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Parental antagonism and parent–offspring co-adaptation interact to shape family life

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The family is an arena for conflicts between offspring, mothers and fathers that need resolving to promote the evolution of parental care and the maintenance of family life. Co-adaptation is known to contribute to the resolution of parent–offspring conflict over parental care by selecting for combinations of offspring demand and parental supply that match to maximize the fitness of family members. However, multiple paternity and differences in the level of care provided by mothers and fathers can generate antagonistic selection on offspring demand (mediated, for example, by genomic imprinting) and possibly hamper co-adaptation. While parent–offspring co-adaptation and parental antagonism are commonly considered two major processes in the evolution of family life, their co-occurrence and the evolutionary consequences of their joint action are poorly understood. Here, we demonstrate the simultaneous and entangled effects of these two processes on outcomes of family interactions, using a series of breeding experiments in the European earwig, *Forficula auricularia*, an insect species with uniparental female care. As predicted from parental antagonism, we show that paternally inherited effects expressed in offspring influence both maternal care and maternal investment in future reproduction. However, and as expected from the entangled effects of parental antagonism and co-adaptation, these effects critically depended on postnatal interactions with caring females and maternally inherited effects expressed in offspring. Our results demonstrate that parent–offspring co-adaptation and parental antagonism are entangled key drivers in the evolution of family life that cannot be fully understood in isolation.

Keywords: facultative parental care; parental investment; food provisioning; conflicts; insect; *Forficula auricularia*

1. INTRODUCTION

Parental care is an important source of conflicts between offspring and parents due to asymmetries in the benefits of care to offspring and the costs of care to parents (e.g. in terms of individual future reproduction [1–4]). Parent–offspring co-adaptation is an evolutionary mechanism known to contribute to the resolution of parent–offspring conflict over parental care by selecting for combinations of offspring demand and parental supply that match to maximize the fitness of family members [5,6]. Co-adaptation occurs because individuals adapt to the parental supply when they are offspring and to the demand they inherit to their own offspring when they are parent [4–7].

Whereas parent–offspring co-adaptation is considered an important process in the evolution of family interactions [4,8,9], it remains unclear to what extent co-adaptation can operate when the two parents exhibit asymmetries in their investment or relatedness towards current offspring (e.g. due to multiple paternity), both of which commonly characterize animal mating systems [10]. For instance, the exclusive interaction between mothers (the caring parent in many taxa) and offspring in uniparental families frees fathers from the pressure to adapt to offspring demand and consequently excludes fathers and paternally inherited effects expressed in offspring from the co-adaptation process [11]. Furthermore, when multiple males sire the progeny of a female, parental antagonism is predicted to select for parent-of-origin specific inheritance mechanisms (e.g. through genomic imprinting [9,12,13] as shown in humans and mice [14–18]), which potentially hamper mother–offspring co-adaptation by preventing females from adapting to an offspring demand mainly shaped by paternally inherited effects [5,6]. In such families, paternally inherited genes expressed in offspring are predicted to selfishly exaggerate offspring demand because siblings are not equally related from their paternal-side and the different patrilines compete among each other for access to the provided maternal care. Conversely, maternally inherited genes expressed in offspring are predicted to limit the level of offspring demand because females suffer from the costs of exaggerated offspring demand and have siblings that are equally related from their maternal side [9]. While a growing number of experimental and theoretical studies show that parental antagonism and parent–offspring co-adaptation are keystones in the evolution of family life [4,8,9], little is known about their simultaneous effects within families and its consequence on family interactions.

Unravelling the simultaneous effects of co-adaptation and parental antagonism on family life requires manipulating the potential sources of conflict by forming families with alternative combinations of maternal, paternal and offspring strategies. A powerful experimental method is to conduct cross-breeding and cross-fostering [7,19,20] using individuals from a population where both evolutionary processes can fully operate to generate

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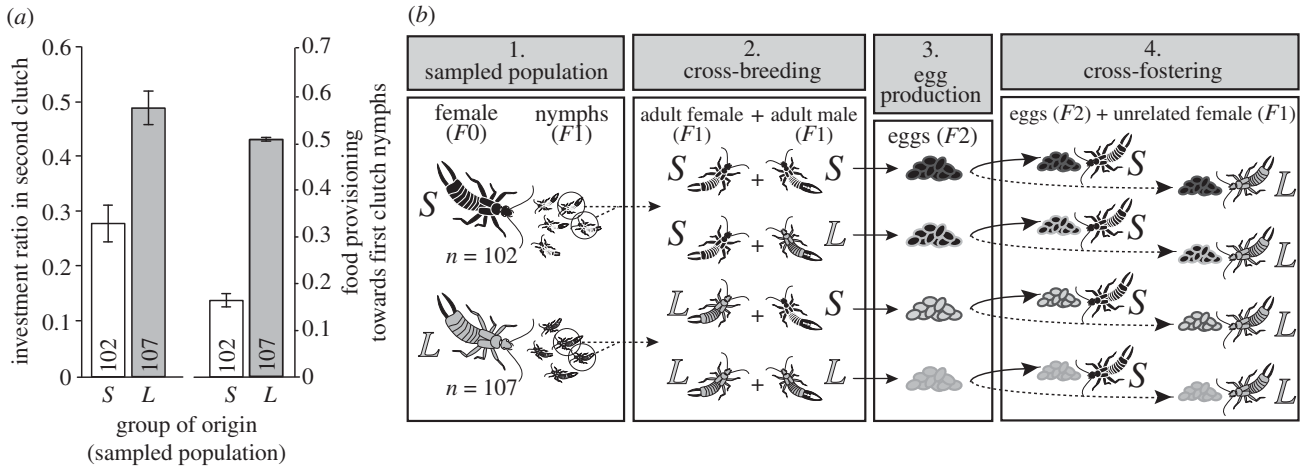

Figure 1. Natural variation in earwig family life and experimental design. (*a*) When compared with *S*-group individuals, *L*-group ones had mothers that exhibited larger investment in second clutch (egg number in second clutch divided by total egg number; Welch *t*-test, $t_{113.5} = 23.4$, $p < 0.0001$) and larger food provisioning (ratio of nymphs that get food from their mother 7 days after hatching; Welch *t*-test, $t_{125.7} = 4.70$, $p < 0.0001$). Error bars represent SEM. Sample size is at the bottom of each bar. (*b*) Details of the experimental design.

or maintain variation in family life. The European earwig, *Forficula auricularia*, is an ideal biological model to disentangle the effects of parental antagonism and mother–offspring co-adaptation on family life. In this species, females do not discriminate between their own and foreign nymphs, mate multiply, protect their eggs and nymphs against natural enemies and provide food to their young during approximately two weeks after hatching [21,22]. Furthermore, this species exhibits ample natural variation in family traits such as female investment in future reproduction (production of either one or two clutches during lifetime [22]) and level of food provisioning towards first clutch nymphs [22,23], which may be shaped by co-adaptation and parental antagonism.

In this study, we carried out a series of cross-breeding and cross-fostering experiments between two groups of earwigs that exhibit potential alternative outcomes of co-adaptation and/or parental antagonism [22]. The selected individuals were offspring from females sampled in a single natural population and exhibiting either small (*S*-group) or large (*L*-group) investment in the second clutch (figure 1*a*). These groups were also characterized by small and large levels of food provisioning towards first clutch nymphs, respectively (figure 1*a*). Scope for conflicts was manipulated by setting up eight types of experimental families wherein the origins of foster mothers (OFM) and of genetic mothers (OGM) and genetic fathers (OGF) of offspring form all possible matched and mismatched combinations of *S*- and *L*- origins (figure 1*b*). Maternal care and fitness correlates of mothers and offspring were then measured in these families.

Under the mother–offspring co-adaptation hypothesis, an interaction between OFM and OGM is predicted to significantly influence the measured traits, with lower values of maternal care and fitness correlates in mismatched than matched combinations [4,24]. Conversely, under the parental antagonism hypothesis, OGM, OGF and/or an interaction between these two factors (indicative of intragenomic epistasis [9,12]) are expected to significantly influence the measured values of maternal care and fitness correlates of mothers and offspring. For instance, if fathers control the level of maternal care through paternally inherited offspring effects (mediated e.g. through genomic imprinting), offspring sired by fathers from *L*-groups (OGF-*L*) are expected to receive more food than offspring sired by fathers from *S*-group (OGF-*S*). Finally, under the simultaneous and entangled effects of mother–offspring co-adaptation and parental antagonism, a two-way interaction between OFM and OGF (indicative of social epistasis [7,25]) or a three-way interaction between OFM, OGM and OGF are predicted to significantly influence our measurements. Overall, our results demonstrate that co-adaptation and parental antagonism are entangled key drivers of family interactions that cannot be fully understood in isolation.

2. MATERIAL AND METHODS

(a) *The study animals*

Males and females used for the breeding design were a first laboratory-born generation (*F*1) of *F. auricularia* (figure 1*b*). They were the offspring of 209 earwig *F*0 females (out of a total of 492 used in another experiment [22]) collected as fourth instars nymphs or newly emerged adults in early June 2009 in a natural population located in Dolcedo, Italy. The laboratory rearing of earwigs is detailed in [22]. Briefly, *F*0 females were set up in plastic containers and reared under standardized laboratory conditions, where they randomly mated with males sampled at the same location. Approximately three months after setup, these females were isolated in Petri dishes (10 × 2 cm) to induce clutch production. Fourteen days after hatching of the first clutch of each female, 20 nymphs per family were isolated in new Petri dishes (= first-clutch families) and reared until adulthood, while the mothers were setup in new Petri dishes to allow second-clutch production. Upon the emergence of *F*1 adults, brothers and sisters from each first clutch were separated to prevent sib-mating. After the 492 *F*0 mothers produced a second clutch or were characterized as single-clutch females (females are unlikely to produce additional clutches 60 days after the

hatching of their first clutch [26]), *F*1 adults of the first-clutch families were assigned to two experimental groups, depending on their mother's relative investment in second clutches, as being in the bottom third (*S*-groups, including both single- and double-clutch producers) or in the top third (*L*-groups, including only double-clutch producers) of the distribution (each group includes 164 families, figure 1*a*). This relative investment, which is the number of eggs produced in second clutch divided by the total number of eggs produced, measures how mothers invested in second relative to first reproduction, while controlling for their overall capacity of egg production.

(b) *Cross-breeding and cross-fostering*

The experimental design is detailed in figure 1*b*. The reciprocal breeding took place approximately one month after the emergence of *F*1 adults and involved individuals originating from 102 *S*-groups and 107 *L*-groups (among which 127 contributed to the experiment with both one male and one female, and 82 with either one male or one female). It was conducted by placing each virgin *F*1 female with one unrelated virgin *F*1 male in Petri dishes containing humid sand, a plastic shelter used as a nest and ad libitum artificial diet (see food composition in [22]). Mating pairs were assigned according to a full-factorial design with males/females being either *L*/*L* ($n = 37$), *L*/*S* ($n = 44$), *S*/*L* ($n = 40$) or *S*/*S* ($n = 48$), see figure 1*b*. Each pair was allowed to freely mate for three months, while their Petri dishes were maintained in a climatic chamber with 14 : 10 h/20 : 15°C light:dark photoperiod cycle. Females were then isolated, placed in complete darkness at 10°C for one week, and then in complete darkness at 15°C conditions until egg-laying and hatching.

Approximately two days after *F*1 females laid their first clutch, we cross-fostered eggs among them to obtain all possible combinations between OGM, OGF and OFM, i.e. a total of eight combinations (figure 1*b*). Foster mothers were always unrelated to the tended eggs. Each of the eight combinations contained mean ± s.e. = 21.1 ± 0.9 replicates. To ensure a balanced experimental design, each combination involved an equal number of foster mothers previously mated with males from *S*- and *L*-groups. To limit handling stress on females, eggs were transferred while females remained in their original Petri dish. No food was provided from egg-laying to hatching [22]. From day 1 after hatching to day 14, Petri dishes received ad libitum artificial diet every other day and were kept under 14 : 10 h light : dark photoperiod and a constant temperature of 20°C. At day 14, mothers were individually setup in new Petri dishes, where they had the possibility to produce a second clutch within the next 46 days (resulting in the total maximal interval of 60 days after hatching of first clutches; see above).

(c) *Measurements*

A total of five measures were taken on nymphs and mothers using standard procedures [22]. The number of eggs and nymphs produced in the first clutch of each female was counted 1 day after egg-laying and hatching, respectively. Foster mothers that did not lay a second clutch within the 60 days following the hatching of their first clutch were defined as single-clutch producers [22]. The survival rate of first clutch nymphs was calculated as the number of nymphs alive at day 14 divided by the total number of nymphs at hatching. The developmental time for first clutch nymphs was estimated by counting the number of days from hatching to the first observation of a second instars nymph in a clutch, a good measure of mean developmental time of the entire brood [22]. Finally, food provisioning towards first clutch nymphs was estimated using four successive steps that started at day 5 and consisted in (i) food depriving mothers and nymphs for 24 h, (ii) isolating females for 1 h while offering them green-coloured food, (iii) putting each female back in contact with 20 of its foster nymphs for 15 h, and (iv) calculating the proportion of nymphs with green gut [22,27]. The actual number of nymphs tended by foster mothers was not significantly correlated with our measure of food provisioning to the 20 nymphs (Pearson correlation test, $r = -0.053$, $p = 0.51$). Food provisioning could not be quantified in two cases owing to the small number of nymphs in the clutch (two and three nymphs, respectively), and in six cases that had mistakenly not been food-deprived on day 5.

(d) *Statistical analyses*

The effects of OFM, OGM, OGF and their interactions were tested on the maternal food provisioning, the likelihood of second clutch production by foster mothers, the relative investment of females into second clutch (in females producing a second clutch), as well as on developmental time and early survival rate of offspring using the statistical models described in table 1. Because previous results reported that some of these traits can be sensitive to variation in clutch size [22], this factor was included as covariate in the model of likelihood of second clutch production, where it refers to the number of first-clutch eggs produced by foster mothers, and in the models of developmental time of nymphs and survival rate of nymphs, where it refers to the number of nymphs attended by foster mothers. Clutch size was not entered in the model of food provisioning because the number of nymphs was standardized for food provisioning measurements and does not correlate with initial clutch size, and in the model of relative investment in second clutch as it was part of the response variable. Because of the strong asymmetry between the number of females that produced and did not produce two clutches during our experiments, the model on second-clutch production (likelihood of second clutch production, table 1) was based on a cloglog-link function [28]. All models were tested for overdispersion and corrected using quasi-GLM models when necessary [28]. To allow for a direct comparison of each tested factor across the five analyses, only four- and three-way interactions that were non-significant across all the statistical models were removed (model simplification based on AIC criteria). Note that results do not qualitatively change when models were simplified individually. All statistical analyses were conducted using the software R v. 2.14.0 (http://www.r-project.org/).

3. RESULTS

(a) *Food provisioning*

As predicted under the entangled effects of co-adaptation and parental antagonism, we find that food provisioning depended on the combined influences of OFM, OGM and OGF, a result shown by the significant three-way interaction between these factors (table 1A). Two non-mutually exclusive evolutionary scenarios could underlie this result. First, mother–offspring co-adaptation may protect mothers from paternally inherited offspring

Table 1. Effects of OFM, OGM and OGF on five family performance traits. Significant *p*-values are in bold.

	A		**B**		**C**		**D**		**E**	
	food provisioning		likelihood of second clutch production		relative investment in second clutch[a]		developmental time of nymphs		survival rate of nymphs	
	LR	*p*	LR	*p*	LR	*p*	*F*	*p*	LR	*p*
size of 1st clutch (CS)	—	—	**9.46**	**0.002**	—	—	**24.93**	**<0.0001**	3.35	0.067
origin of foster mothers (OFM)	2.32	0.128	0.11	0.735	0.82	0.365	0.12	0.727	0.64	0.426
origin of genetic mothers (OGM)	0.62	0.431	<0.01	0.950	**4.42**	**0.036**	0.06	0.800	0.01	0.908
origin of genetic fathers (OGF)	**4.16**	**0.041**	0.82	0.365	0.42	0.518	1.79	0.183	1.38	0.240
CS:OFM	—	—	2.60	0.107	—	—	<0.01	0.989	**9.67**	**0.002**
CS:OGM	—	—	1.07	0.301	—	—	1.04	0.310	0.10	0.756
CS:OGF	—	—	3.71	0.054	—	—	**7.54**	**0.007**	0.68	0.410
OFM:OGM	0.62	0.432	0.93	0.334	0.20	0.658	0.51	0.474	<0.01	0.986
OFM:OGF	0.08	0.775	**15.67**	**<0.0001**	0.42	0.517	0.48	0.490	<0.01	0.951
OGM:OGF	<0.01	0.956	<0.01	0.972	1.11	0.293	0.15	0.700	0.02	0.895
CS:OFM:OGF	—	—	0.36	0.549	—	—	1.62	0.205	1.93	0.164
OFM:OGM:OGF	**5.04**	**0.025**	0.67	0.412	0.45	0.501	1.49	0.224	0.46	0.496
type of statistical model d.f. or *n*	Binomial GLM $n = 161$		Binomial GLM $n = 169$		Binomial GLM $n = 144$		GLM d.f. = 1,156		Binomial GLM $n = 169$	

[a]In females that produced two clutches during the experiment.

effects on provisioning. In line with this hypothesis, OGF had no significant effect on food provisioning in families where OFM and OGM matched (figure 2*a*; binomial GLM, $n = 80$; OGF: likelihood ratio, LR, $\chi^2 = 0.13$, $p = 0.72$; OGM: LR, $\chi^2 = 0.69$, $p = 0.41$; interaction: LR, $\chi^2 < 0.01$, $p = 0.99$), whereas offspring sired by *L*-males received significantly more food than nymphs sired by *S*-males in families where OGM and OFM mismatched (figure 2*a*; binomial GLM, $n = 81$; OGF: LR, $\chi^2 = 5.49$, $p = 0.019$; OGM: LR, $\chi^2 = 0.23$, $p = 0.63$; interaction: LR, $\chi^2 = 0.10$, $p = 0.76$). Second, interactions between effects inherited from genetic mothers and genetic fathers may determine if foster mothers or nymphs influence food provisioning, e.g. due to changes in offspring signals or behaviours. Consistent with this prediction, the origin of foster mothers significantly influenced provisioning when nymphs had mismatched maternal and paternal origins (figure 2*b*; binomial GLM, $n = 81$; OFM: LR, $\chi^2 = 6.69$, $p = 0.010$; OGF + OGM: LR, $\chi^2 = 0.67$, $p = 0.41$; interaction: LR, $\chi^2 = 0.15$, $p = 0.70$), whereas nymphs significantly influenced provisioning when they had matched parental origins (figure 2*b*; binomial GLM, $n = 80$; OFM: LR, $\chi^2 = 0.22$, $p = 0.64$; OGF + OGM: LR, $\chi^2 = 4.31$, $p = 0.038$; interaction: LR, $\chi^2 = 0.94$, $p = 0.33$).

(b) *Investment in second clutches*

The likelihood of second-clutch production by foster mothers was affected by the combined effects of OFM and OGF, as shown by a significant interaction between these two factors (table 1B). This result again supports the hypothesis of an entangled effect of co-adaptation and parental antagonism. Foster mothers were less likely to produce a second clutch when they tended nymphs sired by a male with different origin, regardless of the order of mismatching between OFM and OGF ($L + S$ or $S + L$; figure 2*c*), and the likelihood of second-clutch production was not additively inherited across generations (there were no significant main effects of OFM, OGM or OGF; table 1B). Furthermore, in line with the idea that family interactions and intrinsic female condition have independent effects on second-clutch production, we also found that the likelihood of second-clutch production was positively associated with the size of the first clutch produced by foster mothers (table 1B; mean ± s.e. first clutch size; 59.28 ± 2.62 and 65.64 ± 0.70 for one- and two-clutch females, respectively), a pattern previously suggested to reflect variation in female quality [22]. Finally, restricting the analysis to females that produced two clutches in the experiments, we found that their relative investment in second clutches was influenced by OGM. Foster mothers showed significantly larger relative investment when tending offspring produced by females from the *L*-group (number of eggs produced in second clutch divided by the total number of eggs produced: mean ± s.e. = 0.314 ± 0.009, $n = 70$) than from the *S*-group (0.292 ± 0.009, $n = 74$; table 1C). This relative investment was not significantly influenced by OFM, OGF or any of the interactions among factors (table 1C).

(c) *Offspring development and survival*

Our results revealed that interactions between OFM, OGM and OGF did not significantly influence the developmental time and the survival rate of offspring (table 1D,E), two traits not significantly correlated to

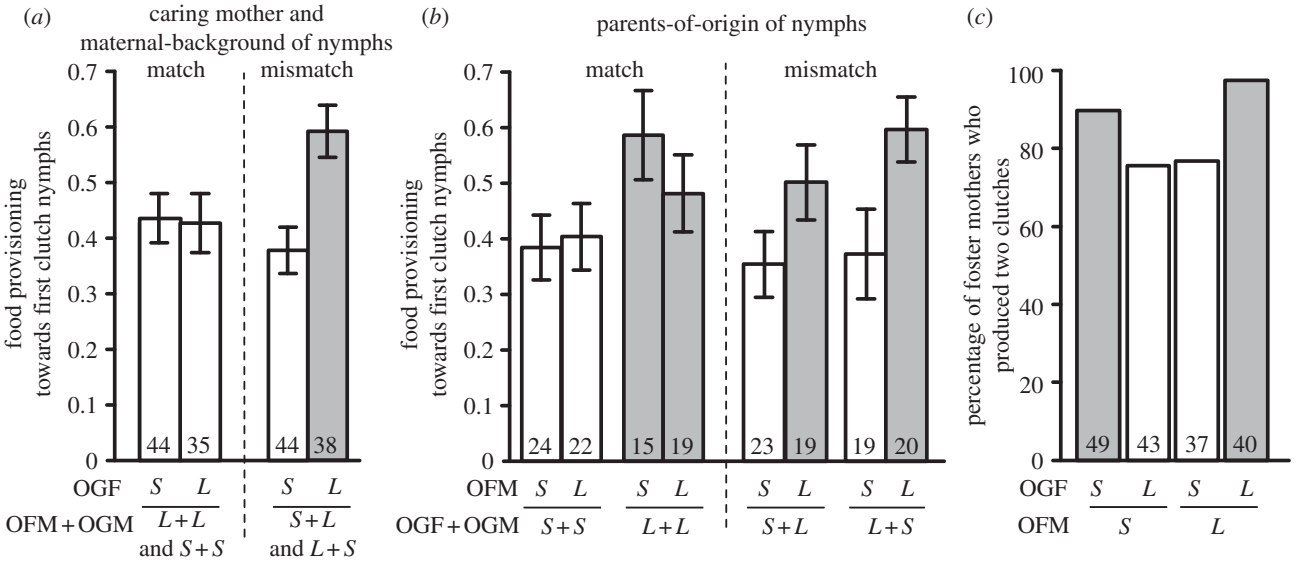

Figure 2. Food provisioning and likelihood of second clutch production by foster mothers. (*a*) OGF significantly influenced food provisioning in families where OFM and OGM mismatched, but not in families where OFM and OGM matched. (*b*) When nymphs had matched maternal and paternal genetic origins, nymphs with both *L*-origins received significantly more food than nymphs with both *S*-origins, independently from the origin of foster mothers. By contrast when nymphs had mismatched maternal and paternal genetic origins, nymphs from the two possible combinations received significantly more food when reared by foster mothers from *L*- than *S*-origins. (*c*) The proportion of females producing two clutches was significantly smaller when OFM and OGF mismatched than matched (*grey* versus *white* bars, $\chi^2 = 9.67$, $p = 0.002$). Error bars represent SEM in (*a*) and (*b*). Sample size is at the bottom of each bar.

each other (Spearman correlation test, $r_s = -0.13$, $p = 0.10$). Nevertheless, developmental time was significantly influenced by an interaction between OGF and clutch size (table 1D), with a positive correlation between developmental time and clutch size only in clutches sired by *S*-males (figure 3*a*); and offspring survival rate was significantly influenced by an interaction between OFM and clutch size (table 1E), due to a negative correlation between survival rate and clutch size only in clutches tended by *L*-foster mothers (figure 3*b*).

4. DISCUSSION

Our findings showed that post-natal interactions between mothers and offspring influenced maternal care and female future reproduction. This result confirms a little tested main assumption in all evolutionary models on parental antagonism, conflict resolution and co-adaptation [6,29], and reveals that offspring not only influence maternal care behaviours, but can also exert selection pressure on the caring females. Uniquely, we demonstrated that parental antagonism and co-adaptation have simultaneous and entangled effects on family interaction outcomes. In particular, we found that (i) the level of food provisioning reflected the combined influence of caring females, genetic mothers and genetic fathers of nymphs; (ii) the likelihood of second-clutch production by caring females resulted from the entangled effects of caring females and genetic fathers of nymphs; (iii) the relative investment of foster mothers in second clutch was shaped by the genetic mothers of nymphs, and finally that (iv) caring mothers and genetic fathers of nymphs independently influenced the developmental time and the survival rate of offspring.

We showed that parent-of-origin specific effects expressed in offspring mediated how nymphs influenced female traits (figure 2), a result predicted under parental antagonism and genomic imprinting [30]. Interestingly, however, we found that parental antagonism did not only occur through interactions between paternally and maternally inherited effects expressed in offspring (as predicted by the kinship theory of genomic imprinting [14–17]), but also through postnatal interactions between paternally inherited effects expressed in offspring and the caring females (a result in line with intergenomic social epistasis [7,25]). Such social epistasis between the caring female and the genetic father of offspring could generate correlational selection on these two family members [31], because matched origins of caring female and genetic father of nymphs (in terms of *S*- and *L*-groups) increased the female's likelihood of second-clutch production. If strong enough and sufficiently consistent over time and across environmental conditions, this correlational selection based on the resolution of family conflicts could favour assortative mating within populations and, ultimately, lead to speciation of individuals from *S*- and *L*-groups [32,33]. Interestingly, a previous study suggested that single and double-brooded earwigs (collected in separate populations) may correspond to two cryptic sister species in *F. auricularia* [34]. However, the support for this suggestion remains limited and our recent work demonstrates full mating compatibility between these two types of individuals (co-occurring within a same population) (see this study and [22]). Another possibility is that the populations remain panmictic, for instance, if no mechanism for assortative mating evolves. In this case, the occurrence of mismatched matings would contribute to the maintenance of variation in family interaction outcomes (as observed in the studied population [22]), thereby limiting long-term resolution of family conflicts. Disentangling these two evolutionary hypotheses requires tests for the presence of cues possibly

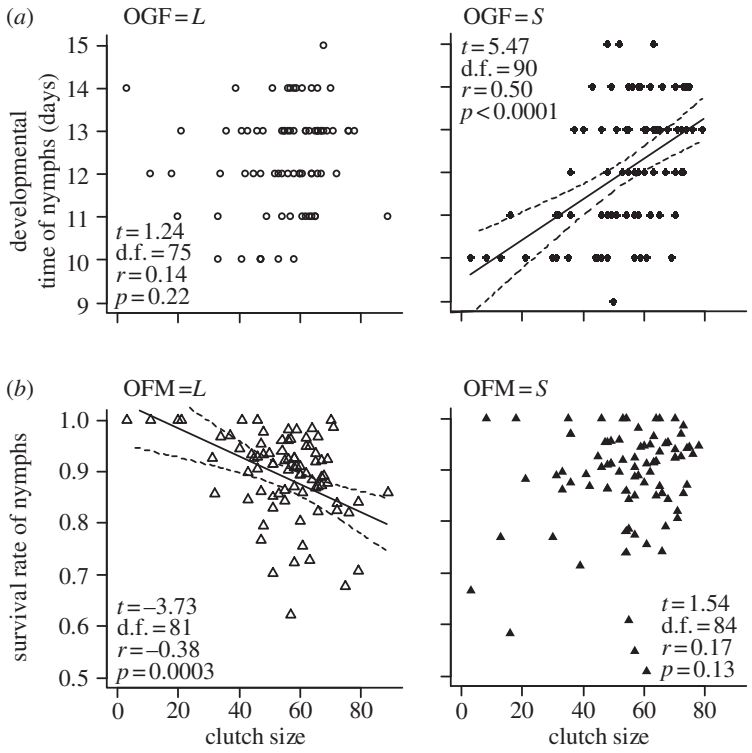

Figure 3. Developmental and survival rate of nymphs. (*a*) Nymph developmental time (number of days until the emergence of a second instars nymph in a clutch) was significantly sensitive to clutch size variation only when *S*-males sired the nymphs. (*b*) Nymph survival rate was significantly sensitive to clutch size variation only when *L*-mothers tended the clutches. Significant regression lines (filled lines) are shown with 95% confidence intervals (dashed lines). Pearson's correlation tests are reported.

involved in group recognition (e.g. chemical signatures [35]), as well as the occurrence of assortative mating and non-random fertilization between individuals from *S*- and *L*-groups.

Neither food provisioning nor second-clutch production was additively inherited from mothers to adult daughters. In particular, the non-significant main effect of OFM on these two traits measured on the females themselves indicates that the environment in which the foster mothers grew up as a nymph (and which is correlated with food provisioning and investment in second clutches, figure 1*a*) and/or the genes inherited from their parents did not predict (alone) second-clutch production and level of food provisioning (table 1A,B). Instead, our results reveal that the environment experienced by females and males as nymphs influences both the strategy they will later transmit to their own nymphs and how the newly produced mothers will react to such offspring strategy (in terms of food provisioning and second-clutch production). The above effects on female nymphs could be due to maternal effects transmitted to the eggs or to the young ones through family interactions, as reported in rats where pups experiencing low levels of care become mothers providing little care irrespective of their genotype [36]. Because fathers are absent during parental care, the above effect on male nymphs is likely to result from epigenetic sperm modification by early-life environments, for example, through induced mutations in DNA sequences, changes in the content of male ejaculate or epigenetic modifications in the male germline [37,38]. The molecular mechanism underlying the parent-of-origin specific effects reported in this study is currently unknown, but the observed patterns of inheritance are consistent with a role for genomic imprinting.

In contrast to the results on maternal traits, we found that cross-fostered offspring did not suffer from mismatched combinations of OFM, OGM or OGF in terms of developmental time and survival rate. The observed discrepancy in the effects of family mismatch on offspring and maternal traits suggests that parent–offspring co-evolution mediated by parental antagonism and co-adaptation is primarily driven by selection through the costs of care to females, rather than the benefits of care to offspring [4]. Nevertheless, we found that parents influenced alternative traits in offspring: genetic fathers influenced offspring sensitivity to clutch size in terms of developmental time (only the nymphs sired by *S*-males were sensitive), whereas foster mothers affected offspring sensitivity to clutch size in terms of survival rate (only the nymphs cared by *L*-females were sensitive). These parent-specific effects on two uncorrelated offspring traits reveal scope for antagonistic co-evolution between the sexes [19,39] over the control of offspring performance, in that a potential positive effect of fathers on offspring fitness (the developmental time of nymphs was not sensitive to clutch size when OGF was *L*) is counterbalanced by a potential negative effect of mothers (the survival rate of nymphs was sensitive to clutch size when OFM was *L*).

Over the past two decades, models of parental antagonism in animals mostly have been tested in placental species [9,13,17–19,40,41], although from a theoretical perspective selection for parent-of-origin specific effects applies more generally. By demonstrating parentally antagonistic effects in an insect species with basal and non-obligate forms of maternal care, our results

emphasize that the evolution of parent-of-origin specific inheritance does not require intricate and obligate interactions between parents and offspring, for instance through a placenta.

In conclusion, our study demonstrates that parental antagonism and parent–offspring co-adaptation act as entangled key drivers of family interactions, even in species with facultative forms of care. This finding highlights the importance to consider these two major evolutionary processes together rather than in isolation to get a better understanding of the mechanisms regulating family interactions and promoting the evolution of social life [11,19,42]. Furthermore, our results demonstrate that the early-life social environment of offspring shape the strategy they later adopt as parents but also that they transmit to their own offspring. As a consequence the nature of mother–offspring interactions can be both cause and consequence of heritable variation in parental and offspring strategies (including the fitness of family members), providing an example for the importance of reciprocal causation in evolutionary biology.

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