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The biology and social life of earwigs (Dermaptera)

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Abstract

Earwigs are often known for the forceps-like appendage at the end of their abdomen, urban legends about them crawling into human ears, and their roles as pest and biological control agents. However, they are much less known for their social life. This is surprising, as many of the 1,900 species of earwigs show social behaviors toward eggs, juveniles, and adults. These behaviors typically occur during family and group living, which may be obligatory or facultative, last up to several months, and involve only a few to several hundred related or unrelated individuals. Moreover, many individuals can alternate between solitary and group living during their life cycle, an ability that probably prevailed during the emergence of social life. In this review, I detail the diversity of group living and social behavior in earwigs and show how further developing this knowledge in Dermaptera can improve our general understanding of the early evolution of social life in insects.

Keywords

family life, facultatively social, parental care, aggregation, subsocial, precosial

1. WHAT ARE EARWIGS?

Earwigs (also known as the order Dermaptera) are free-living, flat, elongated insects characterized by a pair of forceps-like cerci at the end of their abdomen (1). They are often difficult to observe because they are nocturnal and secretive and like to hide in small cavities. Nevertheless, this taxonomic group is ubiquitous: It contains approximately 1,900 described species that can be found on every continent except Antarctica (39, 44). Most earwigs are oviparous. Females generally lay eggs in the soil, often guard the clutch of eggs during development, and sometimes remain with the juveniles (called nymphs) for several weeks (2). Apart from these characteristics, earwigs are often known to the general public for allegedly crawling into the ears of sleeping people, but fortunately, this is just an urban legend (4, 49). Many species have a significant impact on human agrosystems around the world. Some are considered major pests that damage vegetative tissues, flowers, grains, and fruits. Others are proven biological control agents against many insect pests, such as leafhoppers, caterpillars, aphids, and flies. A few species even do both (89). By contrast, the impacts of earwigs on other human interests are quite limited, as they are not known to cause health problems in livestock, pets, or humans and do not damage buildings (39).

The phylogenetic position of Dermaptera among insects and the phylogenetic relationships within this order have been in constant flux in recent decades (21, 38, 84, 123). On the one hand, Dermaptera have been successively proposed as a sister group to almost all of the 10 orders of Polyneoptera (87). This major monophyletic clade of winged insects includes Plecoptera (stoneflies), Orthoptera (crickets), Embioptera (web-spinners), Phasmatodea (stick insects), Mantodea (mantises), Blattodea (cockroaches and termites), and Zoraptera (angel insects). The latest available data retain Zoraptera as the sister group to Dermaptera (123, 124). On the other hand, Dermaptera is traditionally composed of 11 families whose composition and phylogenetic position have also greatly varied throughout the history of systemic entomology. These families typically include Anisolabididae (37 genera/393 described species), Apachyidae (2/15), Chelisochidae (17/95), Diplatyidae (9/143), Forficulidae (67/500), Karschiellidae (2/12), Labiduridae (7/73), Pygidicranidae (18/182), Spongiphoridae (40/499), and the epizoic Arixenidae (2/5) and Hemimeridae (2/12) (39, 84, 85). These families were long structured

around three major clades: the Protodermaptera, which referred to the lower or primitive earwigs; the Epidermaptera, which referred to the derived or higher earwigs; and the Eudermaptera, which comprised earwigs that feature one instead of the ancestral two penises and was contained within the Epidermaptera. However, the recent accumulation of morphometric, anatomical, and genomic data from many species has led to some major changes in this classification. For instance, Protodermaptera is now considered a monophyletic clade nested within the paraphyletic Epidermaptera (i.e., at the same level as Eudermaptera), and Spongiphoridae has become a paraphyletic group and Apachyidae a sister group to the other earwigs (123) (Figure 1).

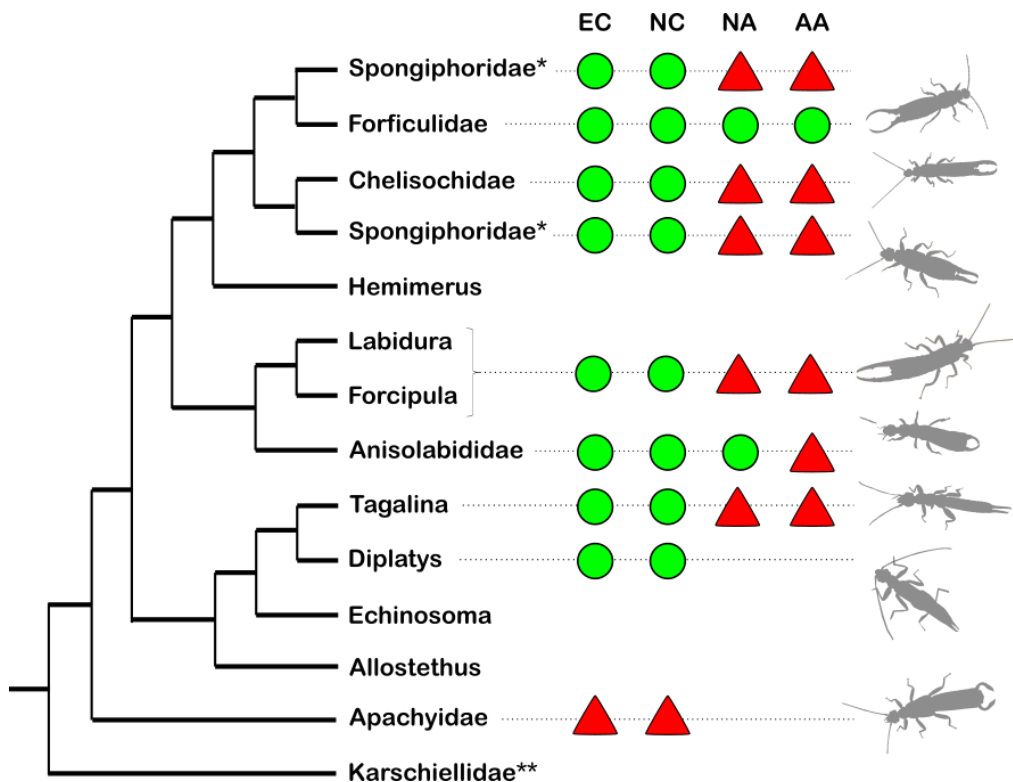


Figure 1 - Reported cases of egg care (EC), nymph care (NC), nymph aggregation (NA), and adult aggregation (AA) across the Dermaptera phylogeny. These social behaviors and forms of group living are present (*filled circle*), absent (*open circle*), or not reported (*no symbol*) in at least one species of the given family. Details per family are provided in Table 1. The proposed phylogeny is based on Wipfler et al. (123). *Spongiphoridae is a polyphyletic group. **The phylogenetic position of Karschiellidae remains unclear.

Besides their agricultural implications and phylogenetic challenges, earwigs have long

attracted attention for their unusual social life in insects. One of the first descriptions of the social life of earwigs dates from 1778 (23a), when the biologist Charles de Geer reported: “At the beginning of June, I found a female earwig under a stone, accompanied by several small insects, which I could not fail to recognize as her own young, of which she was the mother. They stayed by her side, never leaving her, and often placed themselves under her belly, like the chicks of a hen.” (p548). Since then, numerous studies have shed light on the diversity of social life across earwigs. They revealed that it can be obligatory or facultative, last from a few hours to several months, and involve up to several hundred individuals. This broad diversity has recently attracted the attention of evolutionary biologists interested in why some animals are solitary while others live in groups—a long-standing problem in biology. Over the past few centuries, these researchers have typically approached this problem by studying the biology of eusocial insects (e.g., ants; termites; and some bees, wasps, and thrips), which has provided important information about the diversity, function, evolution, and ecological success of this obligate and integrated form of sociality (77). However, this focus has led to the neglect of most other forms of sociality and profoundly biased our current knowledge on many aspects of the early transition from solitary living to all forms of (noneusocial) group living in insects (63, 114). There is, therefore, a great need to find and study new taxa presenting noneusocial forms of social life and to investigate the nature, determinants, and evolution of their sociality (19, 95). Earwigs seem to have all these characteristics, but the information available on their sociality is often partial, sparse, and poorly contextualized. The main aim of this review is to address this issue by presenting the current state of knowledge on the diversity of group living and social behavior in earwigs (based on the 46 species for which this information is available; see Table S1). More generally, it also aims to show why developing our knowledge of this taxon may open up opportunities to improve our general understanding of the early stages of social evolution in insects.

2. GROUP LIVING AND SOCIAL INTERACTIONS OF EARWIGS THROUGHOUT THEIR LIFE CYCLE

During their life cycle, earwigs have multiple opportunities to live in groups and express social behaviors (Figure 2). However, not all species seize all of these opportunities. In this section, I

present the different steps of the life cycle of earwigs and discuss the extent to which they involve social and nonsocial behaviors. It should be noted that most of the available information on the biology and life cycle of earwigs has been obtained under laboratory conditions and/or from observations of a few individuals in the field. Although these studies provide important (and sometimes the only) data for our general understanding of the biology of these species, we cannot exclude the possibility that some information might be different under less standardized conditions (17, 31). It is therefore important to keep these limitations in mind when considering the results of the studies presented in the following sections.

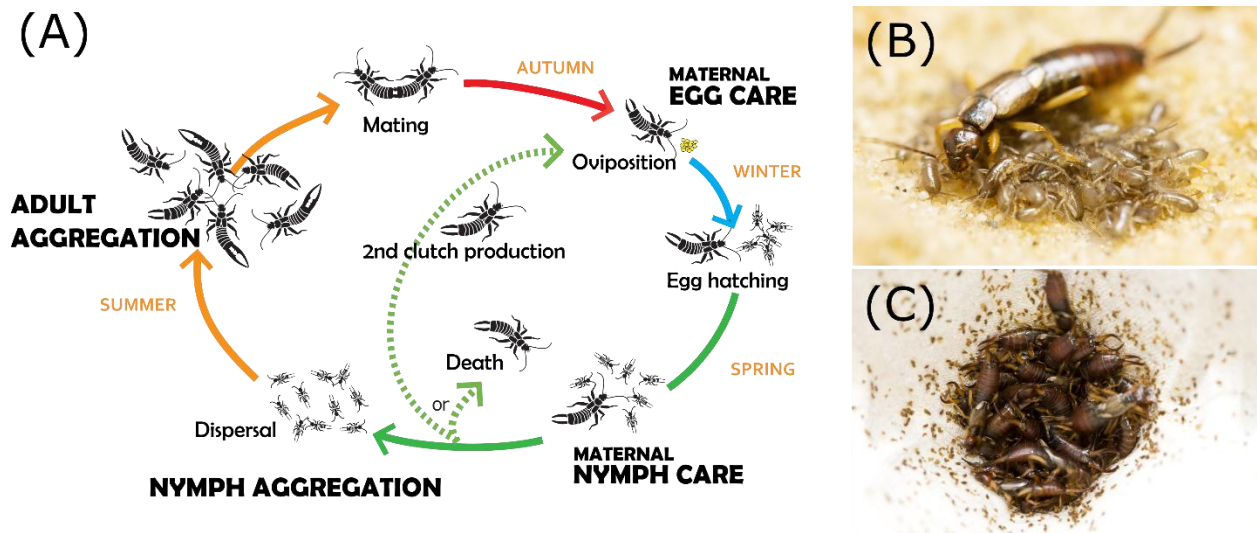


Figure 2 - Life cycle and forms of sociality of the European earwig, *Forficula auricularia*. (a) This species illustrates the different forms of family life and group living of nymphs and adults that can be found in Dermaptera. Seasons are given for natural populations in European regions (89). (b) *F. auricularia* mother tending her clutch of first-instar nymphs. (c) Group of *F. auricularia* adults. Photos by the author.

2.1. Mating

Earwigs must mate to reproduce (sexual reproduction), although parthenogenesis has been reported in one species (20). Social interactions associated with mating usually involve a complex behavioral sequence of approach, antennation, and movements of forceps-like cerci from males to females (81, 93). Earwigs' courtship lasts up to several hours, after which females accept mating by lifting and slightly twisting the tip of their abdomen while the two partners face

opposite directions (13). The mating lasts from a few minutes to several hours—with a record of 20h in *Tagalina papua* (13, 71)—and can be interrupted by other males or females present in the group or near the partners. During copulation, females are generally free to leave, except in a few species such as *Apachyus chartaceus*, where they are held between the forceps-like cerci of their partner for the entire mating duration (98), and *Pseudomarava prominens*, where males grasp the females prior to copulating, insert their penis without twisting their abdomen, and then release the females for the rest of the mating (13). Mating can also be more coercive. This is the case in *Marava arachidis*, where males grab the female's antennae with their mouthparts during mating, while females resist mating attempts by directing their forceps-like cerci at the males (13, 54).

For the most part, earwig females store the sperm received during mating in the spermatheca, although exceptions exist, such as in *Sphingolabis hawaiiensis*, where females do not possess this organ (97). Interestingly, the number of spermathecae, the number of male genitalia, and the size of male genitalia vary across species. For instance, *Diplatys flavicollis* females have six independent spermathecae (51), and *Anisolabis maritima* and *Euborellia plebeja* males have two functional elongated penises (virgae)—one is used during copulation, while the other functions as a spare in case the first one is damaged (53). Moreover, males and females of the pygidicranid earwig *Echinosoma horridum* have extremely long genitalia (85.1% of body length in the male and 386% in the female), while the genitalia is much shorter in *Echinosoma denticulatum* (4.5% of body length in the male and 66.1% in the female) (69).

2.2. Nest Construction and Oviposition

Nest construction and oviposition involve virtually no social interaction in earwigs—even though nest construction is a form of maternal care (76). Females usually begin to build a nest a few days to several months after mating. This construction is done alone after the female has chased away the male and other conspecific individuals. The nest structure is generally simple and ranges from one- or two-chambered nests (6, 65) to slightly more complicated systems of burrows such as those of *A. maritima* (3). They are usually a few centimeters deep (e.g., under large stones) but can reach depths of several meters (18, 65) or, more rarely, be produced at the collar of plants, such as by *Forficula senegalensis* (11). Earwigs lack specific appendices or leg

morphologies facilitating digging and can thus only use their mouthparts to remove soil from the nest (8). Whereas most earwigs only use their nests for egg production and posthatching family life, a few species, such as *Euborellia moesta*, also use it during other parts of their life cycle, e.g., for mating and hunting (8). Adults typically produce an average of 15 to 70 eggs, which develop in 5 to 50 days (Table S1), although a few species are viviparous (39, 47, 56) and others are ovoviviparous, i.e., females lay eggs containing fully developed nymphs that emerge only a few minutes after deposition (52, 90). During egg development, mothers typically provide care to their eggs (see Section 3.1) and stop their foraging activity (59, 101)—the notable exceptions are *A. chartaceus*, where eggs receive no apparent forms of care (98), and *Anisolabella marginalis*, where females bring food into the nest for themselves (103).

2.3. Post-Hatching Family Life

Of the 11 species for which data on maternal behavior after egg hatching are available, four show a posthatching family life (Table 1). Whether or not there is a family life after hatching, earwig nymphs are quickly mobile and often capable of foraging for themselves soon after hatching. This is the case, for instance, in the ovoviviparous *Prolabia arachidis*, where nymphs start their foraging activity only one day after their birth (42), or in the European earwig, *F. auricularia*, where the nymphs can forage as soon as four days after hatching (126). In species where it occurs, family life generally lasts until the nymphs reach the second developmental instar, which can take 2 to 14 days (Table S1). After that time, mothers usually abandon their brood and may then even attack (and consume) their offspring when brought back into contact with them (48, 83). One exception can be found in *Anechura bipunctata*, where mothers stay with their nymphs for several instars and even until their final molt if the mother survives long enough (117). The termination of posthatching family life is often due to environmental constraints such as food shortages. In the hump earwig, *Anechura harmandi*, for example, nymph dispersal occurs faster when nymphs are not provided with food, whereas the usual duration of family life can be restored when food is provided by the mother or by the experimenter (104). In contrast, food limitation does not affect the likelihood of nymphs remaining with their mothers for more than 40 days in the European earwig (126).

Table 1 Overview of the different forms of maternal care and the other types of aggregations reported in eight free-living Dermaptera families. Each cell shows the number of species investigated for each given behavior (in parentheses) and the percentage of said species where the behavior was found. Maternal care follows the categories previously defined by Matzke & Lass (71). The details of each species can be found in Table S1.

Family	Number of species with some data	Maternal egg care					Maternal nymph care						Other types of aggregation	
		Association with eggs	Egg cleaning	Egg transport and pilling up	Aggressive egg defense	Mother assistance for hatching	Association with nymphs	Allogrooming	Aggressive nymph defense	Nymph transport	Male–male contacts	Maternal food provisioning and matrophagy	Old nymphs	Adults
Anisolabididae	9	100% (9)	100% (5)	100% (5)	100% (6)	0% (2)	100% (8)	100% (1)	75% (4)	100% (3)	0% (1)	66% (3)	33% (3)	50% (2)
Apachyidae	1	0% (1)	0% (1)	0% (1)	0% (1)	0% (1)	0% (1)	0% (1)	0% (1)	0% (1)	0% (1)	0% (1)	Unknown	Unknown
Chelisochidae	2	100% (2)	100% (2)	100% (2)	100% (1)	0% (1)	100% (2)	100% (1)	100% (1)	100% (1)	100% (1)	100% (1)	0% (1)	0% (1)
Diplatyidae	2	100% (2)	0% (1)	0% (1)	100% (1)	0% (1)	100% (1)	Unknown	100% (1)	0% (1)	0% (1)	0% (1)	Unknown	Unknown
Forficulidae	16	100% (16)	100% (11)	100% (11)	100% (10)	33% (6)	100% (16)	100% (4)	100% (7)	86% (7)	80% (5)	80% (5)	100% (3)	100% (3)
Labiduridae	6	100% (6)	100% (5)	100% (6)	100% (2)	0% (1)	100% (6)	100% (2)	100% (2)	100% (2)	100% (1)	100% (2)	0% (2)	0% (2)
Pygidicranidae	3	100% (3)	0% (1)	0% (3)	100% (2)	0% (1)	100% (3)	0% (1)	100% (1)	0% (1)	0% (1)	0% (1)	0% (1)	0% (1)
Spongiphoridae	7	100% (4) ^a	100% (3) ^a	100% (3) ^a	100% (3) ^a	40% (5) ^a	100% (6)	100% (2)	100% (3)	80% (5)	50% (4)	33% (3)	0% (1)	0% (1)

^aThis family includes viviparous and ovoviviparous species that are not considered for calculating percentages in maternal egg care.

2.4. Nymph Development and Aggregation of Young Adults

The nymphs typically develop through four to six instars until they reach adulthood (Table S1), which can take from a few weeks to six months (71). After the end of family life, nymphs are often solitary and territorial. They fiercely fight any conspecific they may encounter and are particularly prone to expressing cannibalism (which they also do during family life) (70, 90). However, in some species, juveniles and newly emerged adults regularly form aggregations of a few to several hundred individuals that belong to the same or different earwig species (55, 121) (Table 1). Conspecific aggregations can be found in *A. maritima*, *F. auricularia*, *Forficula decipiens*, *Forficula pubescens*, and *Pseudochelidura sinuata* (40, 91). Conversely, heterospecific aggregations often involve *F. auricularia* together with *F. decipiens* and *F. pubescens* or, more rarely, together with *E. moesta* or *Labidura riparia* (34, 67, 96). The occurrence and size of these aggregations may reflect both habitat limitation (79) and the sex of individuals already present in the shelter (40, 106).

2.5. The Fate of Mothers

After their first clutch (and the departure of their nymphs), earwig mothers often produce additional clutches over the next few months (Table S1)—whether or not they show posthatching care. Remating is typically not necessary, as females may use the sperm stored in their spermatheca (8). The number of clutches that a female can produce in a lifetime varies both between and within species. Multiple factors have been proposed to determine these variations, such as the genetic lineage of females, their number of oocytes at the imaginal molt, their nutritional status at oviposition, and their access to food during development (5, 78, 125, 127). Mothers eventually die after their last-laid clutch at an age of up to 18 months (109a)—if they are not cannibalized beforehand by their own nymphs (see below) or victims of predation events.

2.6. What About Fathers?

The very limited available data suggest that males have no social and reproductive functions after mating. Indeed, the presence of males near or in the nest decreases egg survival in *F. auricularia*, *Doru luteipes*, and *Euborellia annulipes*, either because males directly eat some of

the eggs (even if they may prefer unrelated compared to related eggs; 48) or because females neglect their eggs to chase the male away (23, 48, 66, 94). In *Labia minor*, males defend the nest together with the female for a couple of days before oviposition, after which they generally leave the nest (83). Whether these males provide significant help against egg predators, guard the female to prevent mating with other males, or remain in the nest vicinity to (nonadaptively) eat some of the eggs is unclear. The life expectancy of males is often significantly shorter than that of females (86), although this difference may vary between populations (109a).

3. THE SOCIAL BEHAVIORS OF EARWIGS: THE KNOWN AND UNKNOWN

Despite the multiple social behaviors expressed by earwigs over their life cycle, these behaviors have received a very mixed level of attention in the literature (Table 1). The most-studied social behaviors are maternal egg care during egg development and maternal nymph care during posthatching family life (22, 71, 117). By contrast, much less is known about the nature of sibling interactions during posthatching family life and about the types of social interactions occurring in groups of juveniles and adults. In the following sections, I provide an overview of our current knowledge of these social behaviors. I do not detail the hormonal, chemical, and genetic regulation of (some of) these behaviors, as this has been covered in other reviews (68, 110, 129).

3.1. Egg Care

Egg care is by far the most-studied social behavior in earwigs, probably because it is also the most common among the Dermaptera (Table 1 and Table S1). This prehatching behavior has been reported in all of the species of earwigs studied to date except one: *A. chartaceus*, an ancestral representative of the family Forficulidae (98). This exception could suggest either that maternal egg care is not part of the Dermapteran ground plan, contrary to what has long been assumed, or that maternal egg care has been lost at least once during Dermaptera evolution (123). Additional studies are required to disentangle these two hypotheses. Despite this exception, earwig females usually care for their eggs alone. Communal egg care may occasionally occur, as neighboring females have been shown to gather the eggs and care for them indiscriminately in *A. bipunctata* (118).

There is a wide variety of forms of egg care in earwigs, of which the most studied are egg

grooming, aggressive defenses against predators or conspecifics, and egg-hatching assistance. Egg grooming is a very frequent behavior in which females groom their eggs using their lacea, a small mouthpart appendix covered with a silk brush on its top (48, 118). This behavior has at least three known functions. First, it allows mothers to remove fungal spores and other particles present on the eggshell (10). Mothers of the European earwig, for instance, increase their grooming behavior curatively when eggs are covered with fungal spores (10) and prophylactically when the nesting environment contains entomopathogenic fungi (25). Second, egg grooming allows mothers to renew the chemical protection of their eggs against desiccation by applying cuticular hydrocarbons to the eggshells (10). In the absence of egg grooming, the amount of cuticular hydrocarbons on the eggshells decreases continuously, suggesting that they are not self-produced by the eggs (10). Finally, egg grooming may allow mothers to transfer core microbiota to the eggs. In the maritime earwig, *A. maritima* (37), the presence of the mother determines the abundance and community structure of bacteria on the egg surface including the presence of bacterial strains that have the potential to protect eggs from fungal infection (37). However, it is not always physically possible for earwigs to clean their eggs. In *Diplatys flavicollis*, for instance, mothers produce eggs with adhesive stalks that prevent eggs being moved. These mothers can arrange their eggs shortly after oviposition, before the adhesive stalks have firmly attached the eggs to the substratum, but they cannot easily groom them afterward (99).

Mothers can aggressively defend their eggs using two types of weapons: forceps-like cerci and chemical sprays (28). When facing an intruder, females first try to intimidate their opponents by raising their forceps above their heads or by arching their abdomen to bring their forceps forward above the head. If this is not enough, they then use their forceps as scissors to wound or cut the assailants in half (28, 81). The strength of their forceps allows the females to inflict severe damage to many different attackers, such as pseudoscorpions and spiders. The defensive posture of female earwigs also allows them to spray the intruder with defensive secretions from glands opening on their abdominal tergite. Interestingly, these secretions mostly consist of benzoquinone derivatives (29), which not only deter predators, but also exhibit antimicrobial activity against bacteria and fungi and even against nematodes (35). The spraying of benzoquinone near or on the eggs during egg guarding could thus also be an efficient strategy

for earwig mothers to protect eggs against parasites and pathogens, although this function needs to be tested. Note that some earwigs also spray sulfides similar to the odors of carrion or feces to deter predators such as ants and vertebrates (16).

The third and last well-studied form of egg care in earwigs is maternal assistance in egg hatching. This behavior has been mostly reported in earwig species from ancestral lineages, such as *M. arachidis*, *L. riparia*, and *P. arachidis* (18, 42, 90), where mothers bite the eggs at the time of hatching to aid the emergence of juveniles. Egg-hatching assistance has also been suggested to occur in *F. pubescens* (82), a species belonging to a more recent lineage, although the behavioral process by which mothers of this species help eggs to hatch is still unclear. Otherwise, egg-hatching assistance is absent in most of the other earwig species where it has been investigated, even when egg hatching is concomitant with a molting event that could have benefited from additional help from the mother (71, 108).

Maternal egg care also takes other forms whose function and distribution across Dermaptera remain unclear. For example, the mothers of the European earwig show variable investment in nest construction: Some females build a large, complex nest in the ground, while others lay their eggs directly on the ground (78). The function of the more complex nests could be to protect the eggs from harsh climate conditions and environmental pathogens, but experimental evidence remains scarce (25). Another example of maternal care is egg displacement: Some mothers of the European earwig move their eggs from one location to another during egg development (43, 74). These displacements could be an adaptive response to temperature changes and pathogen presence, as well as a nonadaptive response to maternal stress (25, 109). Finally, it has been reported that *F. auricularia* mothers cover any food remains present in the nest after oviposition with ground material (105). This could be a form of care to prevent the development of pathogenic microorganisms in the vicinity of the eggs, but this has not yet been tested.

In the many species where females care for the eggs, the evolution of this behavior has made maternal presence a necessity to protect the eggs from fungal and predator attack, desiccation, and exposure to suboptimal temperatures (10, 37, 50). However, orphaned eggs of several species can still hatch when experimentally maintained under constant temperature and humidity (48) or when eggs are regularly brushed by an experimenter (18). Moreover, the

sensitivity of earwig eggs to orphaning varies across species, raising questions about the evolutionary drivers maintaining maternal egg care among earwigs. For instance, the survival rate of eggs abandoned during their first 30 days averages only 10% in *F. auricularia* but reaches an average of 70% (and up to 100%) in *F. pubescens* when reared under similar laboratory conditions (82, 112).

Somewhat surprisingly, maternal egg care can be directed to conspecific, unrelated eggs and even to glass beads; tiny stones; and other small, light-colored miscellaneous objects. This high level of acceptance has been reported, for instance, in *F. auricularia* (112), *Doru lineare* (15), and *E. annulipes* (50), where it raises questions about the maintenance of egg care despite the risks of social parasitism by conspecific and heterospecific females (112). This is unlikely to be caused by a lack of signals on the eggs to help mothers recognize their own eggs, as eggshells have a bouquet of cuticular hydrocarbons that may be specific to each group of mothers and juveniles (10, 128). By contrast, it could be due to the intrinsically prominent level of aggressiveness of egg-tending mothers, which makes it very unlikely for another female to deposit its eggs in a foster nest and thus reduces selection pressures to evolve an (error-prone) egg discrimination response. This is consistent with the observation that, when two nests of *F. auricularia* females are accidentally in contact, one female usually chases away the other one and then combines—and cares for—both clutches (33).

3.2. Nymph Care

In contrast to prehatching care, posthatching maternal care has been studied in only a few earwig species (Table 1). Most forms of posthatching maternal care arise as an extension of prehatching care beyond offspring emergence. For instance, mothers show aggressive behaviors toward intruders with their forceps-like cerci, regularly groom their juveniles with their mouthparts, and/or displace their nymphs to another location when the nest is disturbed (72, 101).

By contrast, food provisioning is very specific to this life stage. This form of maternal care consists of mothers bringing food pieces into the nest (101), regurgitating food to the juveniles (100), or sacrificing themselves to feed juveniles with their bodies (58). Mass food provisioning has been reported in numerous earwig species, where mothers forage away from their nest to

obtain diverse types of food (such as prey and plant material) and bring them back to the nest. In the maritime earwig, *A. maritima*, for instance, the amount of food brought to the nest is proportional to the number and nutritional needs of the juveniles, suggesting that this food not only is a nutritional reserve for the mothers, but also serves to feed the juveniles (102).

To the best of my knowledge, food regurgitation has only been investigated in the European earwig. In this species, first-instar juveniles have a cuticle that is transparent enough to show the color of the food that they have ingested. Based on this peculiarity, Staerke & Kölliker (100) first fed *F. auricularia* mothers with green-colored food, then allowed them to interact with their juveniles for 24 hours, and finally showed that some of the juveniles had turned green. As is the case for many forms of posthatching parental care, this food regurgitation is determined by multiple factors, including female condition; the early life experience of tending mothers; and inherited, parent-of-origin-specific effects expressed in juveniles (64, 75, 105, 126, 129). However, recent data suggest that this color transfer could also result from the nymphs' consumption of feces pellets produced by mothers, as some of the feces produced by juveniles are eaten by their siblings (32) and by their mothers (113) during family life. Additional studies are thus needed to disentangle the roles of trophallaxis and coprophagy in the transfer of food from mothers to juveniles.

The last known form of maternal food provisioning is matrophagy. This surprising phenomenon has been reported in a very limited number of earwig species, among which the hump earwig, *A. harmandi* is a prime example. In this species, the first-instar nymphs kill and eat their mothers before dispersing from the nest (58). This behavior must be constitutive of its life cycle because it occurs in every family, and when it is prevented (experimentally), the nymphs are less likely to develop successfully, and the rescued mothers do not reproduce again (even if their spermatheca still contains motile sperm) (104). Cases of matrophagy have also been reported in a few other species, such as *F. auricularia* (122), *Chelidurella acanthopygia* (116), and *E. moesta* (8), but in these cases, it is very likely to reflect the opportunistic consumption of the corpses of prematurely dead mothers.

As with eggs, earwig mothers provide care to foreign nymphs as long as they are in the physiological state of providing care and the nymphs are located in the females' own nest (92,

105). In this case, again, this lack of discrimination can be surprising, as mothers should ensure that their expression of costly forms of care is directed toward their offspring. However, the development of such a discrimination ability may be unnecessary if other family members already discriminate. In the European earwig, such discrimination is performed by the nymphs. By setting up experimental pairs of related and unrelated juveniles, Dobler & Kölliker (26, 27) revealed that foreign (and thus likely unrelated) nymphs are more often victims of aggression and cannibalism than familiar (and thus likely related) nymphs. Thus, nymphs can enforce the expression of maternal care toward related offspring by killing potential intruders, thereby relaxing selection pressure on this trait in the mothers.

In contrast to egg care, it is often assumed that posthatching maternal care is not necessary for the development and survival of earwig nymphs. This idea mostly relies on studies showing that nymphs have early foraging capabilities (42, 126) and that orphaned juveniles exhibit a survival rate comparable to nonorphaned juveniles, such as in *A. maritima* (101) and *P. arachidis* (42) under standard laboratory conditions. In the European earwig, maternal loss can even slightly improve the survival rate of nymphs (under laboratory conditions) and yield adult offspring with a larger body size and longer forceps-like cerci (105, 119). Other studies, however, show that orphaned nymphs do not survive more than 12 h under standard conditions, as in *Spongovostox apicedentatus* (45). Whether *S. apicedentatus* mothers provide elements that are intrinsically necessary to ensure offspring development (e.g., immune effectors and symbionts) remains to be further explored. As all the results presented in this section were obtained under standard conditions, we cannot exclude the possibility that the reported benefits (or costs) of maternal presence for the nymphs may be different under natural conditions, i.e., with more abiotic and biotic constraints such as food limitation and higher risks of predation and pathogen infection. Further work under natural conditions is therefore needed to confirm the reported effects. Nevertheless, these contrasting results suggest possible variation in the level of dependence of nymphs on maternal care, which may have a profound impact on the evolution and duration of family life within Dermaptera.

3.3. Sibling Interactions During Family Life

The social behaviors occurring during family life are expressed not only between parents and

offspring, but also among the offspring. In earwigs, nymphs express frequent and tight behavioral interactions with their siblings in the form of mouth-to-mouth contacts (stomodaeal trophallaxis), mouth-to-anus contacts (proctodaeal trophallaxis), allogrooming, and cannibalism. Mouth-to-mouth contacts between first-instar nymphs have been reported in *P. arachidis* (42) and *F. auricularia* (30, 32), whereas mouth-to-anus contacts are only known in *F. auricularia* (32). In other insects, these contacts often mediate the exchange of food, symbionts, immune components, and other molecules of physiological interest (41, 88). However, the content of fluid exchanged during trophallaxis between siblings remains unknown in earwigs.

Only a few studies have investigated the determinants of food transfer among siblings, and these studies are limited to the European earwig. At the individual level, they showed that the frequency and duration of mouth-to-mouth contact are independent of the level of starvation of the recipient nymph (32). At the family level, they showed that higher rates of sibling food transfer are associated with lower rates of maternal food provisioning (64), as well as with larger clutch sizes when mothers are in a deteriorated state (62). Taken together, these results suggest that sibling food transfer is not a dynamic behavior that depends solely on the needs of the interacting nymph, but may be an ancestral behavior that has been evolutionarily maintained at the family level to reduce the costs of potential mother loss or of being cared for by poor-quality mothers (64).

Information on mouth-to-anus contacts and allocoprophy by nymphs during family life is also very scarce and, again, comes only from studies on the European earwig. By manipulating the relatedness and starvation of pairs of nymphs, Falk et al. (32) revealed that mouth-to-anus contacts are longer between unrelated compared to related nymphs, whereas allocoprophy was more frequent between related compared to unrelated nymphs. Given that access to sibling feces improves nymph longevity in the absence of other food sources (60), these findings suggest that feces could be a public good that is openly shared among related nymphs but monopolized at the source by unrelated nymphs (32). Securing access to nymph feces could also provide immune benefits to consumers, as nymph feces exhibit antimicrobial properties (24).

Finally, allogrooming and cannibalism among siblings have been reported in several species (26, 32, 101), but their functions and determinants remain poorly investigated. Allogrooming is

typically used by other social insects to remove dirt, external pathogens, and parasites from the cuticles of conspecifics, as well as to apply chemical compounds involved in communication (9, 73). Whether these functions apply between nymphs is unknown. Similarly, sibling cannibalism is generally an extreme outcome of sibling rivalry over parental investment in care (80). In *F. auricularia*, this cannibalism is preferentially expressed against siblings with lower body weight (27), which is in line with sibling aggression toward individuals of poor condition.

3.4. Groups of Adults and Old Juveniles

To date, the temporal stability, genetic structure, and social network of groups comprising old juveniles or adults are unclear, as is the nature of the social behaviors readily expressed in these aggregations. Dyadic encounters of *F. auricularia* adults nevertheless suggest that these interactions encompass forms of cooperation, such as allogrooming; mating behaviors; and forms of aggression, primarily between males competing for females (14, 120, 121). In *F. auricularia*, the level of expression of these behaviors is independent of the nutritional needs of the adults, and allogrooming is more frequent in pairs of males compared to pairs of females (121). Further studies are needed to determine the impact of these effects on the functioning of these groups.

Despite our limited knowledge of social interactions in adult aggregations, several lines of evidence suggest that group living shapes important fitness traits in adults. In terms of immunity, for example, the sudden isolation of otherwise gregarious *F. auricularia* females produces stress that reduces the resistance of these females to infection by an entomopathogenic fungus (57). This stress is transient and disappears when females are kept in isolation for several weeks before infection (57), suggesting that females' immunity is altered by the sudden change in the social environment. The composition of this social environment is also important because the replacement of group members by other individuals also affects the level of investment of resident adults in their basal immunity (61). Another study investigated why some *F. auricularia* adults are more or less likely to exhibit aggregation behaviors, and its results suggest that early life experience may be important. In this study, Van Meyel & Meunier (115) reared nymphs either alone or with family members and found that the resulting adults were less gregarious when reared alone. Whether this early life effect can be inherited by the next generation, and

thus ultimately drive the level of aggregations of adult earwigs at the population level, remains to be investigated.

4. CONCLUSIONS

Overall, this review shows how the study of earwigs holds promise for improving our understanding of the evolutionary origins of “simple” social systems and the mechanisms supporting the early evolution of social life in general (63). Dermaptera indeed include a wide variety of solitary and social forms in which adults and juveniles live in small or large groups of related or unrelated individuals and in which mothers show little or high investment in the care of eggs and juveniles. Studying how these variations follow the phylogeny of Dermaptera can therefore help us to better understand the emergence, consolidation, and disappearance of forms of sociality that constitute a transition from solitary to social life and mark the initial steps in the major evolutionary transition to eusociality (12, 63). Moreover, this review stresses that adults and juveniles of several earwig species have the capability to alternate between solitary and group living at any time during their life cycle, with only limited costs to them. Because this capability is likely to have prevailed during the early evolution of social life (32), these species provide an excellent opportunity to explore the factors that drove the initial transition to social life at the individual level.

However, this review also highlights the limitations of our current knowledge of the biology and social behavior of Dermaptera and the need to continue and develop research on this taxon. The presented data cover fewer than 50 of the 1,900 earwig described species, and much of the information is based on mere observations or experiments carried out under laboratory conditions. There is therefore a need to investigate the sociality of other earwig species under natural conditions and to be cautious about generalizing well-studied behaviors in some iconic species (such as the European earwig) to the entire order. Nevertheless, there is room for optimism. Advanced genomic, chemical, microbiological, and behavioral methods have recently been developed for studying several earwig species (7, 87, 111, 129). This may soon attract a broader community of researchers interested in the many aspects of dermapteran biology, paving the way for major improvements in our future understanding of their social life and its

peculiarities in insect evolution.

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