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# Summary

## Abstract

When we think of social insects, earwigs rarely come to mind. This is perhaps not surprising, as the term 'social insect' has often been used in the literature to refer exclusively to 'eusocial insects', i.e. ants, termites and certain bees and wasps. However, earwigs show many aspects of social life. Social interactions in earwigs can occur in groups of up to several hundred individuals, with mothers providing extensive forms of care for their eggs and juveniles, and adults and juveniles showing cooperative behaviour with group members of the same and different ages. In this review, we discuss how research on the European earwig (by far the most studied dermapteran species in terms of its social life) can improve our general understanding of social evolution in insects. After outlining (1) its life cycle and (2) its multiple forms of sociality, we explain how this species advances our knowledge of (3) the interplay between social conflict and cooperation in maintaining facultative social life, (4) the role of pathogens and symbionts in the transition between solitary and social life, (5) the impact of anthropogenic change on social evolution, and (6) the chemical, hormonal and genetic regulation of facultative social behaviour. Overall, this review highlights that the study of social species such as the European earwig can provide unique insights into our general understanding of social evolution and the early evolutionary transitions from solitary to group living.

Keywords: facultatively social, family life, subsocial, parental care, precocial species, Dermaptera

## 1. Introduction

Most studies of insect social life tend to focus on species that live in super-organismal (eusocial) societies, such as ants, termites, some bees and wasps. Eusocial societies have a fascinating form of social life, where a few individuals monopolise reproduction (reproductive division of labour), offspring care for their siblings (cooperative brood care) and there is overlap between generations (Starr 2021). However, social life in insects is not limited to eusociality (Costa 2006a, 2018; Rubenstein and Abbot 2017). Indeed, if we define social life as non-accidental forms of group living involving at least two individuals and reciprocal communication of a cooperative nature (Wilson 1971; Costa 2019; Kramer and Meunier 2019), it can be found in various taxa. For example, social interactions can be found in mere aggregations of caterpillars (Sword 2008), in cooperatively breeding groups of some wasps (Brockmann 1997), or in relatively small family groups with facultative or obligatory parental care as in burying beetles (Capodeanu-Nägler et al. 2016).

The long-standing focus on eusocial insects has provided fundamental information about the evolutionary drivers of this unique form of social organisation. However, it has also hindered our general understanding of the early evolutionary transition from solitary to social life. These early steps in the evolution of social life can be defined as the factors that contribute to the emergence and maintenance of social life. For example, social life may emerge with the appearance of parental care after hatching (Choe and Crespi 1997; Bourke 2011). If offspring remain in the clutch, this evolutionary transition may extend to the consolidation of social life through cooperation between siblings, and sibling assistance to parents (Kramer and Meunier 2019). The long-standing focus on eusocial insects has, therefore, impeded our advancement of insights into all other forms of social life in insects (Elgar 2015; Rubenstein and Abbot 2017; Meunier and Steiger 2018; Biedermann et al. 2021). For example, there is a rapidly growing collection of data on the genetic and epigenetic basis of social interactions in ants and eusocial bees. However, such data remains comparatively scarce in non-eusocial insects (e.g. Cunningham et al. 2015; Wu et al. 2020; Bhattarai et al. 2022), and the genetic and epigenetic basis underlying non-eusocial sociality is therefore still poorly understood (Kronauer and Libbrecht 2018). Another example concerns our understanding of social conflicts. The resolution of social conflicts in insect colonies with reproductive division of labour involves evolutionary processes that are very different from those in groups where every member has

direct access to reproduction (e.g. Smiseth and Royle 2018; Kramer and Meunier 2019). It is, therefore, unclear whether these strategies of conflict resolution are a by-product of eusociality or whether they are ancestral phenomena that aided the transition from solitary to advanced forms of group living. A third example relates to the communication system. Eusocial insects rely heavily on chemical signals, as well as acoustic, tactile and visual communication, to maintain the social structure of their colonies and to coordinate activities such as foraging, nest building, brood care, and defence (Kocher and Cocroft 2019). The extensive knowledge of signals in eusocial insects contrasts sharply with our limited understanding of communication systems in non-eusocial species and how these systems regulate inter-individual behaviours (e.g. parental care, aggression) and processes such as aggregation and recognition of (un)related conspecifics (Mas and Kölliker 2008; Wyatt 2014). Finally, the extent to which group members invest in personal and/or social immunity is determined by the nature, frequency and importance of social interactions and the social structures in which they evolve. These social interactions and structures can differ markedly between eusocial and non-eusocial groups (Cotter and Kilner 2010; Meunier 2015; Van Meyel et al. 2018; Cremer 2019). Whether the evolutionary drivers of social immunity are common to all forms of group living is, thus, still uncertain.

The growing awareness of our limitations on the general understanding of the early evolutionary transition has recently stimulated the need to study the sociality of insect taxa whose non-eusocial life has long been overlooked or neglected. Among these non-eusocial insects (e.g. beetles, caterpillars, aphids), earwigs are excellent candidates. Earwigs are insects of the order Dermaptera, which includes about 1900 species worldwide (Hopkins et al. 2022). Earwigs are easily identified by the presence of a hardened forceps-like appendage at the end of the adult abdomen, a unique feature among insects (Albouy 2020). While no earwig species is currently known to display the three main characteristics of eusocial systems (division of labor, overlapping generations, cooperative brood care), many earwigs do have a social life (Meunier 2024). The most common form of earwig social life takes place within (nuclear) family units. These family units typically include a mother and her dozen or so newly hatched juveniles and may persist for several weeks. The other form of earwig social life takes place in large aggregations. These aggregations contain up to several hundred nymphs and/or adults and can last for several months. However, the temporal stability and genetic composition of these

aggregations remain largely unknown. While forms of cooperative behaviour can be found in both types of groups (Vancassel 1984; Matzke and Lass 2005; Costa 2006b; Meunier 2024), group living remains facultative in all the studied earwig species. In particular, young to old earwigs can switch between solitary and group living at any time in their life cycle. This facultative social life is rare in contemporary insect species, but it is likely to have been dominant at the start of the evolution of social life (Meunier 2024).

Among dermapterans, the European earwig *Forficula auricularia* Linnaeus, 1758 (also called the common earwig) is by far the species whose biology and social life have been studied the most (Figure 1). It began most notably with the seminal work of Lamb (1976a, b) on maternal care and has since been extended to many aspects directly or indirectly related to their sociality. These aspects include, for instance, the expression and determinants of conflict and cooperation in these groups, the impact of pathogens on the maintenance of group living, the genetic and hormonal basis of social life, the chemical communication that governs these social interactions, and the role of anthropogenic factors such as climate change and chemical pollution on the expression of their sociability. We believe that the accumulation of knowledge on this earwig's social life has reached a point where *F. auricularia* has been clearly established as a valuable, timely and promising biological model for studying multiple aspects of sociality (or sociability) and for improving our general understanding of insect social life beyond the textbook examples found in Hymenoptera and Blattodea.

**Figure 1 – Adults of the European earwig *Forficula auricularia*.** Females (left) and males (right) have straight or curved forceps-like cerci at the end of their abdomen, respectively. Photo: J. Meunier.

The two main aims of this study are (1) to provide an up-to-date review of our knowledge of the social life of the European earwig and (2) to show how the study of this species can improve our general understanding of the evolutionary transitions to, between or from non-eusocial forms of sociality. To this end, we first describe the life cycle of this species and highlight the different forms of group living that earwigs may experience during their life. We then explain how recent data pave the way for major advances in our current understanding of four research axes in social evolution, namely (i) the interplay between social conflict and cooperation in maintaining facultative social life, (ii) the role of pathogens and symbionts in the transition between solitary and social life, (iii) the impact of anthropogenic change on social evolution, and (iv) the chemical, hormonal and genetic regulation of facultative social behaviour. Overall, this review lays the foundations for developing future work using the European earwig as a biological model to study the emergence, maintenance or breakdown of social life in insects.

## 2. The multiple aspects of social life of the European earwig

The European earwig encounters multiple forms of social life during its 18-month life cycle, from the egg stage to the death of the new adults (Figure 2). New *F. auricularia* adults emerge in early summer (season given with reference to the northern hemisphere; otherwise, see Orpet et al. 2019) and live in mixed-sex groups composed of up to several hundred individuals (Moerkens et al. 2009). This gregarious life lasts several months, during which females mate with numerous males (Sandrin et al. 2015) and both sexes display competitive and cooperative behaviours (Weiß et al. 2014). In late autumn, the females isolate themselves in a burrow usually dug in the ground and lay an average of 40 to 50 eggs (Meunier et al. 2012; Ratz et al. 2016; Dib et al. 2017). These eggs are guarded by the female for about 40 to 50 days throughout the winter (Figure 3; Lamb 1976b; Ratz et al. 2016). Males are actively kept away from the clutches by mothers (Lamb and Wellington 1974), as males would otherwise attempt to cannibalise the eggs (Meunier 2024). Maternal egg care is obligatory in this species (Boos et al. 2014; Koch and Meunier 2014), and females typically provide multiple forms of care such as aggressive protection against predators and egg cleaning to both remove fungal spores from eggshells and prevent eggs from desiccating (Lamb 1976b; Boos et al. 2014; Diehl and Meunier

2018; Van Meyel et al. 2019). Mothers do not discriminate between their own and foreign eggs (Meunier and Kölliker 2012a; Thesing et al. 2015; Van Meyel et al. 2019).

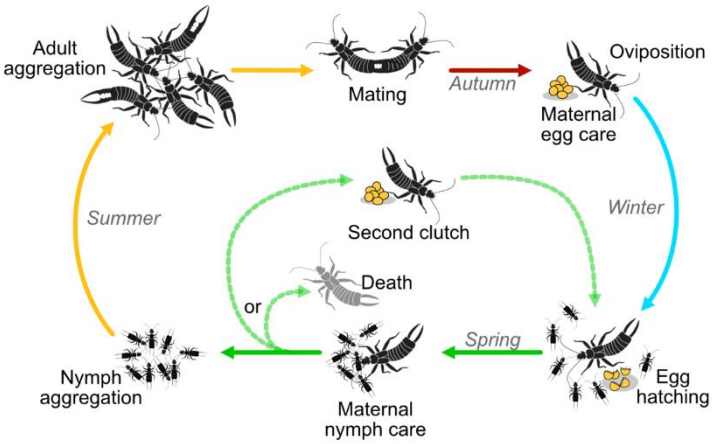


**Figure 2 – Life cycle of the European earwig.** Seasons are given with reference to the northern hemisphere. Reference to the southern hemisphere can be found in Orpet et al. (2019). Figure adapted from Meunier (2024).

**Figure 3 – A female of the European earwig providing care to her clutch of eggs.** Females stay with their eggs throughout the winter, providing multiple forms of care while suspending their foraging activity from oviposition until the eggs hatch. Photo: Marshal Hedin.

In early spring, the eggs hatch into juveniles, which are also called nymphs. Mothers stay with the nymphs for a few weeks (Figure 4), protecting them from predators, grooming and moving them around, and feeding them by regurgitation or by bringing them pieces of food (Lamb 1976b; Vancassel 1984; Staerkle and Kölliker 2008; Meunier et al. 2012). Unlike egg care, nymph care is not required for the development and survival of the nymphs – at least under laboratory conditions (Lamb 1976b; Kölliker 2007; Meunier and Kölliker 2012a, b). Although post-hatching family life appears to be facultative (nymphs can be reared without mother and siblings), mothers remain with their nymphs for two to three weeks, until they reach the second or third instar. During this time, mothers may adopt foreign nymphs, which sometimes seek adoption under natural conditions (Kölliker and Vancassel 2007).

**Figure 4 – A female of the European earwig providing care to her clutch of nymphs.** This family life lasts about two weeks, during which time the mother provides multiple forms of care to the nymphs. Mothers may display competitive behaviour towards the nymphs. The nymphs show cooperative behaviour towards both their siblings and mother, but may display competitive behaviours towards their siblings, which can lead to siblicide. Photo: J. Meunier.

The family then splits naturally, with the nymphs dispersing, forming new groups, and molting two more times before reaching adulthood (Figure 5; Dib et al. 2017; Tourneur et al. 2020). It remains unclear whether family splitting is driven by the mother, the nymphs, or both (Wong and Kölliker 2012), and we still don't know what the rules and dynamics of group formation by nymphs are. After splitting, some mothers may produce a second brood without re-mating (on very rare occasions, some will even produce a third or fourth clutch). The likelihood of producing multiple clutches depends on the population, and the physiological state and genetic background of the female (Lamb 1976a; Meunier et al. 2012; Wong and Kölliker 2014; Dib et al. 2017). The development of the second clutch follows the same steps as the first, and the nymphs become adults before the summer of the same year (Ratz et al. 2016; Dib et al. 2017). Regardless of whether she has produced one or two clutches of eggs, the mother eventually dies during summer. Males are generally thought to die earlier in the winter, although they can live as long as females under laboratory conditions (Tourneur and Meunier 2020).

**Figure 5 – A group of adults of the European earwig.** Adults form mixed-sex groups of up to several hundred individuals. The genetic composition, the temporal stability, and the nature of the social interactions within these groups remain poorly understood. Photo: J. Meunier.

It should be noted that *F. auricularia* is a complex of species that can live in sympatry and are (currently thought to be) morphologically indistinguishable (Wirth et al. 1998; González-Miguéns et al. 2020). The need to use genetic approaches to identify the different species, together with the limited use of these approaches in most laboratories studying the European earwig until the late 2010s, has led to some confusion in the literature where the name *F. auricularia* has been used generically without reference to the exact species in question. As a result, it is currently difficult to determine whether the variation observed between studies for the various traits mentioned above is due to the use of different species in each study or to idiosyncratic differences between populations of the same species (Lamb and Wellington 1975; Ratz et al. 2016; Dib et al. 2017). To date, only a few studies have investigated potential differences in life history traits between two species of this complex, namely *Forficula auricularia* clade A and *Forficula auricularia* clade B (Wirth et al. 1998; González-Miguéns et al. 2020). Compared to clade B, individuals of clade A are more likely to be found at colder temperatures and higher altitudes. Furthermore, females of clade A choose to lay their eggs at colder temperatures, are more likely to produce one (rather than two) clutches, stay with their clutch longer and finally, have nymphs that disperse later (Vancassel 1984; Wirth et al. 1998; Guillet et al. 2000; Quarrell et al. 2018; Tourneur et al. 2022). Apart from these studies, no further information is available on species-specific differences in the behaviour and social behaviour within the European earwig complex. It is, therefore, still unclear whether all members of this complex of species have a similar social life throughout their life cycle. In the rest of the review, we will assume that this is the case or that the putative difference is only marginal. Nevertheless, we urge future studies on the European earwig to identify and clearly state which species they are working on. This could be achieved by sequencing the barcode genes of their specimens or by identifying new taxonomic criteria that allow for clear distinctions.

## 3. Cooperation and social conflicts

Social interactions typical of the European earwig can involve individuals of different ages, sexes and levels of genetic relatedness, occur at different stages of the life cycle, and yet are almost always facultative. Understanding why sociality is maintained while remaining optional in this species has raised fundamental questions about the costs and benefits of these social

interactions. In the following section, we review our current understanding of these costs and benefits in the European earwig and, more generally, how these data have recently led us to reconsider the central role of access to maternal care in the emergence and maintenance of family life in animals (Kramer and Meunier 2019).

### 3.1. The limits of maternal care during family life

A key form of cooperative behaviour in family life is parental care (Meunier et al. 2022), which is defined as 'any parental trait that enhances the fitness of a parent's offspring, and that is likely to have originated and/or is currently maintained for this function' (Smiseth et al. 2012). European earwig mothers caring for their nymphs have been documented for over 250 years (Geer 1778). However, the nature and benefits of this care have only been studied in detail since the late 1970s (Lamb 1976b; Vancassel and Foraste 1980). Some of these studies have focused on mothers and have shown that the level of maternal investment in care is often determined by environmental factors, female condition and her genetic background (Lamb 1976b; Mas and Kölliker 2011a; Gómez and Kölliker 2013; Kölliker et al. 2015; Wu et al. 2020; Merleau et al. 2022). Other studies have focused on nymphs, mostly examining the nature, type and strength of the benefits they receive from maternal presence. Somewhat surprisingly, these studies show that maternal presence leads to very little (if any) improvement in fitness-related traits of nymphs, at least under standard laboratory conditions. This lack of improvement in nymph traits applies to survival, behaviour, and immunity, as well as developmental rate and success (Lamb 1976b; Kölliker 2007; Meunier and Kölliker 2012a, b; Raveh et al. 2016; Vogelweith et al. 2017b).

The intriguing accumulation of data reporting a lack of direct benefits from maternal care raises the question of why nymphs remain with their mothers. One possible answer is that nymphs do not gain direct benefits from maternal presence, but rather incur long-term costs from maternal deprivation. Thesing et al. (2015) explored this possibility by testing the transgenerational effects of maternal deprivation in offspring. The authors set up experimental families in which (1) juveniles were initially reared with or without mothers, (2) the resulting adults were cross-mated according to maternal presence or absence, (3) their subsequent eggs were cross-fostered between mothers, and finally (4) the foster families were maintained under standard laboratory conditions until the new juveniles reached adulthood. The results showed that the absence of a mother during nymphal development reduced the level of care

expressed by the nymphs once they became adults. This transgenerational effect was determined not only by the background of the foster mothers (i.e. whether or not the caregiving mother was an orphan when she was a nymph), but also by the background of the biological parents of the foster nymphs (i.e. whether or not the biological mother or father who produced and fertilised the eggs were orphans when they were nymphs). Whether this reduced care is maintained across generations is unknown, as is its potential cost to offspring. However, the same study shows that maternal deprivation during nymph development entailed short-term benefits (not costs!) for offspring, as it leads to the production of larger adults with longer forceps – two proxies of earwig fitness (Tomkins and Simmons 1998; Rantala et al. 2007). These findings thus suggest that remaining in a family group could be a good strategy for nymphs as it would lead them to provide more care for their own offspring later on, but also a bad strategy as they would become small adults with reduced fitness (see also Kölliker 2007).

Another hypothesis to explain why nymphs stay with their mothers despite the apparent lack of benefits would be that these benefits only occur under stressful conditions (Wilson 1975). However, the studies investigating this hypothesis do not support that mothers provide benefits under stressful conditions. When *F. auricularia* families are maintained under restricted food availability, the presence of mothers reduces – rather than increases - nymph survival rate until adulthood (Meunier and Kölliker 2012b). This is due to the emergence of an (often neglected) conflict between mother and offspring over food access, with mothers monopolising resources to the detriment of their nymphs in order to improve their own investment in the production of a second clutch (Kramer et al. 2017). Other studies also show that when the quality of nymphs is experimentally reduced, thereby increasing nymphs' nutritional needs, mothers again respond by reducing (rather than increasing) their investment in care (Mas et al. 2009; Mas and Kölliker 2011a), and that nymphs demand more care when mothers do not provide enough of it (Kramer and Meunier 2016). Taken together, these data emphasise that nymphs do not necessarily receive care or nutritional benefits from staying with a mother, even though mothers may have higher foraging efficiency than nymphs. All else being equal, this suggests that securing contact with mothers may not be the sole evolutionary driver explaining why earwig nymphs form a family group. However, it is important to note that most studies on *F. auricularia* have been carried out under standard laboratory conditions. This leaves open questions about the impact of other natural risks on the benefits of maternal

presence for earwig nymphs, among which a promising candidate is predation (Trumbo 2012). Future studies are required to test these potential benefits, even though the season during which family life typically occurs in this species (winter and early spring) may limit the number of predators who have access to the earwig nymphs.

### 3.2. Sibling rivalry and sibling cooperation during family life

While the nymphs do not necessarily receive care or nutritional benefits from staying with the mother, they may benefit from other types of social interactions provided by the family members (Kramer and Meunier 2019). One of these is sibling interactions. In animals, sibling interactions are generally considered competitive, with effects on the young ranging from none to lethal (Mock and Parker 1997). However, a growing body of research shows that forms of sibling cooperation are more common in nature than previously thought (Roulin and Dreiss 2012; Kramer and Meunier 2019).

In the European earwig, sibling competition (also known as sibling rivalry) often leads to siblicide and cannibalism. These two behaviours are promoted by weight asymmetry between siblings (Dobler and Kölliker 2011), more frequent towards foreign nymphs than nestmates (Dobler and Kölliker 2010), but are independent of the number of patrilines within the clutch (Meunier and Kölliker 2012b; Wong et al. 2014b). Living with siblings can therefore be seen as a risk of family life for the nymphs. However, recent studies have shown that sibling cooperation also occurs in this species, at least in the form of sibling food transfer. Nymphs can share food both in the presence and absence of the mother, although direct contact with the mother limits the frequency of these exchanges (Falk et al. 2014). Food is exchanged by proctodeal trophallaxis (mouth-to-anus contact) and allo-coprophagy (Falk et al. 2014), but not by stomodeal trophallaxis (mouth-to-mouth contact). The use of each of these routes depends on the genetic relatedness between the juveniles. Food transfer occurs by allo-coprophagy (recipients consume more donor feces) between members of the same family, whereas it occurs by proctodeal trophallaxis (recipients express more mouth-to-anus contacts) when individuals are from different families (Falk et al. 2014).

Sibling food sharing may benefit earwig nymphs in two ways. First, the consumption of sibling feces improves nymph survival in the absence of other food sources (Körner et al. 2016), even if the nutritional needs of a nymph do not influence the level of sibling food transfer (Falk et al. 2014). Second, nymphs cared for by mothers who are unable to provide sufficient food

(e.g., because they are in poor condition) may compensate by increasing their expression of sibling food sharing (Kramer et al. 2015; Kramer and Meunier 2016). Given that *F. auricularia* nymphs are mobile and able to forage only a few days after hatching, this suggests that they may increase foraging in response to having poor quality mothers (Wong et al. 2014a).

The benefits of sibling food sharing might, therefore, be one of the evolutionary drivers for maintaining juveniles in family groups, especially when mothers are not providing sufficient care. However, the importance of sibling food sharing is less clear when food is available *ad libitum*. Under this condition, depriving nymphs of sibling interactions (and thus sibling food sharing) is beneficial, with isolated juveniles developing faster and becoming larger adults than juveniles reared with siblings or with siblings and a mother (Van Meyel and Meunier 2022). These isolated juveniles nevertheless produce adults with deficient gregarious behaviour, suggesting that the presence of siblings during development may have long-term benefits for adult social life (Van Meyel and Meunier 2022).

### 3.3 The signs of offspring assistance during family life

The evolution of family life depends not only on the nymphs' decision to stay with the mother but also on the mother's decision to stay with the nymphs. It is, therefore, legitimate to ask whether *F. auricularia* mothers may also derive direct benefits from living with their nymphs, and whether these benefits might explain (at least in part) the maintenance of family life in this species.

One likely source of benefits from family interaction for mothers is offspring assistance. This phenomenon, also called ‘reverse parental care’ (Nalepa 2016), is defined as ‘cooperative acts of offspring to the benefit of their parents’ (Kramer and Meunier 2019). Two studies present data suggesting that offspring assistance may occur in the European earwig and call for further studies to determine whether this is simply a beneficial by-product of remaining in the offspring group or a form of active cooperation (for the definition of cooperation, see West and Griffin 2024). In the first study, Diehl et al. (2015) show that nymphs sanitise the nest by lining its surface with (their own) feces, which have antimicrobial properties. Remaining in the nest may therefore provide mothers with an external, efficient and costless protection against pathogens provided by their juveniles (more details in part 4). The second study recently revealed that mothers consume the feces of their juveniles during family life (Van Meyel et al. 2022). This suggests that, in addition to consuming antimicrobial compounds provided by their

nymphs, mothers may also have access to a significant amount of food brought back to the nest by their numerous foraging nymphs. If these are confirmed examples of offspring assistance, we cannot rule out the possibility that access to the associated benefits may have encouraged earwig mothers to remain with nymphs. From a broader perspective, the question arises: did the advantages of offspring assistance encourage mothers to return to the nest or to stay longer in the nest, thereby contributing to the development of family life? Disentangling these scenarios is particularly important for our general understanding of the early evolutionary transition from solitary to group living through family life, when young offspring may not have needed their mothers for development and survival (Wong et al. 2013; Falk et al. 2014).

### 3.4. Cooperation and conflict beyond family life

The social life of the European earwig is not restricted to family groups. Before and after family life, the life cycle consists of successive groups: first, young nymphs without mothers; then old nymphs and newly produced adults; and finally adults of both sexes (Albouy and Caussanel 1990; Lordan et al. 2014). Surprisingly little is known about these phases of sociality. For instance, it is still unknown whether these groups include genetically related individuals, whether their composition is stable over time, and whether individuals show high nest fidelity. The recent development of genetic tools such as microsatellites (Sandrin et al. 2015) should allow these questions to be answered shortly. Other questions about these phases of sociality concern the nature of the behavioural interactions that take place in these groups and the costs and benefits they provide to group members. Laboratory experiments between two adults suggest that these interactions involve a combination of cooperative behaviours such as allogrooming, aggressive behaviours (mostly between males) and mating courtships (Walker and Fell 2001; Brown 2006; Weiß et al. 2014). Our (limited) knowledge of the costs and benefits of group living for adults comes from studies that isolate individuals or manipulate group composition. First, studies showed that the sudden isolation of adult females causes transient stress that reduces their resistance to infection by an entomopathogenic fungus (Kohlmeier et al. 2016; Vogelweith et al. 2017a). Second, they also demonstrated that preventing males from interacting with other males improves their resistance to fungal infection, probably by avoiding the costs of male-male competition for females (Kohlmeier et al. 2016). Finally, another study showed that replacing group members by unknown conspecifics increases the level of investment of each adult in its basal immunity, probably as a density-dependent prophylaxis

(Körner et al. 2018). Whereas *F. auricularia* adults can live alone, all these findings show that having a social environment can determine their investment in immunity. However, this is the only piece of information available to suggest that these groups are more than just a collection of individuals. There is, therefore, substantial scope for development of our understanding of the characteristics of these social groups.

## 4. Parasites, pathogens, and symbionts

The evolution of group living requires not only resolving potential conflicts and promoting cooperation between group members, but also overcoming the risk of frequent and close contact with pathogens and parasites (Meunier 2015; Biedermann and Rohlfs 2017). This risk is particularly important in group-living species because social contacts typically facilitate the transmission of pathogens/parasites, group members often share close genetic relatedness that makes them susceptible to the same pathogens/parasites, and groups often live in nests that provide excellent environmental conditions for microbial growth (Cotter and Kilner 2010; Biedermann and Rohlfs 2017). All of these factors are inherent to the biology of the European earwig. Moreover, this species spends a large part of its life cycle in the soil and has a relatively long lifespan (for insects) that includes all seasons and environmental conditions. This brings it into contact with a wide array of pathogens and parasites, ranging from nematodes (Hodson et al. 2011) to gregarines (Ball et al. 1986), pathogenic fungi (Toledo et al. 2008; Orpet et al. 2019) and parasitoid flies (Kuhlmann 1994; Barthell and Stone 1995). The resistance to pathogens and parasites is thus particularly important in the European earwig.

### 4.1 Social immunity

Whilst pathogens have long been thought to be a barrier to the emergence and maintenance of social life (Schmid-Hempel 1998), a recent hypothesis suggests the opposite. In particular, pathogens and parasites could promote the evolution of group living by promoting additional immune protection to each group member in the form of social immunity (Meunier 2015). Social immunity was first conceptualised in eusocial insects, where it has been shown to take multiple forms such as allo-grooming, nest sanitation and adjustment of social networks to pathogen pressure, and to confer crucial advantages over pathogens (Schmid-Hempel 1998; Cremer et al. 2007; Stroeymeyt et al. 2018). It is now accepted as a general mechanism that

can be found in all forms of group living (Cotter and Kilner 2010; Meunier 2015; Van Meyel et al. 2018; Cremer 2019), where it is defined as 'any collective or personal mechanism that has emerged and/or is maintained at least partly due to the anti-pathogen defence it provides to other homospecific group members' (Van Meyel et al. 2018).

The European earwig is a promising model to test whether access to social immunity could promote the evolution of social life, as this species offers the possibility to manipulate pathogen pressure and test whether pathogens affect the likelihood that a nymph or an adult will join or leave a group. However, research on this question is still in its infancy and is currently focused on identifying the immune benefits that might be gained from group living. Most of the available data concerns egg care. *F. auricularia* mothers protect their eggs against pathogens either curatively, by expressing grooming behaviour to remove fungal spores present on the eggshell (Boos et al. 2014), or prophylactically, by expanding nest construction in the presence of live pathogens in the environment (Diehl and Meunier 2018). However, mothers do not avoid nest sites contaminated with live pathogens, nor do they adjust egg production to the risk of pathogen encounters (Diehl and Meunier 2018). Maternal egg grooming also mediates the transfer of cuticular hydrocarbons onto the eggs, which could help to limit pathogen infection (Boos et al. 2014), and may mediate the transfer of bacteria with antifungal properties to the eggshell, as reported in the earwig species *Euborellia maritima* (Greer et al. 2020).

However, it remains unclear whether the benefits of maternal egg care against pathogens extend to the resulting nymphs - and thus whether access to this social immunity could promote the maintenance of family life in this species. For example, mothers are known to groom their nymphs regularly during family life (Mas and Kölliker 2011a), but the function of this behaviour against pathogens remains untested. Some data nevertheless suggest that nymphs may gain direct immune benefits from remaining in the family group. For example, mothers line the nest surface with fecal pellets, which have antimicrobial properties against bacteria and fungi (Diehl et al. 2015). Nymphs could thus benefit from maternal nest sanitation, even if both mothers and nymphs contribute to this possible form of social immunity (see above; Diehl et al. 2015). Interestingly, the level of antimicrobial properties in fecal pellets does not change in the presence or absence of family members (Diehl et al. 2015), indicating that this investment in social immunity is constitutive in *F. auricularia*. Another study suggests that nymphs can gain long-term immune benefits by remaining with their mother during

development. Earwig mothers transfer their immunological experience to their nymphs during the period of post-oviposition maternal care, thereby improving the survival of their resulting adult offspring after infection with a bacterial pathogen (Boucicot, Cheutin, Laverré, Bracquart-Varnier, Verdon, Meunier, *unpub. data*). Interestingly, this transfer only occurs in immune-challenged mothers, as the presence or absence of a non-immune-challenged mother during development does not change the basal immunity of the resulting adult offspring (Vogelweith et al. 2017b). A last study shows that nymph gene expression depends on a complex interaction between pathogens and maternal presence during the period of family life. Using a transcriptomic approach, Körner et al. (2020) showed that the effect of maternal presence or absence on gene expression in the fat body of nymphs (the central site of immunity in insects) is reversed depending on the presence or absence of an entomopathogenic fungus in the nest. This suggests that the immune response is dependent on maternal presence in nymphs, and may be one of the selective pressures acting on the evolution of family life in this species.

### 4.2 Symbionts and gut microbiota

In many animal species, parental care typically enables the vertical transmission of beneficial symbionts and communities of symbionts (e.g., the gut microbiota) from parents to offspring (Onchuru et al. 2018). These symbionts and gut microbiota often play a key role in the biology of offspring by influencing their ability to digest specific food sources, complete their development and fight against pathogens (Douglas 2015). It is not yet known whether the European earwig contains symbionts that are essential for its biology and whether the (gut) microbiota of the parents must be transferred to the nymphs. One study suggests that the gregarine *Gregarina ovata,* a parasite frequently found in the gut of invertebrates, may play an important and beneficial role in this species, as its presence in adults is associated with better resistance to starvation (Arcila and Meunier 2020). However, further studies are needed to show the causality of this association. The bacterial gut microbiota of adult *F. auricularia* females has recently been described and includes the four classical bacterial phyla reported in many insects, namely Proteobacteria, Firmicutes, Bacteroidota and Actinobacteriota (Van Meyel et al. 2021). However, the relationship of the gut microbiota with social behaviours and group living is unclear. First, experimental alteration of the maternal gut microbiota by ingestion of the antibiotic rifampicin does not alter the expression of pre- and post-hatch care behaviours (Van Meyel et al. 2021). This suggests that the bacteria directly or indirectly affected by

rifampicin play a limited role in maternal care. Second, there is no difference in the gut microbiota composition between females with naturally high or low levels of aggregation prior to egg production (Cheutin, Boucicot, Meunier, 2024). This indicates that female aggregation is not due to potential behavioural manipulation by their gut microbiota as a strategy for the microbiota to reach a new host (Stilling et al. 2014; Lewin-Epstein et al. 2017; Biedermann and Rohlfs 2017; Münger et al. 2018; Johnson and Foster 2018; Nalepa 2020). Finally, the gut microbiota of mothers naturally changes between oviposition and egg hatching, with a general increase in Actinobacteriota (Van Meyel et al. 2021). As this phylum is often associated with antimicrobial and antifungal properties in insects (Mattoso et al. 2012; Salem et al. 2013; Greer et al. 2020), this change may suggest that the gut microbiota is responding to the expression of social behaviours, such as egg care, in the context of social immunity. Again, more research is needed to establish the causality of this association between social behaviours and gut microbiota composition.

## 5. Social responses to anthropogenic modifications of the environment

Another long-standing question in social evolution is to understand which environmental constraints can promote the emergence, maintenance or disappearance of social life. Over the last few centuries, human industrialisation has led to rapid, profound and often irreversible changes in the environment for all living organisms, whether through increased urbanisation, climate change or pollution (Johnson and Munshi-South 2017). While eusocial species may be particularly resilient to such environmental stressors because they can tolerate the loss of many individuals (workers) as long as reproductive individuals are maintained (Straub et al. 2015), these stressors often alter the expression of important individual and collective behaviours (Crall et al. 2018), which can dramatically alter colony fitness and ultimately the survival of reproductive individuals.

Studying the effects of anthropogenic stressors in facultatively social species such as the European earwig, can provide important, novel insights into our understanding of the early steps of social evolution. This is because individuals of these species have the flexibility to rapidly evolve towards stable solitary lifestyles or instead maintain (or even strengthen) their social life. This may thus reveal whether social life can be a solution or a cul-de-sac in a world

characterised by rapid environmental changes such as increased chemical pollution and global warming.

### 5.1 Chemical pollution

Recent studies on the European earwig provide promising data regarding how facultative social life can evolve under the effect of anthropogenic stresses such as chemical pollution. This species is common in many crop systems worldwide (where the nature of the crop makes it either a pest control or a pest itself; Orpet et al. 2019), and therefore, often evolves in environments that are regularly exposed to a large diversity of pesticides. Most of these studies have shown that these exposures can be lethal to the European earwig (Ffrench-Constant and Vickerman 1985; Shaw and Wallis 2010; Fountain and Harris 2015) or cause sublethal effects such as morphological abnormalities, reduced weight, and inhibited enzymatic activities (Sauphanor et al. 1993; Malagnoux et al. 2015; Le Navenant et al. 2021). Nevertheless, some recent studies show that the European earwig can develop tolerance or resistance to pesticide exposures (Le Navenant et al. 2019, 2021; Jana et al. 2021). One explanation is that frequent exposure to pesticides ultimately improves detoxification mechanisms such as those involving glutathione-S-transferases, carboxylesterases and acetylcholinesterase (Malagnoux et al. 2014; Le Navenant et al. 2019). Another non-mutually exclusive hypothesis is that pesticide resistance is due to changes in either their expression of social behaviours or in their resilience to changes in the expression of social behaviours. To date, no study has directly investigated this hypothesis. However, data show that direct exposure to low doses of pesticides (deltamethrin, pyriproxyfen) or high concentrations of heavy metals (cadmium) causes almost no change in the expression of post-hatching care by earwig mothers (Meunier et al. 2020; Mauduit et al. 2021; Merleau et al. 2022; Honorio et al. 2023a, b), although it alters non-social behaviours such as prey consumption and mobility (Sauphanor et al. 1993; Malagnoux et al. 2015). These few papers pave the way for future studies to determine whether other social behaviours are also unaffected by chemical pollution, and the implications of social life on the adaptation of individuals to polluted areas.

### 5.2 Global warming

The European earwig has shown a remarkable ability to colonise habitats with contrasting climates around the world, and so is a promising biological model for studying the implications of global warming on the continued evolution of facultative social life. Within a few centuries,

the European earwig has spread from its native range in Europe to almost every continent and many islands (Quarrell et al. 2018b; Tourneur and Meunier 2020), including remote locations such as the Falkland Islands (Maczey et al. 2019). This species is therefore able to colonise areas of extreme heat, as in North Africa, as well as areas of extreme cold such as those found in Canada (Wirth et al. 1998). This successful spread has been linked to several physiological adaptations affecting oviposition date, egg development time, clutch size and number of clutches produced (Ratz et al. 2016; Quarrell et al. 2018; Tourneur and Meunier 2020). However, how this might be linked to behavioural and, in particular, social adaptations has been poorly investigated. Some forms of maternal care appear to vary between populations. This is the case of egg relocation after exposure to extreme cold, which occurs much earlier after egg exposure in St Johns compared to Harvey Station, two sites in eastern Canada (Tourneur et al. 2022). As these two populations belong to different species of the European earwig complex, this behavioural difference may be due to species specificity rather than adaptation to local conditions (Tourneur et al. 2022). This interpretation would be consistent with another study showing that the expression of nymph care is comparable among three European populations (one in France and two in Spain) of *F. auricularia* sp. B, although these populations have contrasting climatic conditions (Ratz et al. 2016). Future work using the large geographic scale approach developed by Tourneur and Meunier (2020) and linking the expression of maternal care to local environmental conditions, should be the next step in further exploring the link between climate change and social evolution in the European earwig.

## 6. Chemical, hormonal and genetic regulation of social behaviours

A further opportunity to improve our current understanding of the first evolutionary steps of social evolution is to elucidate the chemical, physiological and genetic regulatory mechanisms of social interactions that are still facultative, as in the European earwig (Kronauer and Libbrecht 2018). In the following section, we first review our current knowledge of chemical signals, an essential part of insect communication (Blomquist and Bagnères 2010; Steiger and Stökl 2017), in the European earwig. We then detail the very limited, but growing, data available on the hormonal and genetic regulation of social behaviour in this insect, and discuss the new avenues of research that this have and will open up.

### 6.1 Chemical communication

The chemical communication of the European earwig has been investigated since the 1990s mainly through studies of its cuticular hydrocarbons (CHCs). The CHC profile of *F. auricularia* contains about 51 branched and unbranched alkanes, alkenes and alkadienes, ranging from nC21 to nC31 (Quarrell et al. 2016). Surprisingly, we do not yet know whether the different species of the European earwig complex have specific chemical signatures.

As in other social insects, CHCs have a major influence on several forms of social behaviour in *F. auricularia*. First, the chemical signature of nymphs determines the level of care they receive from their mothers. Exposure of mothers to CHCs from well-fed (or poorly-fed) nymphs increases (or decreases) their subsequent expression of care for their own nymphs (Mas et al. 2009; Mas and Kölliker 2011a). This effect translates into the future reproduction of mothers, as exposing mothers to CHCs of well-fed nymphs also induced predictable timing of the second relative to the first clutch (Mas and Kölliker 2011b). Second, the chemical signature of nymphs determines the nature of their social interactions during family life. This was inferred from the fact that the chemical signature of the offspring allowed them to recognise their biological father when the offspring were adults rather than juveniles (Wong et al. 2014b). Since such a paternal signature may promote nepotism and siblicide during family life, it suggested that mothers homogenise CHCs during this period by allogrooming to mask the scent of different patrilines. This may explain why siblicide during family life is no more important in clutches sired by multiple males than in those sired by a single male (Meunier and Kölliker 2012b). In contrast, paternal chemical signatures are essential for adults as they allow individuals to avoid siblicide and inbreeding depression (Meunier and Kölliker 2012b; Wong et al. 2014b). A third function of chemical communication in the European earwig is that maternal CHCs determine the social behaviour of nymphs, with different results depending on the age of the nymphs. Exposure to CHCs from well-fed mothers increases the number of nymphs still present in the nest arena in early broods (probably due to delayed dispersal of nymphs and/or lower rates of sibling cannibalism). In contrast, it reduces the number of nymphs still present in the nest arena in late broods - and vice versa for CHCs from poorly fed mothers (Wong et al. 2014a). All these results show that CHCs are at the core of most of the behaviours expressed in the facultative family life of the European earwig, just as they are in the non-flexible social systems found in eusocial species.

Chemical communication is also involved in the aggregation behaviour of nymphs and adults after the period of family life. The search for putative chemical signals mediating earwig aggregation has been driven since the 1990s by strong economic pressures to control populations of this species in peach and apricot orchards (Walker et al. 1993; Hehar et al. 2008; Quarrell et al. 2016, 2018). The first candidates were chemical cues emitted by the feces, as groups of adults are often surrounded by feces (Walker et al. 1993). However, the use of chemical extracts of fecal material did not induce aggregation under controlled conditions (Hehar et al. 2008). Clustering around feces may, therefore, reflect the simple attraction of earwigs to a valuable, non-specific food source (Körner et al. 2016; Van Meyel et al. 2022). The second candidates were the pungent, highly volatile compounds (mostly benzoquinone) emitted by earwigs, as these compounds were thought to act as alarm pheromones, which are often attractive to conspecifics in eusocial insects (Eisner 1960). However, thorough experimental approaches revealed that these compounds do not attract conspecifics and do not trigger aggregation in earwigs (Quarrell et al. 2016). The final candidates were the CHCs directly present on the cuticle of juveniles and adults, some of which are volatile and others of which are released on the habitat substrate by walking. Although several laboratory studies show that full CHC extracts induce aggregation (or repulsive behaviour), it remains difficult to identify which molecules are specifically involved in this phenomenon (Walker et al. 1993; Quarrell et al. 2016). Moreover, the effect of these extracts is weak in the field and highly variable throughout the insects' activity season (Quarrell et al. 2016). Further studies are thus needed to better understand which chemical signatures regulate group living in *F. auricularia* adults.

### 6.2 Hormonal and genetic regulation of social behaviours

Contrary to the chemical communication of the European earwig, our current knowledge of the physiological and genetic regulatory mechanisms of social behaviours is very limited in earwigs and other insects with a family life (Trumbo 2018, 2019; Cunningham 2020). Nevertheless, a growing body of data and methodological developments provide promising information, indicating that our knowledge could expand rapidly over the next decade.

In terms of hormonal regulation, for example, it has been suggested that juvenile hormone (JH) may determine the ability to express maternal care (Trumbo 2019). In two earwig species, *Labidura riparia* and *Euborellia annulipes*, the synthesis of JH is maximal during

vitellogenesis and falls during egg care, while JH supplementation prematurely terminates care (Vancassel et al. 1984; Rankin et al. 1995). Notably, these two earwig species have extremely short periods of maternal care (Meunier 2024). In *F. auricularia*, however, there is contrasting evidence as to whether JH plays a role in maternal care, and whether this role depends on the age of the recipients. First, genomic data show that *F. auricularia* mothers have higher expression of genes involved in JH production when they care for their eggs. However, this expression is down-regulated when mothers care for their nymphs (Wu et al. 2020). Second, exposure of *F. auricularia* mothers to a JH agonist (pyriproxyfen) during egg care and nymph care did not alter the expression of these maternal behaviours (Merleau et al. 2022). This raises the intriguing hypothesis that JH is already present at high levels during maternal care (in contrast to other earwig species), and that JH could therefore be required to express care in *F. auricularia*. Further studies in this species are thus needed to confirm this hypothesis and investigate its implications for other forms of social life in earwigs. These future studies should also investigate the role of other hormones commonly involved in the expression of behaviour in insects (e.g. ecdysteroids), and whether and how they might restrict (or allow) the possibility to switch between social and solitary life in both juveniles and adults in the European earwig.

As with hormonal regulation, only a few studies investigated the genomic basis of parental care in the European earwig. Yet, the recent availability of the *F. auricularia* genome (Bhattarai et al. 2022; Kobayashi et al. 2023) and transcriptome (Roulin et al. 2014; Körner et al. 2020; Wu et al. 2020), as well as the development of gene knockdown methods using RNAi (Wu et al. 2020), provide opportunities to further investigate the genetic basis of social behaviour and maternal care. For example, Wu et al. (2020) used transcriptomic approaches to compare gene expression between mothers who provided care and those who were prevented from providing care. They showed that nearly 1600 genes had different expression levels between the different types of mothers. While most of these have unknown functions, silencing the expression of *Th* (a gene encoding tyrosine hydroxylase, the rate-limiting enzyme in the dopamine synthesis pathway) in mothers reduced the level of maternal food supply to nymphs, while silencing it in nymphs affected the future reproduction of the tending mother. Thus, this gene appears to promote mutual aid between mother and offspring, highlighting the importance of parent-offspring genetic co-adaptation in the evolution of family life (Kölliker et al. 2015). In another study, Körner et al. (2020) investigated the transcriptomic effects of

maternal absence and presence in nymphs living in a nest with or without pathogens. They showed that the interaction between these two factors was responsible for changes in the expression of 154 genes in the fat body of the nymphs. This finding provides the first insights into how maternal care and pathogens interact to shape offspring gene expression in a species with facultative family life. More generally, it stresses how exploring genetic patterns can improve our general understanding of how environmental conditions, particularly pathogens, can drive the evolution of parental care. There is a need to continue and develop these approaches to investigate the diversity and function of these genes and to determine their role in the emergence, maintenance or disappearance of social life in insects.

## 7. Conclusion

Overall, this review provides an insight into the current state of our understanding of the social life of the European earwig. It demonstrates the diversity and complexity of social behaviours and group living that can be found in this social (but not eusocial) insect and highlights how its study opens up new avenues for advancing our understanding of some of the potential evolutionary pathways to sociality in insects. For example, discovering why and how juveniles and parents form family groups while still retaining the ancestral ability to live solitarily may shed light on the factors that may have favoured the emergence of group living from the solitary state, which is one of the major evolutionary transitions in life (Szathmáry and Maynard Smith 1995; Bourke 2011). Similarly, understanding the driving force behind group living in adults that are perfectly able to live in isolation can tell us something about the conditions that may have favoured the maintenance of group living once it had emerged but was still flexible. Overall, this review demonstrates that the European earwig provides an excellent opportunity to address all these major questions in evolutionary biology. We hope that the information provided here will encourage the development of future research using this species as a model to study the emergence, maintenance and disappearance of social life in insects.

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## Data availability

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