect cuticles and have been shown primarily to serve as protection against desiccation (Blomquist *et al.* 1987). CHCs vary with ecological and social environments and insects biosynthesize most of them, although some may be secreted directly from the diet on the cuticle (Blomquist & Jackson 1973; Tillman *et al.* 1999; Blomquist & Vogt 2003). Interestingly, the variation in alkane ratios has been shown to reflect the environmental conditions in which ant workers were living (Wagner *et al.* 2001) and used by workers to discriminate task-specific workers (Greene & Gordon 2003) or also between nest-mates of a same colony against intruders (Liang & Silverman 2000). These examples illustrate how condition-dependent CHCs, and particularly alkanes, have been co-opted and evolved a secondary signalling function in various social contexts. Our finding of condition-dependent offspring CHC profiles in earwig nymphs suggests that particular CHC compounds may have been selected and co-opted for a secondary signalling function as an offspring signal of quality to their caring mothers. In the future, manipulative studies with individual synthetic CHCs and blends of these compounds should be conducted to provide direct evidence and confirm this signalling function.

Finally, in species where there is a high juvenile mortality, we may expect parents to preferentially feed offspring of higher reproductive value in order to maximize their fitness return on parental investment (i.e. Haig 1990). Kölliker (2007) reported a high juvenile mortality between first instar nymphs and the adult stage in the common earwig. Maternal investment that is allocated to nymphs of low condition associated with low likelihood to survive appears maladaptive for mothers. Since maternal investment has been demonstrated to be costly in this species (Kölliker 2007), we expect selection on mothers to maximize their return on investment by favouring offspring of good quality. Therefore, if specific CHCs of nymphs correlate positively with their nutritional condition as previously discussed, mothers may preferentially feed nymphs displaying them and thus drive the selection for a chemical signal of quality.

In conclusion, our results support the hypothesis that chemical communication evolved in the context of maternal care to regulate food provisioning in the social species *F. auricularia* and that mothers may select for an offspring chemical signal of quality. The current evolutionary theory on parent–offspring conflict resolution has generally assumed that offspring begging signals advertise need but the recent discoveries of offspring signals of quality in different species with parental care suggest that the resolution of conflict may have led to a multitude of signals of different forms (visual, chemical and vocal) and different functions (need, quality) depending on the ecology and social context in which offspring–carer interactions evolved.

We thank Ralph Dobler, Nicole Kalberer and David Duneau for their constructive discussion and two anonymous referees for their valuable comments. This research was funded by a research grant (no. 3100A0-111969 to M.K.) by the Swiss National Science Foundation.

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