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COSTS AND BENEFITS OF ISOLATION FROM SIBLINGS DURING FAMILY LIFE IN ADULT EARWIGS

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SUMMARY

The benefits of parental care are often seen as a cornerstone of family life evolution. However, recent studies show that sibling interactions can also confer substantial benefits to juveniles. Here, we tested a new hypothesis suggesting that the need for juveniles to access sibling interactions may encourage juveniles to remain in a family group, thereby consolidating the early stages of family life evolution when parental care is facultative. We set up juveniles of the European earwig, *Forficula auricularia* (a family-living insect in which maternal care is facultative and juveniles can forage for themselves and cooperate with siblings) either alone, with siblings, or with siblings and their mother, and then quantified the effects on the development, morphology and four fitness-related behaviours of the resulting adults. We found that isolated juveniles reached adulthood more quickly and that these adults were overall larger but showed impaired aggregation behaviour when compared with juveniles raised together with siblings or with siblings and their mother. By contrast, sibling deprivation did not affect offspring survival, male forceps length (an ornament involved in reproductive success) and three other behaviours in adults (boldness, general activity and exploration). All these results were independent of adult sex, although females overall reached adulthood earlier and were larger than males. Altogether, our findings suggest that the potential benefits of sibling interactions measured in this study play a minor role in the maintenance of earwig family life. They also emphasize the need to study the evolutionary drivers of family life in species where all members can switch from family to solitary life, a scenario that probably prevailed in the early evolution of sociality.

INTRODUCTION

Family life is a common phenomenon in animals (Royle et al., 2012). It is taxonomically widespread and can take various forms, ranging from a few individuals to hundreds, lasting from a few hours to several years, and involving one or both parents. Over recent decades, the parents have often been considered to be essential components of family life, as mothers and/or fathers typically provide multiple forms of care to their juveniles during this period (Royle et al., 2012). For instance, parents can offer protection against (1) predator attacks, by hiding juveniles and/or keeping potential predators away from the nest, (2) pathogens, by transferring immune effectors to the juveniles and/or removing parasites from the nest and juveniles, and (3) starvation, by providing juveniles with the food they could not access otherwise (Klug & Bonsall, 2014; Meunier et al., 2022; Royle et al., 2012). Nevertheless, the diversity and magnitude of the benefits associated with parental care come with a substantial risk: when offspring are deprived of their parents, they may suffer from impaired development, physiology, behaviour, reproduction and survival (Balshine, 2012; Dettling et al., 2002; Foster et al., 2012). The strength of these negative effects has long fostered the idea that access to parents is one of the most important evolutionary parameters in the maintenance of family life (Kramer & Meunier, 2019; Royle et al., 2012).

However, the care of parents for their offspring is but one type of social interaction during family life and it has been suggested that other types of interactions, such as interactions among siblings, could also be of major importance in promoting this form of social life (Falk et al., 2014; Kramer & Meunier, 2019; Rebar et al., 2020). The nature of sibling interactions has traditionally been assumed to range from fierce competition for limited parental resources to simple mutual tolerance (Roulin & Dreiss, 2012), suggesting that the presence of siblings may only have a negative or no impact on the maintenance of family life. However, an increasing number of studies reveal that sibling interactions are not competitive by default and may include a great diversity of cooperative interactions providing direct and indirect (due to relatively high genetic relatedness) benefits to siblings (Kramer & Meunier, 2019; Roulin & Dreiss, 2012). For instance, offspring postpone fledging to the benefit of their younger siblings in the house wren, *Troglodytes aedon* (Bowers et al., 2013), form coalitions with litter mates against unrelated

juveniles in the spotted hyaena, *Crocuta crocuta* (Smale et al., 1995), express mutual cleaning in the ambrosia beetle *Xyleborinus saxesenii* (Biedermann & Taborsky, 2011), and may cooperate to improve foraging success in the absence of parents in the burying beetle *Nicrophorus vespilloides* (Prang et al., 2022; Rebar et al., 2020; but see Magneville et al., 2018). Having access to these benefits can have a profound impact on offspring fitness and may thus ultimately favour the maintenance of family life, particularly when parental care is facultative, a phenomenon that probably prevailed in the early evolution of family life (Falk et al., 2014) and (still) prevails in contemporary precocial species (e.g. Capodeanu-Nägler et al., 2016; Pittet et al., 2014; Thiel, 1998). Nevertheless, it is not known whether the deprivation of sibling interactions during the period of family life may have similar short- and long-term costs for precocial offspring to parental deprivation. On a more general level, it hence remains unclear whether the risks associated with sibling deprivation may ultimately encourage juveniles to remain in a family group even when parental care and family life are facultative.

In this study, we tested the new hypothesis that securing access to sibling interactions may ultimately encourage juveniles to remain in a family group in the European earwig, *Forficula auricularia*. In this precocial insect, mothers remain with their juveniles for several weeks after egg hatching, during which time they provide extensive care to the newly produced juveniles (called nymphs) in the form of fierce protection against predators, grooming behaviours and food provisioning (Lamb, 1976). Maternal care is, however, facultative in this species, as nymphs have early foraging capabilities that allow them to reach adulthood in the absence of a mother (Kölliker, 2007). Furthermore, maternal presence can be costly for earwig nymphs under harsh environmental conditions, as mothers then monopolize resources for themselves, leading to excess mortality of their offspring (Kramer et al., 2017; Meunier & Kölliker, 2012a). Nevertheless, the fitness of earwig juveniles depends not only on their interactions with their mother, but also on interactions with their siblings. While earwig siblings sometimes compete fiercely and even eat each other during family life (Dobler & Kölliker, 2011; Meunier & Kölliker, 2012a), they can also cooperate by sharing food (via mouth-to-mouth contacts and allocoprophagy; Falk et al. 2014). Importantly, the level of this form of sibling cooperation has been shown to depend on

the level of maternal care, as sibling cooperation typically increases to compensate for low levels of maternal care and/or low maternal quality (Kramer et al., 2015; Kramer & Meunier, 2016).

To investigate whether access to the potential benefits of sibling interactions can encourage juveniles to remain in a family group, we set up a total of 156 *F. auricularia* juveniles either alone, in a group of siblings or in a group of siblings with a mother, and then quantified effects on key fitness-related traits of the resulting adults in terms of development, survival, morphology and behaviour. In particular, we measured their developmental time and survival rate until adulthood, the minimum interocular distance (which typically reflects body size) and the fresh weight of adults at emergence (two proxies of adult quality; Koch & Meunier, 2014; Meunier et al., 2012), the forceps length of newly produced males (a sexual ornament involved in male reproductive success; reviewed in Kamimura, 2014), and four major behaviours in (social) arthropods: aggregation, boldness, general activity and exploration of a novel environment (Blight et al., 2016; Modlmeier et al., 2012; Rodrigues et al., 2016; Wright et al., 2019). Because numerous life history traits and behaviours are sex specific in the European earwig (Vogelweith et al., 2017; Weiß et al., 2014), we measured the effects of the social environment in both males and females (except for forceps length). If access to sibling interactions can encourage juveniles to remain in a family group, we predicted that the deprivation of sibling interactions during family life has short- and long-term costs for precocial offspring. Specifically, we predicted isolated nymphs would delay their development, survive less well and produce smaller adults with shorter ornaments. Moreover, we expected the resulting adults would exhibit at least some deficient behaviours, for instance in terms of aggregation, boldness, general activity or exploration. Because mothers can modulate the nature of sibling interactions during family life (Kramer et al., 2015; Kramer & Meunier, 2016), we also predicted that the effects of living with or without siblings on nymphs would depend on the presence of a mother.

MATERIAL AND METHODS

Insect Rearing and Experimental Design

We tested whether the presence or absence of siblings and mothers impacts the development, survival, morphometry and behaviour of 156 individuals originating from 26 families of *F. auricularia* (from clade B; González-Miguéns et al., 2020). These families were produced by 26 females field sampled in July 2019 in a pip fruit orchard at Pont-de-Ruan, France, and then maintained under standard laboratory conditions until oviposition and egg hatching (Meunier et al., 2012). One day after egg hatching, we randomly distributed the mother and the nymphs between three treatments: one group of 10 sibling nymphs with their mother (family group treatment), one group of 10 sibling nymphs without mother (sibling treatment) and 10 isolated nymphs (isolation treatment). We did not implement a fourth treatment consisting of a mother with a single nymph, because earwig mothers generally cease expressing maternal care when broods contain only one nymph (J. Meunier, personal observation). Of the 26 families used in this experiment, nine contained between 24 and 27 nymphs. For these nine families, we set up 10 nymphs in the family group treatment, 10 nymphs in the sibling treatment and the remaining four to seven nymphs in the isolation treatment. For the remaining 17 families initially containing more than 30 nymphs, all the supernumerary juveniles were excluded from the experiment. Twenty days later, we removed mothers from the family group treatment to mimic natural family dispersion (Meunier & Kölliker, 2012b), while maintaining all nymphs under standard laboratory conditions to follow their development until adulthood. On the day of adult emergence, each newly produced adult was kept separately from the rest of the group (where applicable) to subsequently conduct morphometric and behavioural measurements (see below).

During the experiment, we maintained each group of nymphs (from both the family group and sibling treatments) in 9 cm diameter petri dishes and each isolated nymph in a 3 cm diameter petri dish. Twenty days after the experiment was set up, we transferred each group of nymphs to a 14 cm diameter petri dish and each isolated nymph into a 9 cm diameter petri dish. We then maintained the newly produced adults in petri dishes of the same sizes until the end of the experiment (i.e. the presence or absence of siblings was maintained throughout the development of the nymphs to adulthood). All petri dishes were lined with moist sand, maintained under a

constant temperature of 20 °C and a 12:12 h light:dark cycle, and received an ad libitum amount of standard food (mostly comprising pollen, carrot and cat food; see details in Kramer et al., 2015) twice a week.

Survival, Development and Morphometry Measurements

We first tested the impact of the presence or absence of siblings and mothers on the survival of nymphs to adulthood, the duration of nymph development until adult emergence, and the size, fresh weight and (male) forceps length of the resulting adults. For the last four measurements, we focused on the first emerging adults per treatment, as the developmental and morphological traits of these adults generally reflect the traits of the entire clutch in this species (Gómez & Kölliker, 2013). We measured the survival rate of nymphs to adulthood by counting the nymphs that became adults out of the 10 (or fewer) nymphs initially set up (individually or in a group) in the different treatments. We measured the duration of development to adulthood by checking each petri dish every day, recording the dates at which we observed the first adult male and female of each treatment and then counting the days from egg hatching. We then measured the size and fresh weight of the first male and female of each treatment per family 1 day after emergence. We weighed each male and female to the nearest 0.01 mg using a microbalance (Discovery DV215CD, OHAUS) and measured their minimum interocular distance (a proxy of their overall size; Arcila & Meunier, 2020) to the nearest 0.001 mm using a camera coupled to a stereo microscope binocular (M80, Leica Microsystems, Wetzlar, Germany) and the Leica Application Suite software. Finally, we measured the forceps length as the mean of left and right outer forceps (Körner et al., 2017) of the first male per treatment (and per family) to the nearest 0.001 mm using the same camera as described above. Because the mean forceps length of *F. auricularia* males is positively correlated with their minimum interocular distance (Arcila & Meunier, 2020; Körner et al., 2017), we calculated a 'residual forceps length' reporting whether males had longer (or shorter) forceps than predicted by their head size. To obtain this residual forceps length, we used the residuals of a polynomial linear model in which we entered the mean forceps length as the response variable and the minimum interocular distance as the explanatory variable (Arcila & Meunier, 2020; Körner et al., 2017).

Behavioural Tests

We measured four behaviours in the first emerging male and the first emerging female of each treatment per family: boldness, general activity, aggregation and exploration of a novel environment. These four behaviours were chosen because they typically have an impact on the fitness of many (social) arthropods (Blight et al., 2016; Modlmeier et al., 2012; Rodrigues et al., 2016; Wright et al., 2019). We measured boldness on day 7 after adult emergence, as the reaction to a simulated predator attack (Mauduit et al., 2021). On that day, we carefully removed the lid from each petri dish, waited 5 min to ensure that the individual was immobile, poked each adult on the pronotum with a glass capillary in a standardized manner (1 poke/s), and then counted the pokes required until the individual moved more than one body length away from its initial position. In general, females that did not move away after a poke either slumped on their legs to secure their position or raised their forceps in a defensive posture. High values thus indicate high levels of boldness (Mauduit et al., 2021).

We measured the general activity of males and females 1 h after the boldness test (i.e. on day 7 after adult emergence). We gently transferred each individual to the centre of a square arena (9 × 9 cm and 0.5 cm high) held between two glass plates and maintained on an infrared light table. We then videorecorded the movement of each individual for 25 min and defined its general level of activity as the total distance covered during this time (Mauduit et al., 2021).

We measured aggregation on day 8 after adult emergence using a Y-shaped 3D-printed arena held between two glass plates and maintained on an infrared light table. This Y-shaped arena (Fig. 1a; 14 × 20 cm and 0.4 cm high) consisted of an introduction chamber connected to a central chamber, which was itself connected to both an aggregation chamber and a nonaggregation chamber. Each chamber was circular (4 cm diameter) and connected via 0.4 cm wide corridors that were large enough to allow earwig movement between chambers. The aggregation chamber was connected to another chamber containing four same-sex conspecifics (from a standard earwig lab rearing, changed at every trial), whereas the nonaggregation chamber was connected to an empty chamber. The connections to these last two chambers

occurred via 0.15 cm wide corridors that were large enough to allow odour circulation and antennations but small enough to prevent an earwig moving through them. We started the test by placing each individual in the introduction chamber, waiting 1 min for acclimatization, and then videorecording its movement for 25 min. The position of the aggregation chamber was swapped with the position of the nonaggregation chamber every other test to avoid laterality bias. As a measure of aggregation, we recorded the total time each individual spent in the aggregation chamber (i.e. near conspecifics). Of the 156 tested individuals, 52 spent more than 90% of their time in the introduction chamber (i.e. they were mostly inactive) and were thus excluded from the statistical analyses. Note that this apparent inactivity was independent of the social treatment (generalized linear model with binomial error distribution: likelihood ratio, LR $\chi^2_2 = 1.59$, $P = 0.451$), the sex (LR $\chi^2_1 = 0.44$, $P = 0.505$) or an interaction between these two factors (LR $\chi^2_2 = 0.82$, $P = 0.664$).

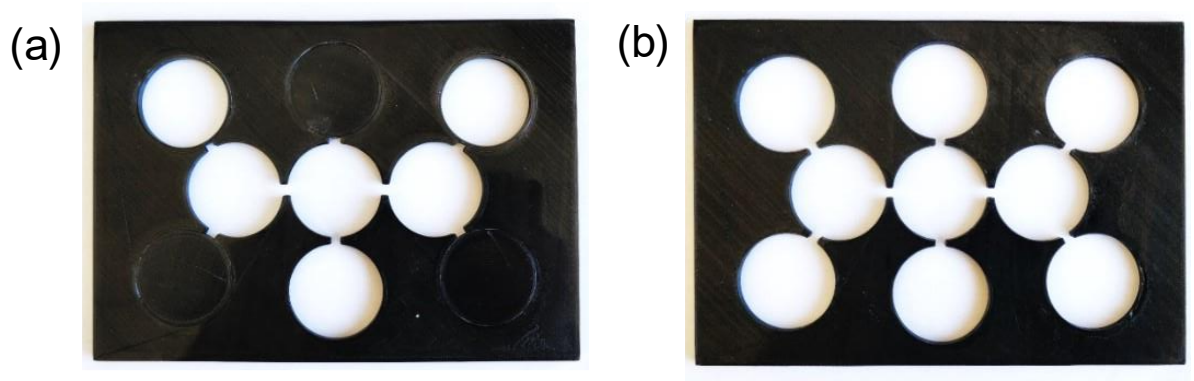

Figure 1. Apparatus used to measure (a) aggregation and (b) exploration of a novel environment in earwig adults. For aggregation measurements, the bottom chamber was the introduction chamber, while the top chambers were the aggregation and nonaggregation chambers. These two chambers were connected to the other chamber via a small opening allowing the circulation of volatile chemicals and antennation but preventing access to earwigs. For exploration measurements, the central chamber was the introduction chamber, while the other chambers received the unfamiliar, chemically distinct objects.

Finally, we measured the exploration of a novel environment 1 h after measuring aggregation (each individual was maintained in its original petri dish in between the two measurements). We adapted a standard protocol originally developed in ants (Modlmeier et al., 2012). We used another 3D-printed arena (Fig. 1b) held between two glass plates and maintained on an infrared light table. This exploration arena (14 × 20 cm and 0.4 cm) contained nine circular chambers (4 cm diameter), each connected to one to four chambers by 0.4 cm wide corridors allowing earwig movement. While the central chamber was empty (introduction chamber), the eight other chambers each contained 0.2 ml of an unfamiliar, chemically distinct object: dried pieces of cumin, cinnamon, mint plus vervain, ginger, coffee, coriander, paprika or evaporated water. The aim was to provide novel stimuli for the individual to explore. All objects were exchanged in between trials. We carefully introduced each tested individual into the central chamber, retained them for 1 min in this chamber for acclimatization, then opened the chamber and started videorecording the movements for 25 min. As a measure of exploration of a novel environment, we counted the chambers that an individual entered during the 25 min of observation (Modlmeier et al., 2012).

Overall, we conducted the four behavioural tests sequentially and in the same order. We recorded all videos in the dark (as earwigs are nocturnal) with infrared light and high sensitivity cameras (BBCA 1300, Basler AG, Ahrensburg, Germany; MediaRecorder v4.0, Noldus Information Technology, Wageningen, The Netherlands). The resulting videos were used to automatically extract the distance walked by the tested individuals using the software ToxTrac v2.92 (Rodriguez et al., 2018) and/or to analyse their movements and behaviours using the software BORIS v.7.9.7 (Friard & Gamba, 2016). Each arena was cleaned with alcohol after each trial to remove any potential pheromone marking. All morphometric and behavioural measurements were conducted blindly regarding the social environment of the tested individual.

Statistical Analyses

We performed all statistical analysis using the software R version 4.1.1 (R Core Team, 2021) loaded with the packages car, emmeans, lme4 and DHARMa. Overall, we used a series of seven

mixed linear models (LMER), one generalized mixed linear model (GLMER) with Poisson error distribution, and one GLMER with binomial error distribution. In these models, we entered either the proportion of surviving nymphs (GLMER with binomial errors), number of days to reach adulthood (LMER), minimum interocular distance (LMER), fresh weight at emergence (LMER), residual forceps length (LMER), number of pokes (GLMER with Poisson error), log-transformed total distance covered (LMER), number of newly visited chambers (LMER) or the log-transformed time in the aggregation chamber (LMER) as a response variable, while social environment (family group, siblings only or isolated), sex and the interaction between these two factors were entered as explanatory factors. Sex was not entered in the analyses on the residual forceps size in males. Because each family contributed to six values per experiment (three treatments and two sexes per treatment), we used family ID as a random effect in every model. The proportion of surviving nymphs was entered using the cbind function, which combines the total number of adults produced and the total number of nymphs that died before reaching adulthood. All models were checked for homoscedasticity and normal distribution of model residuals using the package DHARMa in R. When appropriate, we conducted pairwise comparisons between social environments based on estimated marginal means (i.e. model contrasts) and we corrected *P* values for multiple testing using the Tukey method (Lenth, 2022).

RESULTS

Sibling deprivation did not determine the survival rate of nymphs until adulthood (Fig. 2a; LR χ^2_2 = 2.03, P = 0.362) but influenced the development time of the first emerging adults (Fig. 2b; LR χ^2_2 = 6.12, P = 0.047). In particular, nymphs became adults more quickly when maintained in isolation rather than in a family group (i.e. with siblings and a mother; t_{122} = 2.44, P = 0.042), whereas there was no difference in development time between nymphs maintained with siblings and in isolation (t_{123} = 0.87, P = 0.659) and between nymphs maintained with siblings and in a family group (t_{122} = 1.55, P = 0.273). Independent of this effect, nymphs also reached adulthood faster when they were females compared with males (Fig. 2c; LR χ^2_1 = 12.11, P < 0.0001; interaction between social treatment and sex: LR χ^2_2 = 0.91, P = 0.635).

The social treatment also influenced the interocular distance (Fig. 3a; LR χ^2_2 = 24.87, P < 0.0001), fresh weight (Fig. 3b; LR χ^2_2 = 38.21, P < 0.0001) and (male) residual forceps length (Fig. 3c; LR χ^2_2 = 7.70, P = 0.021) of the first emerging adults. Adults raised in isolation exhibited a greater interocular distance and a heavier fresh weight than adults raised with siblings (t_{111} = –3.75, P = 0.0008 and t_{123} = –4.32, P = 0.001, respectively), and than adults raised in a family group (t_{112} = –4.73, P < 0.0001 and t_{122} = –5.98, P < 0.0001, respectively), while males raised with siblings had longer forceps than males raised in a family group ($t_{45.4}$ = –2.71, P = 0.025). By contrast, interocular distance and fresh weight were comparable between newly produced adults raised with siblings and in a family group (t_{113} = –0.89, P = 0.646 and t_{122} = –1.61, P = 0.244, respectively), and there was no difference in the forceps length of newly produced males raised in isolation and with siblings ($t_{45.1}$ = –0.88, P = 0.657), and males raised in isolation and in a family group ($t_{45.4}$ = 1.82, P = 0.176). Next to the effects of the social treatment on adult morphometrics, newly produced females overall had a greater interocular distance than males (Fig. 3d; LR χ^2_1 = 8.18, P = 0.004), but were as heavy as males (Fig. 3e; LR χ^2_1 = 1.41, P = 0.235). No interaction between sex and the social environment shaped the interocular distance (LR χ^2_2 = 0.08, P = 0.963) and fresh weight (LR χ^2_2 = 0.59, P = 745) of newly produced adults.

Finally, sibling deprivation altered the aggregation behaviour of the first emerging adults (Fig. 4a; LR χ^2_2 = 14.98, P = 0.0006), but did not affect their boldness (Fig. 4b; LR χ^2_2 = 5.58, P = 0.062), general activity (Fig. 4c; LR χ^2_2 = 3.69, P = 0.158) and exploration of a novel environment (Fig. 4d; LR χ^2_2 = 0.30, P = 0.863). Adults raised in isolation were less gregarious than adults raised with siblings ($t_{87.5}$ = 2.83, P = 0.016) and adults raised in a family group ($t_{88.7}$ = 3.73, P = 0.001), while there was no difference in the level of aggregation between adults raised with siblings and in a family group ($t_{84.3}$ = 0.82, P = 0.691). There was also no effect of sex on aggregation (Fig. 4e; LR χ^2_1 = 0.03, P = 0.871), boldness (Fig. 4f; LR χ^2_1 = 2.78, P = 0.096), general activity (Fig. 4g; LR χ^2_1 = 0.90, P = 0.343) and exploration (Fig. 4h; LR χ^2_1 = 0.24, P = 0.621), as well as no effect of an interaction between sex and the social environment on these traits (LR χ^2_2 = 1.15, P = 562; LR χ^2_2 = 0.33, P = 0.846; LR χ^2_2 = 1.33, P = 0.516 and LR χ^2_2 = 2.23, P = 0.329, respectively).

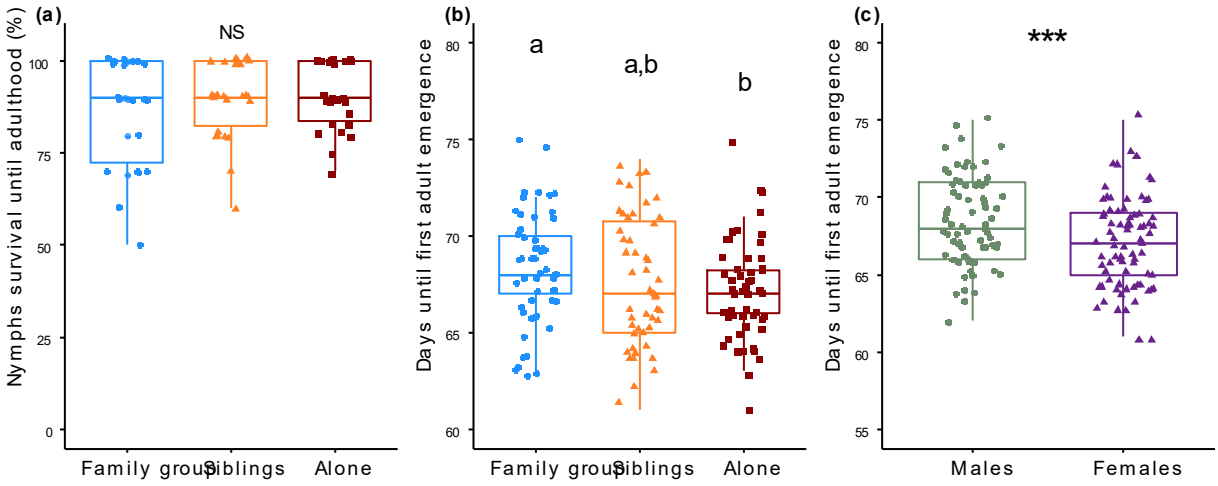

Figure 2. (a) Effect of the social environment on juvenile survival until adulthood; (b) effect of the social environment on the number of days between egg hatching and the first adult emergence per treatment; (c) effect of sex on the number of days between egg hatching and the first adult emergence per treatment. Box plots illustrate median (middle bar) and interquartile range (light bar), with whiskers extending to 1.5 times the interquartile range and dots representing jittered experimental values. Different letters indicate a significant difference at $P < 0.05$; ***$P < 0.001$.

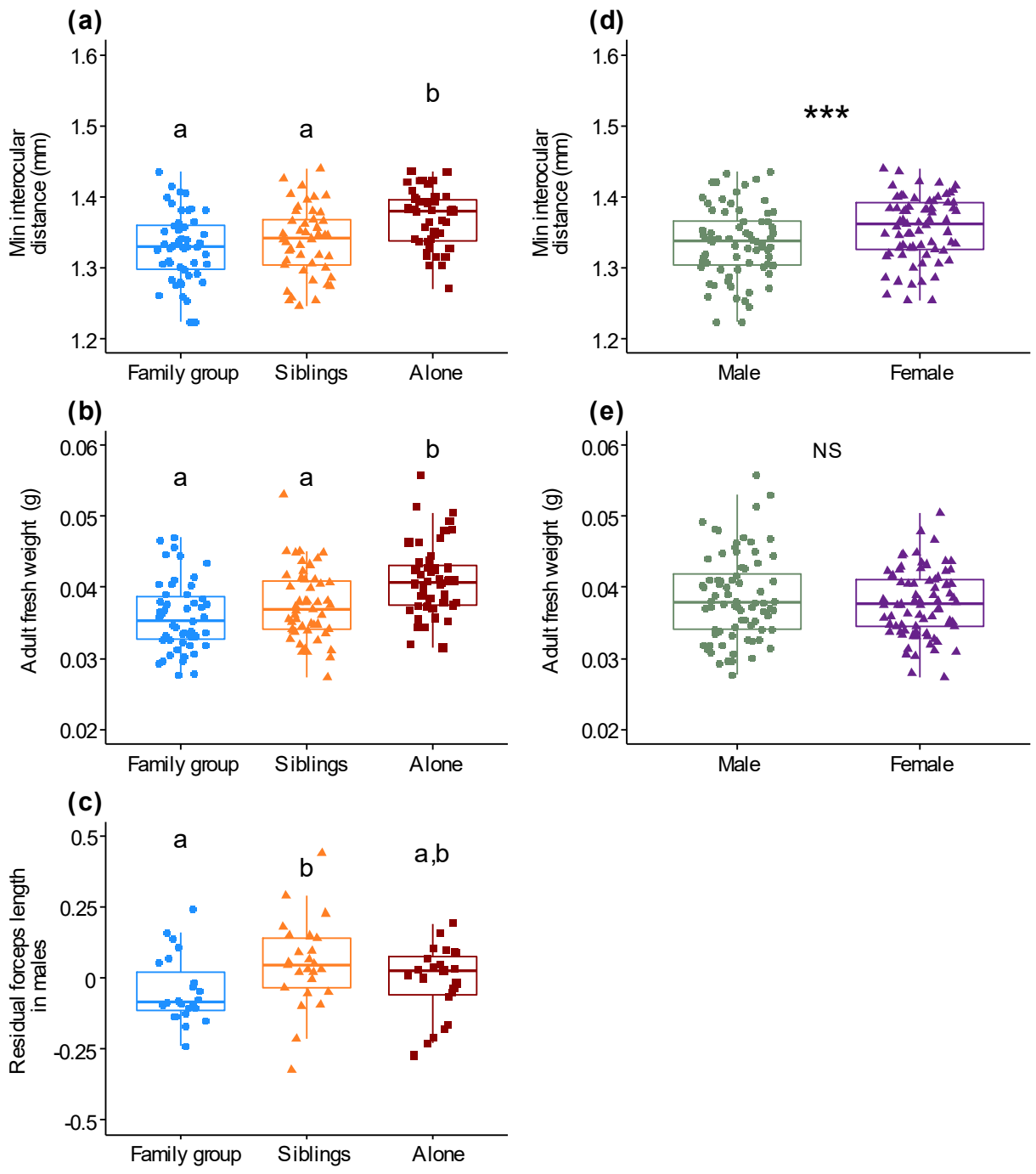

Figure 3. Effect of (a, b, c) the social environment and (d, e) sex on (a, d) the minimum interocular distance, (b, e) fresh weight and (c) residual forceps length (in males) of newly produced adults. Box plots illustrate median (middle bar) and interquartile range (light bar), with whiskers extending to 1.5 times the interquartile range and dots representing jittered experimental values. Different letters indicate a significant difference at $P < 0.05$; ***$P < 0.001$.

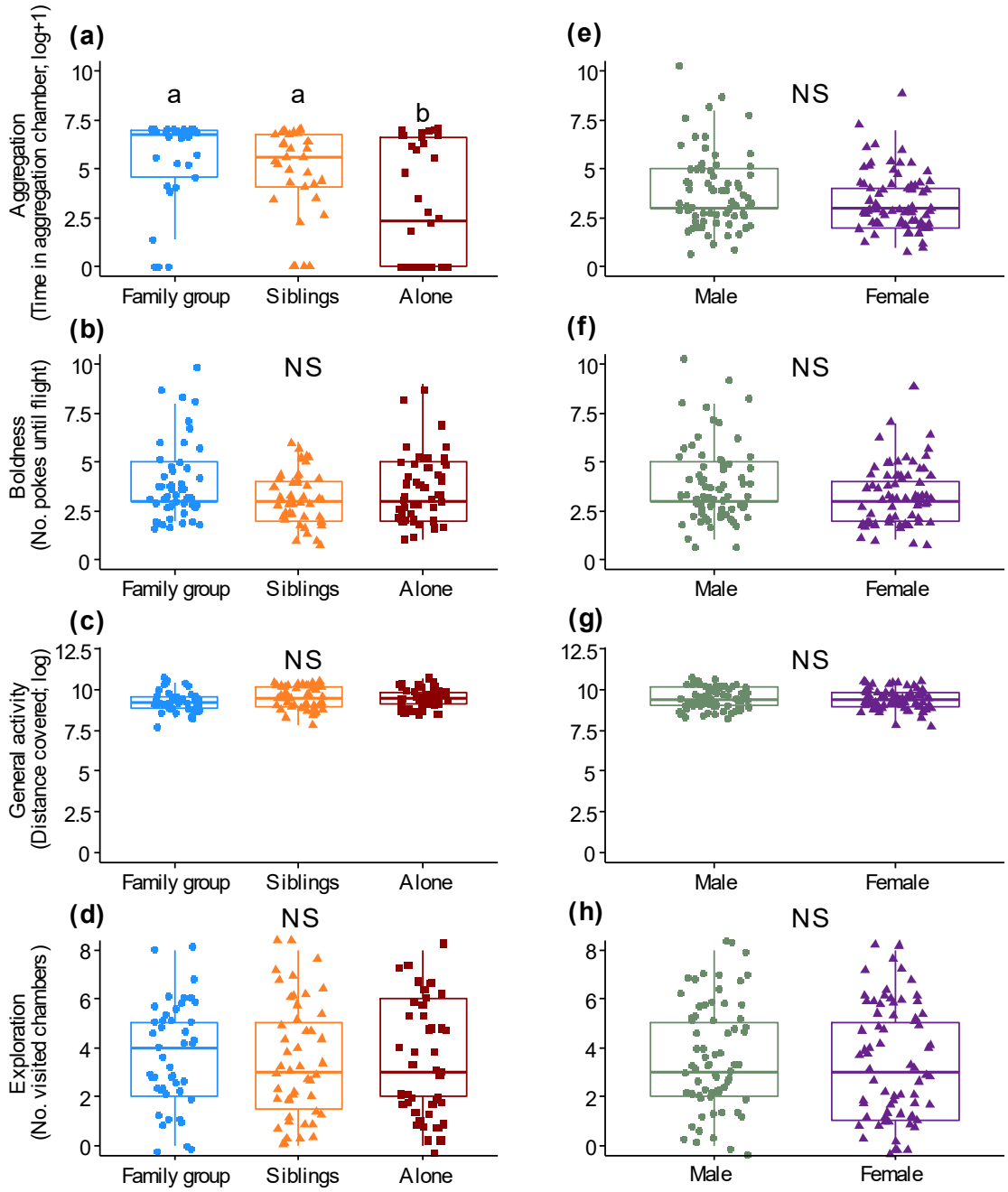

Figure 4. Effect of (a, b, c, d) the social environment and (e, f, g, h) sex on (a, e) aggregation, (b, f) boldness, (c, g) general activity and (d, h) exploration scores of newly produced adults. Box plots illustrate median (middle bar) and interquartile range (light bar), with whiskers extending to 1.5 times the interquartile range and dots representing jittered experimental values. Different letters indicate a significant difference at $P < 0.05$.

DISCUSSION

While a growing number of studies highlight that sibling interactions can confer important benefits to juveniles during family life in species with precocial offspring (Kramer & Meunier, 2019; Roulin & Dreiss, 2012), it remains surprisingly unclear whether the deprivation of such sibling interactions can result in short- and/or long-term costs to precocial offspring, such as those typically reported following parental deprivation (Andres et al., 2013; Dettling et al., 2002; Foster et al., 2012; Smiseth et al., 2012; Thesing et al., 2015). Our results reveal that the deprivation of sibling interactions during family life entails both benefits and costs for juveniles in the European earwig. Earwig nymphs raised in isolation reached adulthood more quickly and produced larger adults, but these first emerging adults exhibited less aggregation behaviour than nymphs reared with siblings or with siblings and their mother. The absence of siblings during the family life period did not affect the survival rate of nymphs to adulthood, nor did it affect their boldness, general activity or exploration behaviour. Overall, the (absence of) effects of sibling deprivation on development, survival, morphology and behaviour did not depend on the sex of the resulting adults, although females overall reached adulthood earlier and had a larger head width. Finally, we found that the presence or absence of siblings did not affect the forceps length of the resulting males, but this length was overall longer in males raised with siblings only rather than with siblings and their mother.

Sibling deprivation led nymphs both to develop into adults more quickly and to produce larger adults. Faster development speed and larger body size are often associated with better reproductive success as they allow individuals to have access to breeding partners earlier in the season and/or offer them better reproductive capabilities (Kingsolver & Huey, 2008; Meunier et al., 2012; Saleh et al., 2014; Yoshimura et al., 2003). Hence, our results suggest that the presence of siblings (under standard conditions) entails costs to earwig juveniles and that maternal presence does not mitigate these costs. These results contrast with previous studies showing that *F. auricularia* nymphs can have short-term benefits from sibling cooperation under harsh environmental conditions (Falk et al., 2014; Körner et al., 2016; Kramer et al., 2015) and thus highlight the importance of environmental conditions (e.g. absence of predators and pathogens, ad libitum access to food) on the nature and outcome of sibling interactions during earwig family

life. The reported costs of sibling interactions are unlikely to reflect competition for limited parental resources (i.e. sibling rivalry; Mock & Parker, 1997), as we found that offspring development and adult size were independent of maternal presence. Instead, they could be due to social harassment, a notion supported by the frequent behavioural contacts and frequent occurrence of cannibalism among earwig nymphs (Dobler & Kölliker, 2010, 2011; Van Meyel & Meunier, 2020). Since the expression of social harassment is likely to be energetically costly for individuals and therefore requires them to be in good shape, this could explain why we found that the costs of sibling interactions exceed the potential benefits of sibling cooperation under good environmental conditions and why the benefits of cooperation exceed the costs of sibling rivalry under harsh environmental conditions. Future studies should investigate this hypothesis, especially by manipulating the quality of environmental conditions. They should also confirm the absence of long-term costs of faster development and transformation into larger individuals for juveniles to validate that the apparent benefits of sibling deprivation reported here reflect an adaptive strategy.

Apart from the effects on development and body size, we showed that sibling deprivation produced less gregarious adults. Aggregation is a key behaviour in *F. auricularia*, as this species is typically found in clusters numbering from a dozen to several hundred individuals (Sauphanor & Sureau, 1993), where adults express both competitive and cooperative behaviour (Weiß et al., 2014) and find mating partners (Sandrin et al., 2015). Expressing reduced aggregation behaviour could therefore limit the mating opportunities of adult earwigs and/or hamper other classical benefits of aggregation such as protection against predators and pathogens (e.g. by preventing the expression of social immunity or density-dependent prophylaxis; Diehl et al., 2015; Santana et al., 2017; Van Meyel et al., 2018; Wilson & Cotter, 2009). This overall indicates a cost of sibling deprivation, possibly due to the lack of sibling interactions during the first 2 weeks of life and/or to the social isolation during the 2 months of nymph development (Kohlmeier et al., 2016). This notwithstanding, the fact that sibling deprivation did not influence nonsocial behaviours such as boldness, general activity and exploration of a new environment also suggests that the lack of social interaction during development specifically hampered the learning of social behaviours (or social odours; Wong et al., 2014) expressed in adults. This is consistent with a previous study

showing that mothers provide less care to their juveniles when they grew up without a mother than with a mother (Thesing et al., 2015). Effects of the early social environment on social learning have been reported in rodents and primates, in which temporary maternal deprivation alters the brain development of juveniles and thereby impairs hormonal and neurobiological processes involved in the expression of social behaviours such as parental care (Champagne & Curley, 2005; Keverne, 2014). In arthropods such as honey bees and dung beetles, the absence of brood care also delays the development of sensory and integrative brain centres in juveniles, even if the impact on social behaviour remains unclear (Farris, 2013; Farris & Sinakevitch, 2003). Future studies are thus required to identify the mechanisms underlying the phenotypic effects of sibling deprivation in earwigs and to test whether these effects are determined by early life experience alone and/or whether they are due to overall development in isolation.

Somewhat surprisingly, we found that males had a longer residual forceps length (i.e. their forceps were longer than predicted by their body size) when reared in sibling groups without rather than with their mothers, whereas males reared in isolation had a residual forceps length that was not different from either of the other two treatments. In earwig males, having long forceps generally ensures better reproductive success, as forceps length is positively associated with the duration, frequency and success of copulations, as well as with fighting abilities against competitors (reviewed in Kamimura, 2014). While forceps length is partly heritable in this species (Pike et al., 2017), high population density also favours the production of males with long forceps, as the superior fighting abilities of these males are more frequently rewarded at high encounter rates (Tomkins & Brown, 2004). Earwig males therefore have direct benefits from growing long forceps, particularly when they develop in dense groups. On the other hand, producing long forceps can be energetically costly and juveniles must therefore have access to sufficient or specific resources during development to allow such an investment in weapon size (Körner et al., 2017). Our results may therefore suggest that growing up in the presence of siblings encourages males to produce longer forceps for future competitive interactions, but that this overexpression is inhibited by maternal presence. While follow-up studies are required to unravel the drivers of this inhibition, we propose two potential mechanisms. First, earwig mothers could have prevented nymphs from accessing sufficient food to produce oversized ornaments, even if this is

unlikely as the food was provided ad libitum (Meunier & Kölliker, 2012a; Kramer et al., 2017). On the other hand, orphaned nymphs could be unable to receive resources that are exclusively provided by the mothers and that are required to develop long forceps. In insects, for instance, parental care often allows the transfer of symbionts that help their juveniles to digest specific food sources and obtain the resulting nutrients (e.g. specific symbionts; Onchuru et al., 2018). The occurrence of such a transfer remains to be investigated in earwigs (Van Meyel et al., 2021).

To conclude, our study reveals that sibling deprivation does not result in major costs to juveniles of the European earwig, such as those typically reported in altricial and precocial species due to parental deprivation (Andres et al., 2013; Dettling et al., 2002; Foster et al., 2012; Smiseth et al., 2012; Thesing et al., 2015). While we showed that early social interaction with siblings increases the later expression of aggregation behaviour in adults (a keystone of their reproductive biology), we showed that sibling deprivation shapes none of three other key behaviours in social arthropods (i.e. boldness, general activity and exploration of a new environment; Modlmeier et al., 2012; Wright et al., 2019) and even provides apparent benefits in terms of developmental time and adult size. Earwig nymphs thus appear to be free to switch from solitary to sibling group living (with or without mothers) with only limited fitness consequences, at least under standard laboratory conditions and regarding the measured traits. Interestingly, earwig mothers can also switch from solitary to family life with limited fitness consequences. When *F. auricularia* mothers abandon the nest, their offspring suffer only small costs or even get benefits in terms of development, survival, immunity, future reproductive strategies and future expression of maternal behaviours (this study; Kramer et al., 2017; Meunier & Kölliker, 2012b; Meunier & Kölliker, 2013; Thesing et al., 2015;). Moreover, nymphs can mitigate poor maternal care by increasing sibling cooperation (Kramer et al., 2015) and mothers can benefit from abandoning their nymphs as it allows them to produce a second clutch earlier (Kölliker, 2007). By demonstrating that lack of access to sibling interactions has as small a detrimental effect as lack of access to maternal care for earwig nymphs, our study raises questions about the evolutionary constraints favouring family maintenance in this species, among which predation risk is a likely candidate (Cocroft, 2002). More generally, our results also demonstrate that the study of these evolutionary constraints in precocial species can provide

novel insights into our current understanding of the evolutionary transition from solitary to social life when individuals can still adopt both lifestyles, a scenario that probably prevailed in the early evolution of family life (Falk et al., 2014).

AUTHOR CONTRIBUTIONS

S.V.M.: Conceptualization; Data curation; Formal analysis; Writing original draft; Review & editing. J.M.: Conceptualization; Data curation; Formal analysis; Funding acquisition; Supervision; Writing original draft; Review & editing.

DATA AVAILABILITY

Data and R script are provided as Supplementary Material at https://doi.org/10.1016/j.anbehav.2022.09.003

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