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Maternal attendance and the maintenance of family groups in common earwigs (*Forficula auricularia*): a field experiment

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Abstract. 1. Understanding the evolution of subsocial behaviour and parental care requires experimental tests of the functional significance of such behaviours and the role of tending parents in the maintenance of family groups. Studies in subsocial insects addressing these issues experimentally and in the field are still relatively rare.

2. In such a field experiment, it is demonstrated here that the presence of tending females enhances the maintenance of family groups in common earwigs, *Forficula auricularia* (Dermaptera; Forficulidae). Experimental removal of tending mothers resulted in substantially decreased recovery of occupied nest burrows and larvae. This effect may have been because of decreased survival among experimental larvae, although a possible role for enhanced larval dispersal could not be fully ruled out.

3. Experimental (motherless) larvae were partly observed in family groups with a tending female, in both experimental and control nest burrows, suggesting that these larvae had been adopted by family groups moving to new nest burrows, and/or that experimental larvae may have actively joined other family groups.

4. This study demonstrates under field conditions the functional importance of maternal attendance for the maintenance of family groups in common earwigs, and suggests that adoption and clutch-joining are factors affecting the social structure of this species.

Key words. Adoption, clutch-joining, Dermaptera, family groups, *Forficula auricularia*, larval dispersal, parental care, subsocial behaviour.

Introduction

Subsocial insect species are characterised by the temporary formation and maintenance of aggregated family groups (Wilson, 1971). Subsociality also typically involves care provided by parents to their offspring (Wilson, 1971, 1975; Clutton-Brock, 1991), such as the protection against pathogens and predators and the provisioning of food (Tallamy, 1984; Tallamy and Wood, 1986; Trumbo, 1996). The evolution of parental care is expected under conditions with substantial benefits of care for juvenile survival (Wilson, 1975), but also when associated reproductive costs to parents are small (Smith and Fretwell, 1974; Clutton-Brock, 1991). The latter is more likely to be the case, for instance, in species with single or few reproductive attempts (i.e. semelparous species), because investment spent on current reproduction only marginally impacts future reproductive potential (Tallamy and Brown, 1999).

Common earwig (*Forficula auricularia:* Dermaptera; Forficulidae) females typically lay their eggs in a burrow where they guard the clutch and care for the eggs by cleaning them from fungi spores and possibly other pathogens (Weyrauch, 1927). After hatching, the mothers continue to guard their clutch of nymphs and also provision them with food (Lamb, 1976; Vancassel and Foraste, 1980; Liu, 1991). While maternal care clearly enhances larval development and survival, earwig larvae can survive without tending mothers through early dispersal and independent foraging (Vancassel, 1984). The duration of post-hatching care differs between what has recently been identified to be two distinct species (Wirth *et al.*, 1998). Species A, which was used for the study presented here, tends to occur in colder,

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higher altitude areas, reproduce once, hence is semelparous, and shows long maternal clutch attendance durations and late larval dispersal (Vancassel, 1984; Guillet *et al.*, 2000). Conversely, species B typically lives in more temperate areas, reproduces twice, and shows shorter maternal clutch attendance durations and earlier larval dispersal (in particular during the first reproductive attempt; Vancassel, 1984; Wirth *et al.*, 1998; Guillet *et al.*, 2000).

Maternal attendance may play a crucial part in the maintenance of family groups (both behaviourally and evolutionarily) because tending mothers are largely responsible for providing the major benefits of family life. If the mother abandons her clutch or dies, much of these benefits are lost and nymphs may have considerably lower survival prospects by remaining aggregated in their nest. Dissolving the family group by dispersing and independent foraging and/or joining other family groups (as observed in the hemipteran *Sehirus cinctus*; Agrawal *et al.*, 2004) may in the absence of a tending mother actually be an adaptive behavioural strategy for nymphs. Here, results from a field experiment are reported where the role of female attendance in the cohesion of family groups was addressed in common earwigs.

Materials and methods

The field experiments were carried out in late spring in the French Pyrenées at Mijanes, France, at an altitude of approximately 1500 m above sea level. The population at Mijanes belongs to the semelparous species (species A) of the *F. auricularia* species complex (Wirth *et al.*, 1998), characterised by long maternal attendance of clutches and delayed juvenile dispersal as compared with the iteroparous species B (Vancassel, 1984).

Nests containing hatched earwig nymphs and their tending mothers were found in late May during daytime underneath stones on subalpine pastures. The searched area covered approximately 1 ha (10 000 m^2). When a nest was found, as many larvae as possible were caught together with the tending females. Each nest was then allocated to one of two groups: (i) a control group where the larvae were put back into their nest together with their mother, leaving them as intact family group, and (ii) an experimental group where the larvae were placed back in their burrow without their mother. Nests were allocated to the control and experimental group in an alternating fashion, resulting in a random distribution of control and experimental nest burrows over the study area. The nymphs were marked by clipping the forceps (cerci) on one side of their body. Depending on treatment, the left or right cerci were clipped, allowing long-term distinction of larvae from the control and the experimental group. The tending females were not marked.

A total of 93 nests were involved in the experiment, and 2027 nymphs (1025 control, 1002 experimental) were marked. Nests were marked and numbered using plastic tags that were positioned on the down side of the rocks that covered the nest burrows. The control group consisted of 47 and the experimental group of 46 nests. Given that these 93 nests were randomly distributed on an area of approximately a hectare, nest burrows were on average roughly 10 m apart. One month after the manipulation and marking, the nests were checked for the presence of nymphs and females, the number of larvae was counted and their experimental origin noted (based on the side on which the cerci were clipped). An area within a radius of approximately 1 m around each nest was intensely searched (i.e. all rocks in this area were turned) for control/experimental earwig nymphs that may have dispersed. Of the 47 control and the 46 experimental nests, 43 and 44 nest burrows were retrieved respectively.

The dependency of the relative frequencies of these categories (empty nest burrows, nests with larvae only, nests with larvae and tending female) on the experimental treatment was analysed by contingency tables and associated statistical tests using SAS statistical software (SAS, 1999). To avoid pseudoreplication, statistical tests were only performed on data available on the basis of the nest burrow.

Results

The composition of families found in the nest burrows depended on our experimental treatment (likelihood ratio $\chi^2_2 = 17.43$, $P = 0.0002$; Fig. 1). There was a much smaller overall number of occupied nest burrows in the experimental than the control group (Fig 1; 16% vs. 58%; likelihood ratio $\chi^2_1 = 17.43$, $P < 0.0001$). The proportion of clutches tended by a female was, however, virtually identical for the two groups (control: 0.72 (0.51–0.88 95% CI); experimental: 0.71 (0.29–0.96 95% CI)). Thus, even though mothers were removed in the experimental group, nymphs from this treatment were found in female-attended family groups.

In terms of individual larvae, 116 nymphs were found from the control and 53 from the experimental treatment. Thirty-seven of the 53 retrieved larvae (i.e. 70%) from the experimental treatment were found in association with a tending female, partly in control and partly in experimental nest burrows. No dispersed nymphs were found in the area other than in the nests that were part of the study.

Discussion

The prediction that maternal clutch attendance would enhance the viability and maintenance of family groups in common earwigs was supported by the results of this study. Significantly fewer nests containing live larvae (as well as a lower number of larvae) were retrieved from the experimental than the control group. This effect could not unambiguously be attributed to larval dispersal or mortality (or both) under field conditions. The result that no larvae were found in the vicinity of the nest burrows, however, while larvae were found changing family groups among nests, suggests that this decreased recapture success may be largely because of higher mortality of nymphs in unattended family groups. Unattended larvae might have suffered from reduced food supply and starvation (due to lack of maternal provisioning), and/or higher predation pressure and pathogene infection (due to lack of maternal defence). Further studies are needed to untangle how exactly maternal attendance enhances larval survival under field conditions.

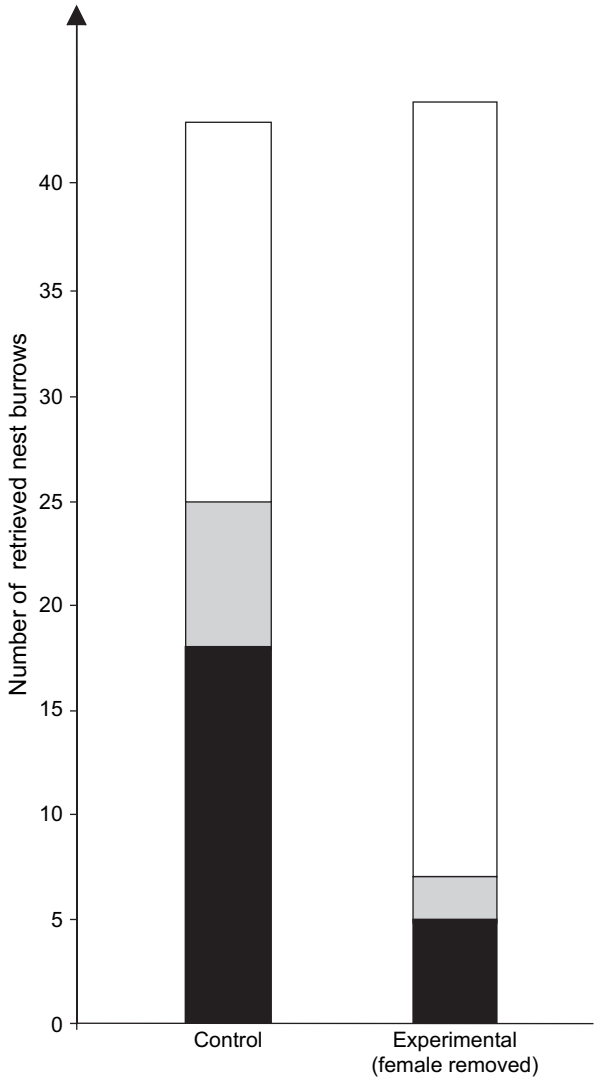

Fig. 1. Effect of experimental female removal on the number and composition of retrieved nest burrows. Controls are nests where the female was left tending her clutch. White bars: empty nest burrows. Grey bars: nest burrows with unattended nymphs. Black bars: nest burrows containing nymphs and a tending female (i.e. intact family groups).

Given that female earwigs are well known for their care behaviours that involve protection and food provisioning, an effect of maternal attendance on larval survival was anticipated, but previously untested under field conditions. The observed substantial benefits of maternal attendance for larval survival, combined with the semelparous life history (i.e. low costs to females), may be a critical basis for the evolutionary stability of subsociality in this species.

From a larval perspective, remaining aggregated in the nest burrow may be the best strategy as long as a female provides food and protection. If the female dies or abandons the burrow, however, the benefit of staying in the burrow is largely lost, and larvae should disperse and seek protection and food sources outside their burrows, despite the likely risks associated with a premature departure from a burrow.

Indeed, the few recaptured nymphs from the experimental group were mostly found attended by females in experimental nest burrows, even though females had been removed in these nest locations. This observation suggests that abandoned larvae may get adopted by intact family groups that switch nest burrow (e.g. after a disturbance such as our experimentation). A few nymphs from the experimental group were observed in control nests, suggesting that they may have actively joined other family groups by dispersing. Unfortunately, the used marking technique (clipping of cerci) was too crude to trace larvae to their original nest burrow (it was only possible to assign larvae to experimental or control burrows), and females were not marked, precluding conclusions on the frequencies of these behaviours and the dispersal distances. Despite these limitations, the data show that clutch-joining through adoption and/or active larval dispersal occurs in common earwigs. More detailed studies with females and larvae marked on the basis of their nest burrow will be required to further investigate this phenomenon.

Both behavioural mechanisms underlying clutch-joining (i.e. female adoption of foreign nymphs and nymph following and joining of family groups) are further supported by evidence on proximate mechanisms underlying nymphal and maternal decision making in this species. Mothers do not discriminate own from foreign nymphs (Radl and Linsenmair, 1991), and nymphs are capable of discriminating clutch-tending from reproductively inactive females, likely based on altered cuticular hydrocarbon profiles (Liu, 1991). As expected, nymphs show a preference to associate with tending females. It remains to be tested if nymphs use these chemical cues to join intact family groups when they encounter adult females during dispersal. The observation of clutch-joining raises questions on why females accept to care for unrelated nymphs (Radl and Linsenmair, 1991). While the benefits of adoption seem straightforward from a nymph's perspective, this is not the case from a female's perspective, potentially resulting in conflicts. The presumably low cost of care in a semelparous species as the common earwig, species A, may be a likely explanation (Tallamy and Brown, 1999). The low evolutionary costs of care imply weak selection on mothers to discriminate against unrelated nymphs.

It was shown in this field experiment that the presence of female earwigs affects the maintenance of family groups, probably by enhancing clutch viability through the provisioning of care. It was further observed that the social dynamics of earwig populations involves adoption of nymphs by female-tended family groups and, possibly, active nymphal joining of family groups through dispersal. More detailed investigations using individual markings and closer observations will provide better estimates for the importance of adoption and clutch-joining in earwig populations.

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