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**ABSTRACT**

Many animals consume the feces of their conspecifics. This allo-coprophagy can have benefits, such as access to nutrients and symbionts, but also risks for consumers, mainly due to direct contact with pathogens that develop on feces. In the European earwig *Forficula auricularia*, mothers and juveniles live in nests lined with their feces. This surprising habit allows juveniles to consume the feces of their siblings during family life and provides them with nutritional benefits when mothers provide low care. However, it was unclear whether earwig mothers also practice allo-coprophagy, and whether this behaviour is motivated by their nutritional needs. Here, we set up four types of experimental families in which we manipulated the nutritional needs of mothers and/or juveniles and measured the effects on the production of feces by the juveniles, and the consumption of these feces by the mothers. Our results first show that fed juveniles produced more feces pellet in presence of fed compared to food-deprived mothers. We also found that, overall, about 50% of the mothers consumed juveniles feces. This consumption was both more likely and larger when the feces were produced by fed compared to food-deprived juveniles, while the proportion of feces pellets eaten was larger in food-deprived compared to fed mothers. Overall, our results reveal that allo-coprophagy involves every family member and suggest that it can have both nutritional and non-nutritional benefits for earwig mothers. Allo-coprophagy could thus favour the maintenance of mothers in the nest and, more generally, promote the early evolution of family life.

**INTRODUCTION**

The consumption of feces produced by conspecifics is a taxonomically widespread phenomenon in animals (Weiss, 2006). When present, its expression is generally associated with three main types of benefits. First, it may provide an additional source of food (including enzymes, metabolites and undigested particles) to consumers (Nilsson, 1983; Nalepa, Bignell, & Bandi, 2001). This can be decisive to improve resistance against starvation when other food sources are absent, as reported in the German cockroach *Blattella germanica* (Kopanic et al., 2001). Second, the consumption of feces may improve the efficiency of food utilization. This is because the microorganisms and microbes that rapidly colonize feces often initiate the digestion of organic compounds (e.g. cellulose), detoxify allelochemicals and soften the substrate (Nalepa et al., 2001; Weiss, 2006), which overall make coprophagy a source of enzymes and metabolites that would be otherwise difficult to access. This phenomenon is called the "external rumen" and has been reported, for instance, in Passalidae beetles (Halffter, 1997; Dillard, 2019). Finally, coprophagy may ensure the transfer of gut mutualistic micro-organisms among conspecifics. A growing body of literature indeed demonstrates that the acquisition of these gut microbes can be essential for recipients (Moran et al., 2019), as they are involved in numerous physiological, reproductive, and behavioural functions of the host. For instance, the gut microbiota can affect the digestion of specific food sources (Cleveland, 1923; Mirabito & Rosengaus, 2016), hormone signalling, metabolism and ageing (Broderick & Lemaitre, 2012), immunocompetence (Wei et al., 2017; Itoh et al., 2018; Wang et al., 2020), general activity (Hosokawa et al., 2008), and behavioural tasks (Jones et al., 2018). This transfer of gut mutualistic micro-organisms could be particularly important in insects, as their inherent

moulting events typically lead to a repeated defaunation of their gut, which thus requires simple mechanisms (such as coprophagy and mouth-to-anus contacts) allowing regular reinfections by the microbiota – a process that could promote the general evolution of complex forms of social life such has eusociality (Nalepa, 2015, 2020).

Whereas allo-coprophagy should be facilitated when producers and consumers share a nesting area and thus have direct access to each other's feces, this phenomenon seems to be rare in group-living species (Weiss, 2006). The main reason is that a wide range of pathogenic bacteria and fungi are known to use feces as a substrate for their development (Bailey, 1955; Bucher, 1957) and the associated risk of contact and infection for the host dramatically grow when host density is high and/or living space is confined (Weiss, 2006; Jackson & Hart, 2009; Schmid-Hempel, 2017). As a result, many group-living species do not show coprophagy and/or have evolved sanitation behaviors to limit contacts with feces from conspecifics (Meunier, 2015). Classical examples of these behaviors are expelling feces out of the nest (Thomson, 1934; Weiss, 2003; Biedermann & Taborsky, 2011) and restricting defecation to a single location (Dethier, 1980; Farji-Brener et al., 2016).

In the European earwig *Forficula auricularia*, individuals actively maintain their feces in the nest. In this subsocial insect, mothers remain with their clutch of eggs during winter and then stay with the newly emerged juveniles (called nymphs) during the first two weeks following egg hatching (Lamb, 1976; Kölliker, 2007; Van Meyel et al., 2019; Tourneur & Meunier, 2020). During this post-hatching family life, mothers and nymphs actively maintain their feces in the nest and line its walls and ground with this material (Körner et al., 2016). Mothers provide multiple forms of post-hatching care to their nymphs, including fierce

protection against predators, grooming behaviours and food provisioning through regurgitation (Staerkle & Kölliker, 2008; Mas & Kölliker, 2011; Ratz et al., 2016) and they typically favour nymphs in good compared to poor conditions (Mas et al., 2009; Mas & Kölliker, 2011). Nevertheless, earwig nymphs exhibit early foraging capabilities and are thus relatively independent of maternal care (Kölliker, 2007; Thesing et al., 2015; Vogelweith et al., 2017). Some studies even showed that nymphs survive better in the absence compared to the presence of their mothers when the environment contains limited food resources (Meunier & Kölliker, 2012; Kramer et al., 2017), raising fundamental questions about why earwig mothers stay with their juveniles.

Recent works propose that the maintenance of feces in the nest could mediate a form of social immunity and/or allow the expression of allo-coprophagy, which could overall promote family life for earwig mothers and juveniles. A previous study showed that the feces of both mothers and nymphs exhibit antimicrobial properties, their maintenance in the nest could thus be a form of social immunity preventing the development of mould and other potential pathogens in the offspring vicinity (Diehl et al., 2015). This phenomenon has also been reported in the subterranean termite *Coptotermes formosanus* (Chouvenc et al., 2013) and the burying beetle *Nicrophorus vespilloides* (Rozen et al., 2008). On the other hand, some studies have shown that the feces produced by earwig nymphs are consumed by their siblings during family life (Falk et al., 2014). This consumption increases when mothers reduce their investment in maternal care (Kramer et al., 2015; Kramer et al., 2017) and the feces produced by earwig nymphs exhibit nutritive value that promotes sibling survival in absence of any food source or in presence of maternal feces only (Körner et al., 2016). Hence, the maintenance of feces in the

nest could (also) serve as food stock for nymphs (that is self-protected from the competition with microbes via its antimicrobial properties), which may help to mitigate the risks associated with food deprivation and/or a lack of maternal food provisioning. Whether this food stock can also be used by mothers and thus whether it can encourage mothers to stay with their (foraging) offspring remained untested.

In this study, we investigated whether and why mothers consume feces produced by their juveniles in the European earwig *F. auricularia* L. Using a 2x2 full factorial experiment, we tested whether 1) earwig mothers consume feces pellets produced by their nymphs, and whether 2) mothers adapt their level of coprophagy to their own nutritional needs and/or the nutritional condition of the feces-producing nymphs (which may, for instance, shape the nutritional quality of the feces ; Körner et al. 2016). We also investigated whether offspring could actively assist their mothers via allo-coprophagy by testing whether 3) nymphs adapt their production of feces (e.g. via a modified foraging activity and/or food intake) to the nutritional needs of their mother. We set up four types of experimental families in which we provided food either to the mothers, the nymphs, both mothers and nymphs, or none of them. We then counted the number of feces pellets produced by nymphs and the occurrence and level of maternal consumption of these nymphal feces pellets. If mothers exhibit allo-coprophagy, we predicted that mothers would consume at least some feces pellets produced by their nymphs. If the level of allo-coprophagy is driven by the nutritional needs of the mother, we predicted feces consumption would be higher in food-deprived compared to non-food deprived mothers. Finally, if nymphs actively promote allo-coprophagy when tended by food-

deprived mothers, we predicted that nymphs would produce more feces when they were tended by a food-deprived compared to a fed mother.

## MATERIALS AND METHODS

### Experimental setup

The experiment involved 95 earwig families produced by 95 *F. auricularia* females (from the clade B of this species; Wirth et al. 1998; González-Miguéns et al. 2020) field-sampled in June 2018 in Pont-de-Ruan (France) and then maintained under standard laboratory conditions until egg-laying (Nov-Dec 2019) and then egg hatching (Jan-Feb 2019; details of the standard rearing conditions are provided in Meunier et al., 2012). One day after egg hatching, each family was randomly assigned to one of four treatments consisting of the provisioning of food to either i) the mother ($N=24$), ii) the nymphs ($N=24$), iii) both the mother and the nymphs ($N=23$) or iv) none of them ($N=24$). To this end, the number of nymphs per family was first standardized to 25 (initial mean ± SE number of nymphs per clutch = 34.52 ± 0.57; nymphs were never mixed between clutches) and the resulting experimental family transferred in Petri dishes (10 cm diameter) lined with moistened sand and maintained under 20°C and 12h:12h light: dark cycle.

The manipulation of food provisioning was done by temporarily separating mothers and nymphs in two small Petri dishes (5 cm diameter) lined with moistened sand, then providing them with an *ad libitum* amount of food or no food (depending on the treatment) for two hours, and finally returning mothers and their nymphs to their original large Petri dishes. Food provisioning was manipulated two, four, six and eight days after egg hatching. Earwig family life

typically lasts 14 days and nymphs can survive up to 15 days without food access (Körner et al., 2016). Mothers were fed with a standard food preparation (mostly containing pollen, carrots, and cat food; see detailed food composition in Meunier et al., 2012) on each of these days. By contrast, nymphs were fed with the standard food preparation on days two and four, whereas they were fed with green-coloured pollen pellets on day six and eight (Kramer et al., 2015). The consumption of green pollen allowed the subsequent production of green feces pellets by juveniles, which facilitated both their counting by the experimenter and the discrimination between nymph and (when present) mother produced feces (Falk et al., 2014).

Immediately after our last manipulation of food provisioning on day eight, 15 nymphs per family were isolated in a new container to allow feces production. Fourteen hours later, we removed the nymphs, counted the number of feces pellets in the container (without touching them as they are very fragile and cannot be removed and/or moved) and then transferred each mother to the container with the feces of their own nymphs. These 14 hours of isolation are unlikely to mask the (potential) effect of mothers' nutritional condition on nymphs feces production, because (1) the effect of maternal condition on nymph behaviours is known to operate during at least 1 day without direct contacts with mothers (Wong et al., 2014) and because (2) feces production is the outcome of a long physiological process, which thus here, is more likely to reflect the impact of the 8 previous days of direct contacts with a mother rather than the 14h of isolation.

Two hours later, we counted the number of remaining feces pellets in the container. The very few feces pellets produced by mothers during these two hours (when present) were typically non-green and larger than the ones produced by nymphs and were thus excluded from

this counting. To minimize observer bias, the feces counting was done blindly regarding the treatment applied to the mothers and their nymphs. For feces production (day 8) and feces consumption (day 9), family members were transferred to new Petri dishes (10 cm diameter) lined with a piece of white, moistened filter paper (Macherey-Nagel GmbH & Co. KG, Düren, Germany) to facilitate the counting of green feces pellets.

We defined the number of feces pellets eaten by a mother as the number of green feces pellets present in the container before minus after maternal introduction. Somewhat surprisingly, this number was negative in 4 of the 95 replicates (4.2%). A likely explanation for these values is that even if mothers typically produce feces pellets that are non-green and larger compared to the feces of their nymphs, a few mothers might have produced some 'small' indistinguishable feces pellets during the experiment and this production happened to be larger than the number of nymph's feces pellets they have possibly consumed in these four replicates. Among these four females, two belonged to the treatment where both females and nymphs had no food access (our calculation led to -1 and -1 eaten feces pellets, respectively), one to the treatment where both females and nymphs had food access (-2 eaten feces pellets) and one to the treatment where only the nymphs had food access (-1 eaten feces pellets). For consistency, we removed these four values in all our statistical analyses. Nevertheless, either changing these values to zero, removing or maintaining them in our analyses do not qualitatively change the results (see details in Table S1). Note that only a few replicates contained the typical 'large' non-green maternal feces pellets, which suggests that maternal feces production was overall very limited during the 2h of our experiment. Thus, the potential limit of the method discussed above is unlikely to affect our general conclusions.

**Statistical analysis**

We analyzed the effects of nymphs' and mothers' food status on the production of feces pellets using a linear general model (LM), in which the number of feces pellets produced by the fifteen nymphs was entered as a response variable, while nymphs' food status, mothers' food status and the interaction between these two factors were entered as explanatory factors. Because many mothers did not consume any fecal material produced by their nymphs (see results and Figure S1), this data was analysed using two successive approaches. We first analyzed the effects of nymphs' and mothers' food status on the consumption of at least one nymphs' feces pellet by a mother using a generalized linear model (GLM) with binomial error distribution. In this model, whether a mother was or was not coprophagous (1 or 0, respectively) was entered as a response variable, while nymphs' food status, mothers' food status and the interaction between these two factors were entered as explanatory factors. Second, we analysed the effects of nymphs' and mothers' food status on the level of feces consumption by coprophagous mothers using an additional GLM (with binomial error distribution corrected for overdispersion) and an additional LM, in which the proportion and the absolute number of feces pellets eaten by a coprophagous mother, respectively, were used as a response variable, while nymphs' food status, mothers' food status and the interaction between these two factors were entered as explanatory factors. The proportion of feces pellets eaten by the coprophagous mothers was entered using the *cbind* function in R, in which we used the number of feces pellets eaten and non-eaten. To fulfil model assumptions and thus ensure both homoscedasticity and a Gaussian distribution of LM residuals, we log-transformed both the number of feces pellets produced by nymphs and the absolute number of feces pellets eaten by

mothers. When required, we conducted pairwise comparisons between treatments using estimated marginal means of the LMs and GLM, and Tukey-adjusted $P$-values. All these models were conducted with R v4.0.2 (R Core Team, 2017) loaded with the packages *car* and *emmeans*.

**RESULTS**

Overall, the groups of nymphs produced from 2 to 194 feces pellets (mean ± SE = 48.32 ± 4.97; Figure S1A), which corresponds to an average of 3.2 feces pellets per nymph per 14h. The consumption of at least one nymphs' feces pellet by the mother was present in 46 of the 91 (50.5%) trials. This maternal coprophagy was overall more frequent when the feces were produced by fed compared to food-deprived nymphs (Figure 1A; LR $\chi^2_1$ = 5.99, P = 0.014), whereas it was independent of mothers' food access and of an interaction between mothers' and nymphs' food access (Table 1).

In the 46 coprophagous mothers described above, the absolute number of nymphs' feces pellets eaten by each female varied from 1 to 125 (mean ± SE = 12.98 ± 3.28; Figure S1B). These numbers correspond to 1 % to 75 % (mean ± SE = 20.05 ± 2.80 %) of the total number of nymphs' feces pellets available during the tests, indicating that coprophagous mothers never consumed all the feces pellets produced by their nymphs. The proportion of feces pellets eaten by these coprophagous mothers was higher when mothers were starved compared to fed (LR $\chi^2_1$ = 20.65, $P$ < 0.0001), whereas it was independent of nymphs' access to a food source and of an interaction between nymphs' and mothers' food access (Table 1). By contrast, the absolute number of feces pellets eaten by coprophagous mothers was higher when the feces were

produced by fed compared to food-deprived nymphs (Figure 1; $F_{1,42}$ = 12.28, $P$ = 0.001), whereas it was independent of mothers' food access and of an interaction between nymphs' and mothers' food access (Table 1).

The number of feces pellets produced by the nymphs was shaped by an interaction between nymphs' and mothers' food access (Figure 2; $F_{1,91}$ =7.57, $P$ = 0.007; see table 1 for full model description). Contrary to our predictions, however, this interaction reveals that the fed nymphs produced more feces when they were tended by fed compared to food-deprived mothers (pairwise comparison: $t_{91}$ = -3.37, $P$ = 0.006) and that this effect was absent in the food-deprived nymphs (pairwise comparison: $t_{91}$ = 0.50, $P$ = 0.959).


**DISCUSSION**

Whereas earwig juveniles actively consume the feces produced by their sibling during family life (Falk et al., 2014), whether earwig mothers may also exhibit allo-coprophagy remained unknown. Here we first show that about 50% of the mothers indeed consumed feces produced by their juveniles. The likelihood that a mother became coprophagous was higher in the presence of feces produced by fed compared to food-deprived nymphs. Similarly, we found that the level of feces consumption by coprophagous mothers was higher when the feces were produced by fed compared to food-deprived nymphs (for the absolute number of feces eaten, only), and higher when mothers had no access compared to previous access to a food source (for both proportion and absolute number of feces eaten). Finally, our data show that the fed nymphs did not increase their production of feces when their mothers were food-deprived (i.e.

no sign of offspring assistance), and instead that the fed nymphs produced more feces when they were tended by fed compared to food-deprived mothers.

Our results first confirm that earwig mothers can consume the feces of their juveniles. In the context of family life, allo-coprophagy typically serves to clean the nesting area and/or to provide nutritional benefits to consumers (Nilsson, 1983; Kopanic et al., 2001; Weiss, 2006; Mirabito & Rosengaus, 2016). In earwigs, feces consumption is unlikely to be a simple nest cleaning behaviour, as nests' walls and grounds are actively covered with mothers and nymphs feces and these feces have antimicrobial properties (Diehl et al., 2015; Körner et al., 2016). Our findings also suggest that the nutritional benefits of allo-coprophagy only partly determine its expression by earwig mothers. This is because we found that the proportion of feces consumed was overall higher in coprophagous mothers that were previously starved compared to well-fed, but also that the nutritional needs of mothers did not shape their likelihood to become coprophagous nor the absolute quantity of feces they have eaten. Allo-coprophagy might thus have other (additional) functions in earwig mothers, among which access to specific nutrients, mutualists symbionts and/or immune components are likely candidates (Diehl et al., 2015; Arcila & Meunier, 2020; Van Meyel et al., 2021).

Our data also reveal that fed nymphs (and only fed nymphs) produced more feces when their mothers were already well-fed. Under standard pathogen-free environments, increased production of feces typically results from a higher food intake. Our results thus suggest that fed nymphs received an additional amount of food from their fed mothers, probably during the periods of family interactions. Interestingly, this pattern was absent with starved nymphs: these nymphs did not increase feces production in presence of fed mothers. This implies that fed

mothers did not provide food to starved nymphs and thus that mothers control this food transfer. This might be the case if mothers provide food to their offspring mostly via regurgitation (Staerkle and Kölliker 2008) and not via allo-coprophagy on maternal feces. Overall, our findings also emphasize that fed mothers provided food to nymphs that were already well-fed and thus likely to be of good condition, and not to nymphs that were starved and in poor condition. This is in line with previous works showing that earwig mothers increase their investment into care (i.e. foraging activity, allocation of food resources and grooming behaviours) when they are exposed to chemical cues extracted from well-fed compared to poorly-fed juveniles (Mas et al., 2009; Mas & Kölliker, 2011). These results support a general prediction stating that parents preferentially feed offspring of higher reproductive value to maximize their fitness return on parental investment (Haig, 1990). More generally, they highlight that earwig mothers do not provide unconditional care during family life (Meunier & Kölliker, 2012; Kramer et al., 2017) and may neglect juveniles that are the most in need of care (see also Mas et al. 2009).

To conclude, our experiments revealed that earwig mothers can consume the feces of their juveniles during family life, that this consumption is only partly driven by the nutritional needs of the mother and that juveniles do not adapt their feces production to the nutritional needs of their mothers. These findings call for future studies investigating the effects of nymphs starvation on the quality of their fecal pellets and exploring the non-nutritive drivers of maternal consumption of juveniles feces, among which the transfer of gut microbiota could be a prime candidate (Van Meyel et al., 2021). They also call for studies disentangling whether this behaviour is a mere product of selection for immediate food access with no further implication

in the early evolution of family life, or whether it may have such an implication by selecting for

the maintenance of mothers in the vicinity of their foraging juveniles and thus, by ultimately

promoting the emergence and consolidation of facultative family living from a solitary state.

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**REFERENCES**

Arcila, F. and Meunier, J. (2020). Friend or foe? The apparent benefits of gregarine

　　(Apicomplexa: Sporozoa) infection in the European earwig. International Journal for

　　Parasitology, 50, 461–469.

Bailey, L. (1955). The epidemiology and control of nosema disease by the honey-bee. Annals of

　　Applied Biology Appl Biol, 43, 379–389.

Biedermann, P. H. W. and Taborsky, M. (2011). Larval helpers and age polyethism in ambrosia

　　beetles. Proceedings of the National Academy of Sciences of the United States of America,

　　108, 17064–17069.

Broderick, N. A. and Lemaitre, B. (2012). Gut-associated microbes of Drosophila melanogaster.

Gut Microbes, 3, 307–321.

Bucher, G. (1957). Disease of the larvae of tent caterpillars caused by a sporeforming

bacterium. Canadian Journal of Microbiology, 3, 695–709.

Chouvenc, T., Efstathion, C. A., Elliott, M. L., and Su, N. (2013). Extended disease resistance

emerging from the faecal nest of a subterranean termite. Proceedings of the Royal Society

of London B: Biological Sciences, 280, 20131885.

Cleveland, L. R. (1923). Symbiosis between termites and their intestinal protozoa. Proceedings

of the National Academy of Sciences of the United States of America, 9, 424–428.

Dethier, V. G. (1980). The world of the tent-makers: a natural history of the eastern tent

caterpillar. Amherst: University of Massachusetts Press.

Diehl, J. M., Körner, M., Pietsch, M. and Meunier, J. (2015). Feces production as a form of social

immunity in an insect with facultative maternal care. BMC Evolutionary Biology, 15, 15:40.

Dillard, J. R. (2019). Effects of breeding ecology on parental care and family living in passalid

beetles. Insectes Sociaux, 66, 581–592.

Falk, J., Wong, J. W. Y., Kölliker, M. and Meunier, J. (2014). Sibling cooperation in earwig

families provides insights into the early evolution of social life. The American Naturalist,

183, 547–557.

Farji-Brener, A. G., Elizalde, L., Fernández-Marín, H. and Amador-Vargas, S. (2016). Social life

and sanitary risks: evolutionary and current ecological conditions determine waste

management in leaf-cutting ants. Proceedings of the Royal Society of London B: Biological

Sciences, 283, 20160625.

González-Miguéns, R., Muñoz-Nozal, E., Jiménez-Ruiz, Y., Mas-Peinado, P., Ghanavi, H. R. and García-París, M. (2020). Speciation patterns in the *Forficula auricularia* species complex: cryptic and not so cryptic taxa across the western Palaearctic region. Zoological Journal of the Linnean Society, 190, 788–823.

Haig, D. (1990). Brood reduction and optimal parental investment when offspring differ in quality. The American Naturalist, 136, 550–556.

Halffter, G. (1997). Subsocial behavior in Scarabaeinae beetles. In J. Choe and B. Cresspi (Eds.), The Evolution of Social Behaviour in Insects and Arachnids (pp. 237–259). Cambridge, UK: Cambridge University Press.

Hosokawa, T., Kikuchi, Y., Shimada, M. and Fukatsu, T. (2008). Symbiont acquisition alters behaviour of stinkbug nymphs. Biology letters, 4, 45–48.

Itoh, H., Tago, K., Hayatsu, M. and Kikuchi, Y. (2018). Detoxifying symbiosis: Microbe-mediated detoxification of phytotoxins and pesticides in insects. Natural Product Reports, 35, 434–454.

Jackson, D. E. and Hart, A. G. (2009). Does sanitation facilitate sociality? Animal Behaviour, 77, e1–e5.

Jones, J. C., Fruciano, C., Marchant, J., Hildebrand, F., Forslund, S., Bork, P., Engel, P. and Hughes, W. O. H. (2018). The gut microbiome is associated with behavioural task in honey bees. Insectes Sociaux, 65, 419–429.

Kölliker, M. (2007). Benefits and costs of earwig (*Forficula auricularia*) family life. Behavioral

   Ecology and Sociobiology, 61, 1489–1497.

Kopanic, R. J., Holbrook, G. L., Sevala, V. and Schal, C. (2001). An adaptive benefit of facultative

   coprophagy in the German cockroach Blattella germanica. Ecological Entomology, 26, 154–

   162.

Körner, M., Diehl, J. M. and Meunier, J. (2016). Growing up with feces: benefits of allo-

   coprophagy in families of the European earwig. Behavioral Ecology, 27, 1775–1781.

Kramer, J., Körner, M., Diehl, J. M., Scheiner, C., Yüksel-Dadak, A., Christl, T., Kohlmeier, P. and

   Meunier, J. (2017). When earwig mothers do not care to share: Parent-offspring

   competition and the evolution of family life. Functional Ecology, 31, 2098–2107.

Kramer, J., Thesing, J. and Meunier, J. (2015). Negative association between parental care and

   sibling cooperation in earwigs: a new perspective on the early evolution of family life?

   Journal of Evolutionary Biology, 28, 1299–1308.

Lamb, R. J. (1976). Parental behaviour in the Dermaptera with special reference to *Forficula*

   *auricularia*. The Canadian Entomologist, 108, 609–619.

Mas, F., Haynes, K. F. and Kölliker, M. (2009). A chemical signal of offspring quality affects

   maternal care in a social insect. Proceedings of the Royal Society of London B: Biological

   Sciences, 276, 2847–53.

Mas, F. and Kölliker, M. (2011). Differential effects of offspring condition-dependent signals on

   maternal care regulation in the European earwig. Behavioral Ecology and Sociobiology, 65,

341–349.

Meunier, J. (2015). Social immunity and the evolution of group living in insects. Philosophical Transactions of the Royal Society B: Biological Sciences, 370, 20140102.

Meunier, J. and Kölliker, M. (2012). When it is costly to have a caring mother: food limitation erases the benefits of parental care in earwigs. Biology Letters, 8, 547–550.

Meunier, J., Wong, J. W. Y., Gómez, Y., Kuttler, S., Röllin, L., Stucki, D. and Kölliker, M. (2012). One clutch or two clutches? Fitness correlates of coexisting alternative female life-histories in the European earwig. Evolutionary Ecology, 26, 669–682.

Mirabito, D. and Rosengaus, R. B. (2016). A double-edged sword? The cost of proctodeal trophallaxis in termites. Insectes Sociaux, 63, 135–141.

Moran, N. A., Ochman, H. and Hammer, T. J. (2019). Evolutionary and ecological consequences of gut microbial communities. Annual Review of Ecology and Systematics, 50, 20.1-20.25.

Nalepa, C. A. (2015). Origin of termite eusociality: trophallaxis integrates the social, nutritional, and microbial environments. Ecological Entomology, 40, 323–335.

Nalepa, C. A. (2020). Origin of Mutualism Between Termites and Flagellated Gut Protists: Transition From Horizontal to Vertical Transmission. Frontiers in Ecology and Evolution, 8, 1–15.

Nalepa, C. A., Bignell, D. E. and Bandi, C. (2001). Detritivory, coprophagy, and the evolution of digestive mutualisms in Dictyoptera. Insectes Sociaux, 48, 194–201.

Nilsson, C. (1983). Coprophagy in larval Culiseta bergrothi (Diptera: Culicidae). Hydrobiologia,

98, 267–269.

R Core Team. (2017). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Ratz, T., Kramer, J., Veuille, M. and Meunier, J. (2016). The population determines whether and how life-history traits vary between reproductive events in an insect with maternal care. Oecologia, 182, 443–452.

Rozen, D. E., Engelmoer, D. J. P. and Smiseth, P. T. (2008). Antimicrobial strategies in burying beetles breeding on carrion. Proceedings of the National Academy of Sciences of the United States of America, 105, 17890–5.

Schmid-Hempel, P. (2017). Parasites and Their Social Hosts. Trends in Parasitology, 33, 453–462.

Staerkle, M. and Kölliker, M. (2008). Maternal food regurgitation to nymphs in earwigs (*Forficula auricularia*). Ethology, 114, 844–850.

Thesing, J., Kramer, J., Koch, L. K. and Meunier, J. (2015). Short-term benefits, but transgenerational costs of maternal loss in an insect with facultative maternal care. Proceedings of the Royal Society of London B: Biological Sciences, 282, 20151617.

Thomson, D. (1934). Some adaptations for the disposal of faeces. The hygiene of the nest in Australian birds. Proc Zool Soc Lond, 104, 701–708.

Tourneur, J.-C. and Meunier, J. (2020). Variations in seasonal (not mean) temperatures drive rapid adaptations to novel environments at a continent scale. Ecology, 101, e02973.

Van Meyel, S., Devers, S., Dupont, S., Dedeine, F. and Meunier, J. (2021). Alteration of gut

microbiota with a broad-spectrum antibiotic does not impair maternal care in the

European earwig. Journal of Evolutionary Biology, jeb.13791.

Van Meyel, S., Devers, S. and Meunier, J. (2019). Love them all: Mothers provide care to foreign

eggs in the *European earwig Forficula auricularia*. Behavioral Ecology, 30, 756–762.

Vogelweith, F., Körner, M., Foitzik, S. and Meunier, J. (2017). Age, pathogen exposure, but not

maternal care shape offspring immunity in an insect with facultative family life. BMC

Evolutionary Biology, 17, 69.

Wang, G. H., Berdy, B. M., Velasquez, O., Jovanovic, N., Alkhalifa, S., Minbiole, K. P. C. and

Brucker, R. M. (2020). Changes in microbiome confer multigenerational host resistance

after sub-toxic pesticide exposure. Cell Host and Microbe, 27, 213-224.e7.

Wei, G., Lai, Y., Wang, G., Chen, H., Li, F. and Wang, S. (2017). Insect pathogenic fungus

interacts with the gut microbiota to accelerate mosquito mortality. Proceedings of the

National Academy of Sciences of the United States of America, 114, 5994–5999.

Weiss, M. R. (2003). Good housekeeping: why do shelter-dwelling caterpillars fling their frass?

Ecology Letters, 6, 361–370.

Weiss, M. R. (2006). Defecation behavior and ecology of insects. Annual review of entomology,

51, 635–61.

Wirth, T., Guellec, R. Le, Vancassel, M. and Veuille, M. (1998). Molecular and reproductive

characterization of sibling species in the european earwig (*Forficula auricularia*). Evolution,

52, 260.

Wong, J. W. Y., Lucas, C. and Kölliker, M. (2014). Cues of maternal condition influence offspring
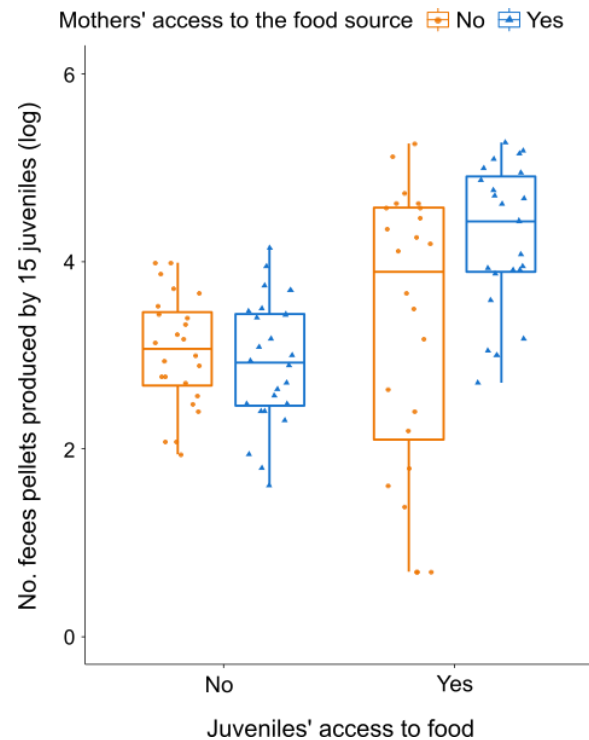
selfishness. PloS one, 9, e87214.

**Table 1** – Statistical overview of the effects of juveniles' or mothers' access to a food source during family life on (a) the number of feces pellets produced by nymphs, (b) the likelihood of maternal coprophagy, as well as (c) the proportion and (d) number of feces pellets eaten by mothers. Significant p-values are in bold. LR = Likelihood Ratio.

| | (a) No. feces pellets produced by nymphs | | (b) Likelihood of maternal coprophagy | | (c) Proportion of nymphs' feces eaten by mothers | | (d) No. nymphs' feces eaten by mothers | |
|---|---|---|---|---|---|---|---|---|
| | $F_{1,91}$ | P | LR $\chi^2_1$ | P | LR $\chi^2_1$ | P | $F_{1,42}$ | P |
| Juveniles | 16.25 | **0.0001** | 5.99 | **0.014** | 1.38 | 0.240 | 12.28 | **0.001** |
| Mothers | 4.07 | **0.047** | 0.39 | 0.532 | 20.65 | **<0.001** | 1.57 | 0.217 |
| Interaction | 7.57 | **0.007** | 1.50 | 0.220 | 3.18 | 0.075 | 3.87 | 0.056 |
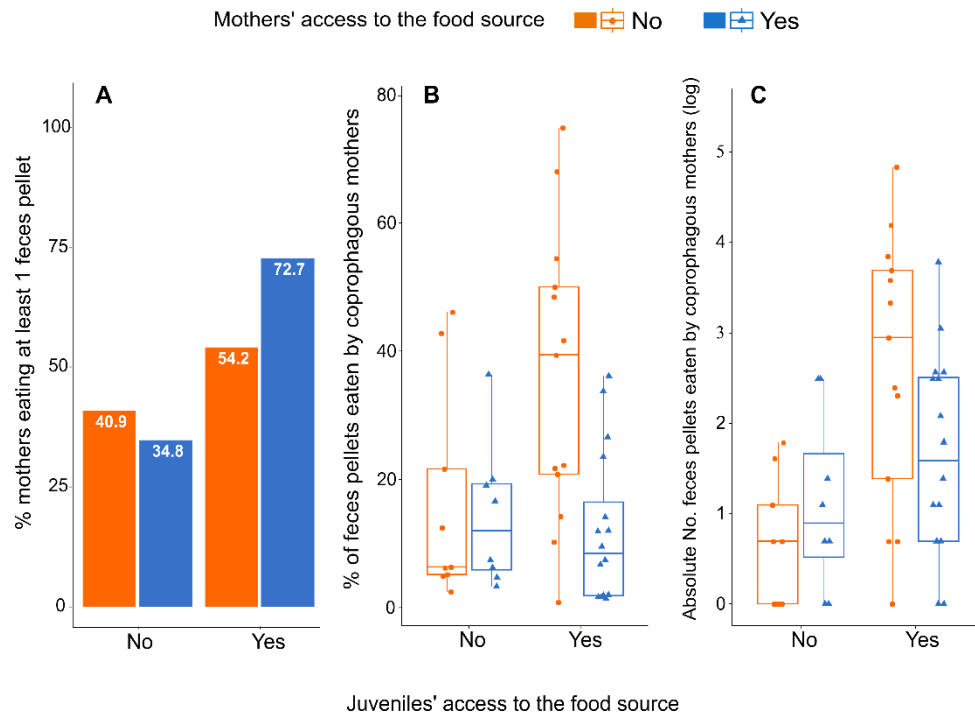
**Figure 1 -** Effect of juveniles' or mothers' access to food during family life on the (a) likelihood of mothers to eat at least one nymphs' feces pellet, (b) proportion of nymphs' feces pellet eaten by a coprophagous mother and on the (c) absolute number of nymphs' feces pellet eaten by a coprophagous mother over 2h. Boxplots depict median and interquartile range, with whiskers extending to 1.5 times the interquartile range and dots representing experimental values.

**Figure 2** - Effects of juveniles' or mothers' access to a food source during family life on the number of feces pellets produced by fifteen juveniles over 14h. Boxplots depict median and interquartile range, with whiskers extending to 1.5 times the interquartile range and dots representing experimental values.