Love them all: mothers provide care to foreign eggs in the European earwig *Forficula auricularia*

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ABSTRACT

The rejection of foreign individuals is considered a central parameter in the evolution of social life. Within family units, parents are typically thought to reject foreign offspring to ensure that their investment into care is directed towards their own descendants. Whereas selection for such kin bias is expected to be high when parental care is extended and involves numerous and energetically costly behaviours, it can be reduced when the acceptance of foreigners provide subsequent benefits to offspring and when alternative parental strategies limit the risk of clutch parasitism. In this study, we investigated the outcome of these conflicting selection pressures in the European earwig. Our results overall demonstrate that mothers do not eliminate foreign eggs, provide the same level of care to both foreign and own eggs (egg grooming, egg defense and maternal return) and pay the same costs of care in terms of weight loss and immunity when tending each type of eggs. We also show that foreign and own eggs exhibit similar development time, hatching success and lead to comparable juvenile quality. Interestingly, our results reveal that tending eggs (of any origin) reduces mothers' weight loss during this long period, possibly due to egg cannibalism. Hence, these findings emphasize the difficulty to predict the occurrence of kin bias, and stress the need to broaden our knowledge on the net benefits of egg rejection for parents to better understand the general importance of kin bias in the evolution of pre-hatching parental care.

Keywords: Parental care, Egg recognition, Kin discrimination, Kin recognition, Dermaptera, Social insect

1-INTRODUCTION

The capability of an individual to reject unrelated conspecifics is often considered a hallmark of the evolution of cooperation and group living (Tang-Martinez 2001; Penn and Frommen 2010). This is because such form of kin bias can enhance the direct and/or indirect fitness of donor individuals by allowing them to direct costly cooperative behaviors to recipient individuals sharing (at least) some of their genes (Hamilton 1964). Examples of kin bias can be found across a large number of species and contexts, ranging from colony defense in Belding's ground squirrels and eusocial insects (Sherman 1977; Polizzi and Forschler 1999; Duffy et al. 2002; Meunier et al. 2011), over matrilineal kinship in hierarchies of Japanese monkeys (Kawai 1958; Kawamura 1958), to cooperative courtship in the wild turkey (Krakauer 2005).

Parental care is one of the main contexts in which kin bias is expected to evolve. Parental care is a taxonomically widespread phenomenon, and involves a broad diversity of processes, such as the defense of eggs and juveniles against predators and pathogens, as well as the provisioning of juveniles with food (Royle et al. 2012; Kramer and Meunier 2018). While these processes typically enhance offspring development and likelihood to reach adulthood (see Royle et al. 2012 for review), parental care come with significant costs for parents: Investing into care can increase parents' energetic expenditure and risk of predation, both of which ultimately reduce parental investment into future reproduction (Trivers 1972; Alonso-Alvarez and Velando 2012). Evolving the capability to

reject foreign offspring may thus help parents optimizing the fitness returns of their investment into care by ensuring that it is directed at their own offspring (Hamilton 1964).

Several parameters, however, may inhibit the evolution of kin bias in family living species (Penn and Frommen 2010). For instance, kin bias typically comes with an important risk of error for parents (rejecting their own offspring), so that it is expected to evolve only when parents have a high likelihood to encounter foreign offspring in their nest, e.g. due to heterospecific or conspecific clutch parasitism (Tallamy 2005). Kin selection may also inhibit kin bias and promote the acceptance of foreign offspring when clutch parasitism is primarily done by related conspecifics, e.g. in populations where individuals exhibit low dispersal capabilities (Hatchwell and Komdeur 2000). Selection for kin bias may also be relaxed if the net costs of care are low for parents, e.g. if care mostly involves passive processes such as thermal protection (Klug and Bonsall 2014). Finally, a relaxed selection for kin bias may occur if the net costs of care for parents are outweighed by direct benefits of tending larger clutches, e.g. if it reduces the risk of predation of their own offspring through a dilution effect (Krause and Ruxton 2002). Investigating the presence (or absence) of kin bias in family living species may thus offer a unique opportunity to shed light on the effects of the above parameters on the expression of parental care, and more generally, on their importance in the evolution of complex family systems (Hatchwell and Komdeur 2000; Samuk and Avilés 2013).

Whereas females of the European earwig *Forficula auricularia* provide extended and complex forms of care to their eggs (Lamb 1976), it remains unclear whether mothers accept foreign eggs and/or adjust their level of care to egg origin. In this insect, each female constructs a burrow during late autumn, in which they take 1 to 3 days to produce a first clutch of about 40 eggs (Boos et al. 2014; Koch and Meunier 2014; Ratz et al. 2016; Diehl and Meunier 2018). Females remain with their eggs for the subsequent 1-2 months, during which they provide multiple forms of egg care. This includes, for instance, the removal of fungal spores from the egg shell, the application of chemical protection against desiccation through egg grooming, the relocation of the clutch under stressful conditions, and a fierce protection against predators (Boos et al. 2014; Koch and Meunier 2014; Diehl and Meunier 2018). Egg care is likely to be costly for females, as they typically stop their foraging activity between egg laying and hatching (Kölliker 2007) and thus only have severely limited resources to spend on both their own survival and egg care for several months. Whereas the presence of conspecific clutch parasitism is unknown in this species, several parameters suggest that it can be present. First, populations have high densities (Moerkens et al. 2009) and exhibit great inter-individual variation in the timing of egg production, with late females laying eggs more than 1 month after early ones (Meunier et al. 2012; Ratz et al. 2016). Tending mothers are thus likely to encounter conspecific females looking for a burrow to lay their eggs (and possibly to parasitize). Moreover, females retain the capability to produce a replacement clutch after a few days if they lose their eggs (J Meunier, pers. obs.), which could be used to replace foreign eggs with their

own ones if the occasion arose (e.g. if females eliminate all eggs of their parasitized clutch). Whether this capability evolved as a strategy to combat conspecific clutch parasitism is, however, unknown.

In this study, we investigated whether *F. auricularia* mothers discriminate against foreign conspecific eggs. In particular, we tested whether females eliminate foreign eggs or alter the level of care they provide to these eggs, whether this potential alteration reduces the cost of care for mothers, and whether it reduces the quantity and/or quality of the resulting offspring. We set up four experimental treatments in which either mothers tended their own eggs, mothers tended foreign eggs, mothers had no eggs to tend, or eggs had no tending mother. We then took four measurements over the entire period of egg development. First, we measured the levels of three important forms of egg care: egg grooming, clutch defense and maternal return (Diehl and Meunier 2018). To shed light on the potential costs of tending foreign eggs for mothers, we then measured changes of maternal weight between egg laying and hatching (a proxy of maternal investment into egg care (Koch and Meunier 2014)), and changes in the basal immunity of mothers (a costly physiological trait that often trades-off with investment into care (Reavey et al. 2014)). Finally, we investigated the potential costs to offspring of being tended by a foreign mother by measuring egg development time, hatching success and the weight of emerging juveniles. If *F. auricularia* mothers exhibit kin bias, we predict that (i) females are more likely to abandon or kill their clutch when tending foreign compared to their own eggs, and/or that (ii) females alter their level of care when tending foreign

eggs. Reducing the amount of care toward foreign eggs might allow females to save energy (for future reproduction) while limiting the costs of discrimination errors. If egg care comes with physiological costs, we also predict (iii) a higher weight loss and (iv) a higher change in the levels of basal immunity from egg laying to hatching in mothers tending their own compared to foreign eggs – both values being higher when compared to mothers tending no eggs. If low investment in egg care incur costs to offspring, we predict that (v) eggs reared by a foreign mother exhibit a slower development, are less likely to hatch and that the resulting offspring are lighter compared to offspring from eggs reared by their own mothers – the three measurements reflecting an overall higher quality when compared to eggs with no tending mother.

2-MATERIALS AND METHODS

2.1-Experimental setup

We tested whether *F. auricularia* females discriminate against foreign eggs using a total of 85 families. The females used in this study were collected in June 2017 in Pont-de-Ruan, France, and maintained under standard laboratory conditions until egg production (Meunier et al. 2012). Mothers and eggs were manipulated five days after egg laying to allow females freely interacting with their own eggs during this period of time and by doing so, to allow females to form a template that would allow them to discriminate between their own eggs and foreign (Penn and Frommen 2010). At that time, we set up

the four following experimental treatments: (i) mothers tending their own eggs ("own eggs treatment", n = 28), (ii) mothers tending foreign eggs ("foreign eggs treatment", n = 28), (iii) mothers tending no eggs ("no eggs treatment", n = 29) and (iv) clutches of eggs without any tending mother ("no mother treatment", n = 29; eggs taken from the no eggs treatment). The two last treatments were conducted to test whether the costs of tending foreign eggs are higher than the costs of tending no eggs for a female, and whether the costs of receiving care from a foreign mother are lower than receiving no care for eggs. During our manipulations, all eggs were counted and females received foreign clutches of the same size as their own clutches, i.e. clutches were not trimmed or mixed (mean difference between the number of eggs produced and received ± SE = 0.01 ± 0.02). Manipulations were done by first isolating mothers assigned to different treatments (i.e. females from own eggs, foreign eggs and no eggs treatments) and their full clutch of eggs in two small Petri dishes (diameter 5 cm), then transferring the eggs in the Petri dish of the corresponding mother (own eggs or foreign eggs treatments) and finally returning the recipient mother to its original Petri dish. Females and eggs from every treatment were treated the same way, except for the no mother treatment, where eggs were transferred to a new Petri dish. Note that mean clutch sizes were similar across the four treatments (own eggs treatment: mean clutch size ± SE = 36.93 ± 0.93; foreign eggs treatment = 36.68 ± 0.56 and no eggs/no mother treatments = 37.03 ± 0.83; LM, $F_{2,82}$= 0.054, p = 0.948). Moreover, we did not observe any female egg laying (and thus replacement clutches) after setting up of the four treatments.

2.2-Measurements

After the setup of each experimental family, we measured the expression of three forms of maternal care: the time spent on egg grooming, the level of clutch defense and the delay of maternal return, which were all measured using standard protocols (Thesing et al. 2015; Diehl and Meunier 2018). Egg grooming was measured one day after the setup of experimental families (i.e. five days after egg laying) by isolating mothers for 30 minutes, then returning them to their Petri dish at a distance of 5 cm from the eggs and recording their behaviors for the subsequent 15 minutes on camera (SONY© Handycam HDR-CX700 camera). Movies were analyzed using the software BORIS v4.0.3 (Friard and Gamba 2016) and the total duration of egg grooming was defined as the total amount of time each female spent on cleaning eggs with their mandibles (Boos et al. 2014). Clutch defense, which reflects females' willingness to protect their eggs from predator attacks (Thesing et al. 2015), was measured five days after the setup of experimental families (i.e. 9 days after egg laying). This measurement was performed by poking females on the pronotum with a glass capillary in a standardized manner (one poke per second). We started poking when females were motionless on the brood (or just motionless for "no eggs" treatment). The number of pokes required until the female moved more than one body length away from its initial position was then recorded. Finally, maternal return represents the delay after which females return to their clutch after being chased away by a simulated predator attack (called clutch abandonment in Thesing *et al.*, 2015). It was measured by recording the time the female took to return to its clutch after the end of

the clutch defense measurement. We decided to fix the time of maternal return at 20 minutes. Beyond this delay we indicated that female take more than 20 min to return to its clutch. Note that only one female (from the own eggs treatment) did not return to its clutch in less than 20 minutes after being chased away. All these measurements were conducted on females from own eggs and foreign eggs treatments, they were performed under red light due to the nocturnal nature of earwigs and researchers were blind regarding the treatments. Clutch defense was also measured in females from the no eggs treatment to test the importance of egg presence on the number of pokes before withdrawal, and thus to confirm that the measured behavior indeed reflects a form of egg care.

The costs of maternal investment into egg care in terms of weight loss and immunity changes were measured by recording maternal fresh weight and basal immunity both three days after egg laying and one day after egg hatching. The fresh weight of each female was measured to the nearest 0.001 g using a microbalance (OHAUS© Discovery DV215CD). To measure basal immunity, each female was first anesthetized with CO_2 for 30 seconds. We then extracted 1 µL of hemolymph using a glass capillary and diluted it in 25 µL of cold sodium cacodylate/$CaCl_2$ buffer (0.01 M Na-Cac, 0.005 M CaCl2; pH 6.5). The concentration of hemocytes was measured immediately after hemolymph extraction by transferring 10 µL of the diluted hemolymph on a Neubauer chamber and counting using an optical microscope (magnification ×400). Note that the mean hemocyte numbers per female were similar at the setup of the three treatments

(own eggs treatment: mean hemocyte numbers ± SE = 86.78 ± 8.39; foreign eggs treatment = 98.37 ± 7.96; no eggs treatment = 99.44 ± 9.06; LM, $F_{2,78}$= 0.65, p = 0.524). When eggs did not hatch (or were absent due to the treatment), the second measurements were done 50 days after egg laying, which is similar to the mean number of days between egg laying and egg hatching in the other females (mean duration of egg development ± SE = 50.7 ± 0.13). All these measurements were done blindly regarding the treatments and conducted in females from the own eggs, foreign eggs, and no eggs treatments.

Finally, egg development time was defined as the number of days between egg laying and hatching. Conversely, hatching success was measured by dividing the number of juveniles present one day after egg hatching by the number of eggs counted during experimental setup. Note that all eggs from a clutch typically hatch within a day (Koch and Meunier 2014). The mean weight of the resulting juveniles was measured to the nearest 0.001 g by weighing a group of up to 10 juveniles per clutch with a microbalance (OHAUS© Discovery DV215CD). These measurements were conducted in clutches from the own eggs, foreign eggs, and no mother treatments following a blind protocol.

2.3-Statistical analysis

Egg grooming and clutch defense were analysed using a general linear model (LM) and a generalized linear model (GLM) with Poisson error distribution, respectively. In each

model either the number of pokes or the total duration of egg grooming were used as the response variable, whereas the treatment (own eggs, foreign eggs, or no eggs) were used as the explanatory factor. The delay of maternal return was tested using a Cox proportional hazard regression model allowing for censored data to account for females that did not return to their eggs at the end of the observation time (see data in the results). Note that this analysis assumes that females' delays to return have hazard functions that are proportional over time for the different treatment. Females' changes in basal immunity and fresh weight were analysed using a GLM and a LM, respectively. In these models, the relative change in hemocyte number (or fresh weight) between egg laying and hatching was entered as the response variable, while the treatment (own eggs, foreign eggs, or no eggs) was used as an explanatory variable. These relative changes were obtained by subtracting the number of hemocytes (or the females' fresh weight) at egg laying from the number of hemocytes (or the females' fresh weight) at hatching, and then dividing the result by the number of hemocytes (or the females' fresh weight) at egg laying. Positive values therefore indicate that females gained hemocytes or fresh weight during the period of egg care, and vice versa. The egg development time and mean weight of juveniles were tested using two additional LM, in which the treatment (own mother, foreign mother or no mother) was entered as the response variable. Finally, the hatching success was analysed using a GLM with a quasibinomial error distribution to correct for overdispersion. The hatching success was entered as a response variable using the *cbind*

function in R (number of nymphs at hatching, number of egg received), whereas the treatment (own mother, foreign mother, or no mother) was used as a factor in the model.

When required, pairwise comparisons between treatments were conducted using the estimated marginal means (in the LMs and GLMs) and the *survdiff* function (in the Cox models) and corrected for multiple testing using Tukey methods. To fulfill homoscedasticity and normal distribution of model residuals, the number of pokes and mean nymph weight were log-transformed. All statistical analyses were performed with the software R v3.4.3 (http://www.r-project.org/) loaded with the packages *car* (Fox and Weisberg 2011), *survival* (Therneau 2015) and *emmeans* (Lenth 2018)

3-RESULTS

Whether mothers tended their own or foreign eggs did not affect the expression of egg grooming, clutch defense, and maternal return (Table 1a, Fig 1). Moreover, tending either their own or foreign eggs did not shape how much maternal weight and hemocyte number changed over the period of egg care (Table 1b, Fig 2). Similarly, the two types of experimental families did not differ in terms of egg development time, hatching success, and nymphs' fresh weight at hatching (Table 2, Fig 3).

As expected, our measurement of clutch defense reflected a form of egg care: the number of pokes required until mothers move away from their initial position was overall smaller when mothers tended eggs compared to no eggs (Table 1a, Fig 1b). Somewhat

surprisingly, however, the proportion of fresh weight lost by mothers during the period of care was larger in absence compared to presence of eggs (Table 1b, Fig 2a). By contrast, the presence or absence of eggs did not shape maternal variation in hemocyte number (Table 1b, Fig 2b). Finally, the presence or absence of a tending mother had no effect on egg development time and nymph weight at hatching, even if the absence of a mother dramatically reduced the proportion of successful egg hatching (Table 2, Fig 2).

4-DISCUSSION

Theory predicts that the net costs of parental care may compel tending parents to reject foreign eggs, for instance by eliminating these eggs and/or reducing the amount of care they provide to foreign eggs (Hamilton 1964). In this study, we showed that mothers of the European earwig do neither. The presence of either their own or foreign eggs entailed no change in the three measured forms of maternal care, and no change in two physiological costs often associated with maternal care, i.e. weight loss and altered basal immunity. Somewhat surprisingly, females lost more weight in absence compared to presence of (any type of) eggs, whereas egg presence had no effect on females' changes in basal immunity. The experimental treatment to which these mothers were subjected (i.e own versus foreign eggs) also had no effect on egg development time, egg hatching success and on the weight of the resulting juveniles. Finally, the absence of a mother

dramatically reduced egg hatching success, whereas for the few surviving eggs, it had no effect on development time and juvenile weight.

Our data first show that earwig mothers do not eliminate foreign eggs and that they provide extensive forms of care to foreign conspecific eggs just as they do to their own eggs. This is in line with results obtained in other subsocial arthropods, such as the hemiptera *Tectocoris diophthalmus* (Giffney and Kemp 2016), the wolf spider *Pardosa milvina* (Culley et al. 2010) and many eusocial Hymenoptera (Bourke 1994; Strassmann et al. 2000). It also supports results from several cross-fostering studies in *F. auricularia* showing that eggs reared by foreign mothers can exhibit a high hatching success (Meunier and Kölliker 2012; Boos et al. 2014; Boos et al. 2015; Thesing et al. 2015). Here, our finding suggests that (i) eggs do not possess cues (e.g. chemicals on egg surface) that are specific to their own mother and can be used by females to express kin bias or that (ii) there is no or limited selection pressures promoting the rejection of foreign eggs. The first hypothesis is unlikely to explain our results. Earwig mothers are known to immediately and regularly apply a bouquet of cuticular hydrocarbons on the surface of their eggs (Boos et al. 2014), the composition of this bouquet is family specific (Wong et al. 2014) and it has been proposed that this bouquet mediates kin discrimination between juveniles (Dobler and Kölliker 2010). The second hypothesis is more likely to explain our results. First, that is because conspecific clutch parasitism could be absent in this species, as no study ever reported (or actually investigated) its occurrence in *F. auricularia*. This would suggest that even if females may compete for limited nest availability (due to the combination of high

population densities and inter-individual variation in the timing of egg production), it is not necessarily associated with parasitic behaviours during egg laying. Second, earwig females may have evolved alternative strategies to prevent clutch parasitism. For instance, some females close their nest during the period of egg care and most females remain close to their eggs until they hatch, which may have evolved to limit the risk of intrusion by conspecifics (Meunier et al. 2012; Diehl and Meunier 2018). Thirdly, kin selection may actually promote the adoption of conspecific foreign eggs. That is because *F. auricularia* individuals are likely to live in populations with high genetic relatedness (due to low dispersal capabilities (Moerkens et al. 2010)), so that females might be related to most foreign conspecific eggs and could thus increase their inclusive fitness by tending them. Finally, the acceptance of foreign eggs by a mother could be selected to provide nutritional benefits to its own juveniles later on, as these latter selectively cannibalise foreign juveniles during earwig family life (Kölliker and Vancassel 2007; Dobler and Kölliker 2010). Future studies should be conducted to disentangle which of these four parameters lead to the absence of the reported kin bias in our model species.

Independent of the absence of kin bias, our results confirm that maternal presence is crucial to maximize hatching success in earwigs (Boos et al. 2014). Across species and taxa, the presence of mothers with eggs often mitigates the costs of external stressors acting during egg development, such as predation (Swennen et al. 1993; Machado and Oliveira 2002; Requena et al. 2009; Miller et al. 2011), pathogen infection (Grindstaff et al. 2003; Herzner and Strohm 2007; Kudo et al. 2011; Trumbo 2012; Boos

et al. 2014), desiccation (Aubret et al. 2005; Poo and Bickford 2013), and other environmental changes (Green and McCormick 2004; Smiseth et al. 2012). Given the standard laboratory conditions used in the present study, our findings suggest that maternal presence buffers the otherwise lethal effects of small variation in the nesting environment, e.g. humidity and/or the development of non-pathogenic microbes such as mold (see also Boos *et al.*, 2014). Nevertheless, our results also reveal that maternal presence does not change the intrinsic quality of the eggs – as defined by a faster development and the production of heavier juveniles (Körner et al. 2016; Körner et al. 2018). This suggests that the natural variation in egg quality reported between *F. auricularia* clutches (Diehl and Meunier 2018) does not reflect alternative strategies consisting in increasing (or reducing) the level of pre-hatching care to compensate for low (or to benefit from high) investment into egg quality, respectively.

Although *F. auricularia* mothers stop their foraging activity during the period of egg care (Lamb 1976), our data surprisingly show that mothers lost three times less weight when they tended (any type of) eggs as compared to no eggs at all. This difference in weight loss could be due either (i) to a stress-triggered excess of metabolic activity when mothers lost their full clutch of eggs, or (ii) to the lack of opportunity for isolated mothers to cannibalise their own eggs. The first hypothesis is unlikely to explain our results: we found no effect of egg presence/absence on the basal immunity of females, a physiological trait that is typically shaped by stress in animals (Adamo 2012). By contrast, filial egg cannibalism might be more likely to explain our results. This phenomenon has

been reported in several earwig species, including *F. auricularia* (Miller and Zink 2012; Koch and Meunier 2014). Filial egg cannibalism is generally considered as an adaptive process if it either (i) targets damaged, parasitized or diseased eggs, (ii) reduces the future level of sibling competition for limited resources, (iii) allows parents to re-allocate their resources into future reproduction after a sudden deterioration in their environmental conditions or (iv) if it targets unfertilized trophic eggs and is used as a regular food source to parents when other food sources are scarce (Bartlett 1987; Crespi 1992; Lindström and Sargent 1997; Thomas and Manica 2003; Lourdais et al. 2005; Klug et al. 2006; Miller and Zink 2012; Zeng et al. 2017). This fourth hypothesis could operate in earwigs, as mothers constantly remain in their nest over the period of egg care (Kölliker 2007) which largely occurs during the period when food sources are typically very limited (Lamb 1976). To determine whether egg cannibalism is the main driver of our results and to disentangle its underlying processes, further research will investigate the effects of physical damage and pathogen infection on egg cannibalism, test whether earwig females produce unfertilized trophic eggs and explore the link between changes in environmental conditions and egg cannibalism.

To conclude, our study shows that *F. auricularia* mothers do not reject foreign conspecific eggs. This emphasizes that prolonged and extensive periods of maternal egg care, together with the absence of foraging activity and the capability to produce a replacement clutch do not necessarily select for maternal adjustment of egg care in function of eggs origin. Moreover, our results stress the importance of other parameters

such as the risk of clutch parasitism, the development of alternative strategies to fight against clutch parasitism and the potential benefits of adopting additional eggs, in the selection for a broad tolerance toward foreign eggs. Hence, improving our knowledge on these parameters and their associated net benefits (or costs) for parents will be of central importance to get a better understanding of the role of kin bias in the evolution of parental care across species and taxa.

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DATA ACCESSIBILITY

Analyses reported in this article can be reproduced using the data provided by (Van Meyel et al. 2019).

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FIGURES AND FIGURES LEGENDS

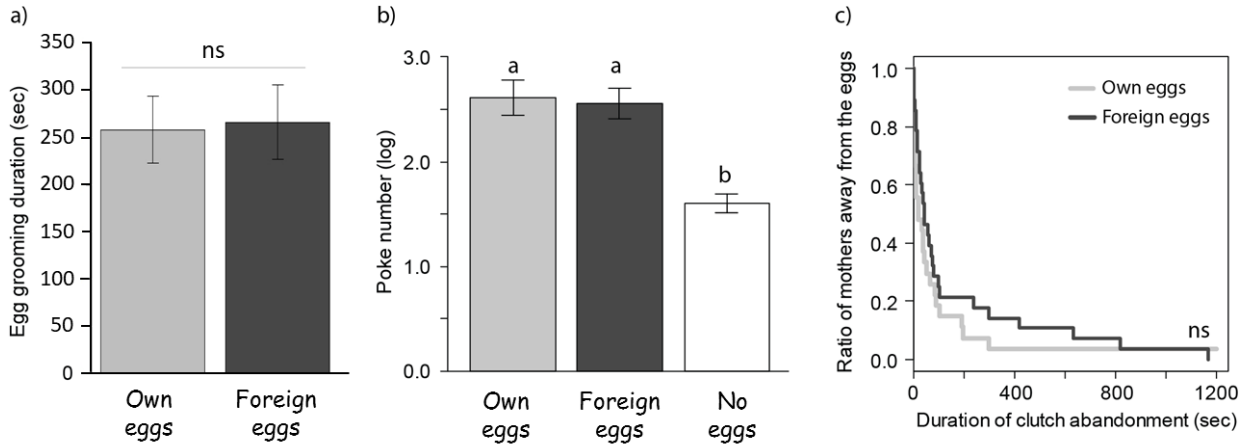


Figure 1 - Effect of treatment on females' egg care. (a) Egg grooming, which is the sum of the times spent by female to clean the eggs. (b) Egg defense against a simulated predator attack, which represents the number of pokes required to deter mothers from tending their clutch of eggs and (c) Delay of maternal return, which indicates how long mothers remain away from their eggs after poking. Different letters correspond to p-values < 0.0001, ns = not significant. Values are means ± s.e.m. The number of replicates is indicated at the bottom of each bar or between brackets.

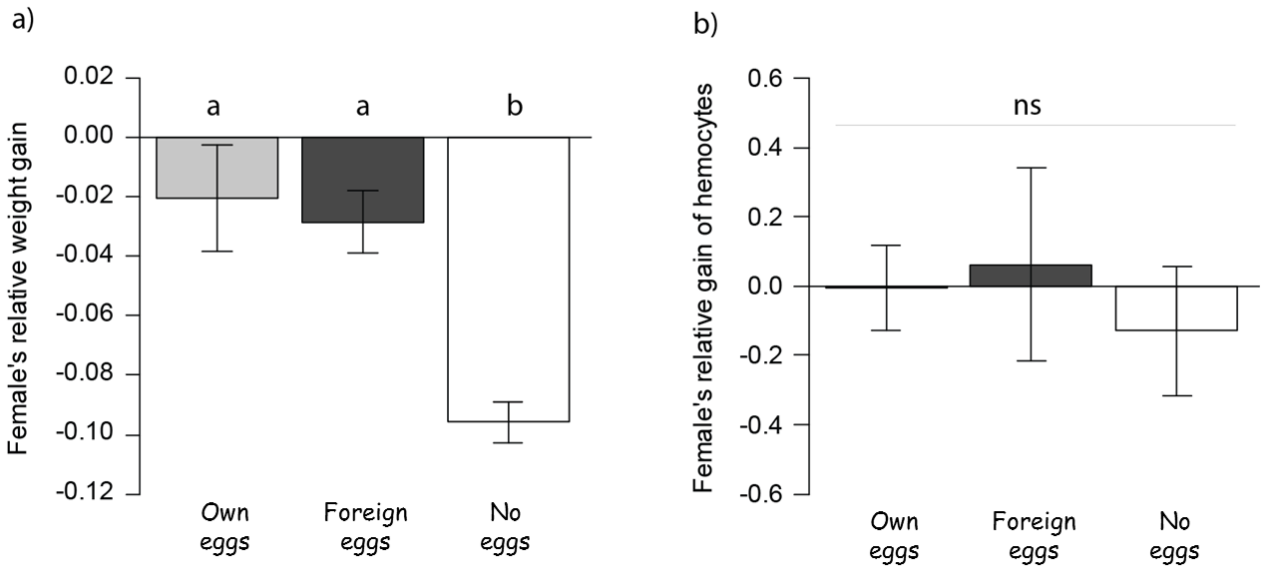


Figure 2 - Effect of treatment on females' body condition reflecting their investment on egg care. (a) Female's relative differences in weight between egg laying and egg hatching, negative values show a weight loss. (b) Female's relative gain of hemocytes between the egg laying and the egg hatching. Different letters correspond to p-values < 0.01, ns = not significant. Values are means ± s.e.m. The number of replicates is indicated at the bottom of each bar.

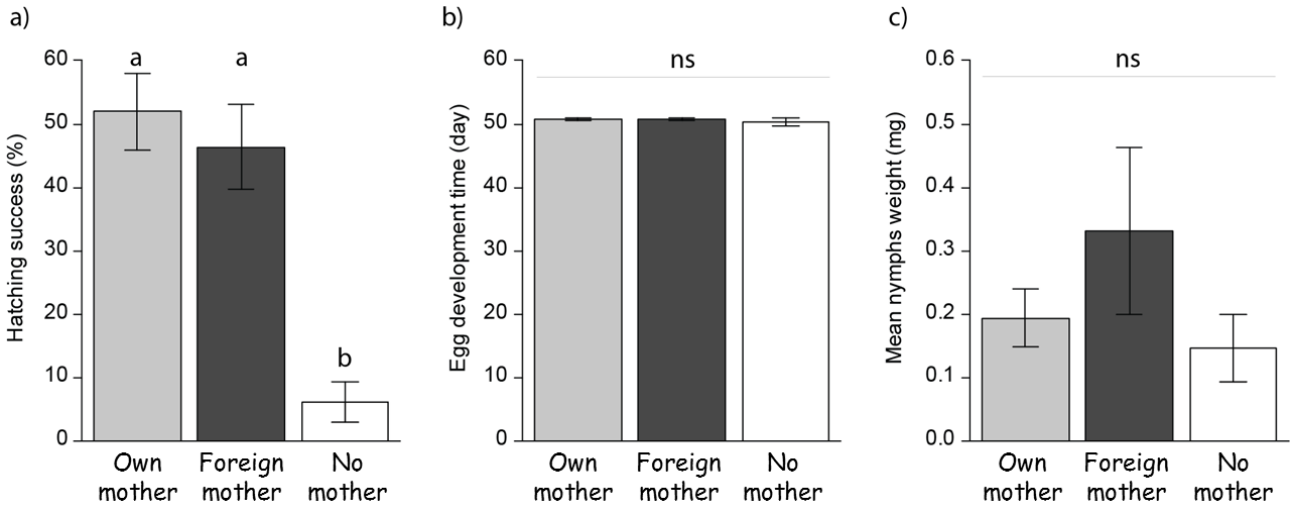


Figure 3 - Effect of treatment on egg quality in terms of (a) hatching success, (b) duration of egg development and (c) mean of nymph weight at hatching. Different letters correspond to p-values < 0.0001, ns = not significant. Values are means ± s.e.m. The number of replicates is indicated at the bottom of each bar.

TABLES AND TABLE LEGENDS

Table 1. Effect of treatment (own eggs, foreign eggs, or no eggs) on the three measured forms of maternal egg care and on the relative changes in hemocyte number and maternal fresh weight. Significant p-values are in bold.

	Treatment			Post-hoc tests (Tukey)		
	Model	Statistical values	P-values	Related vs Unrelated	Related vs No eggs	Unrelated vs No eggs
a) Levels of maternal care						
Clutch defense	GLM	LR $\chi^2(2) = 8.69$	**0.0130**	0.9904	**0.0248**	**0.0352**
Maternal return	Cox	$\chi^2(1) = 1.06$	0.3043	-	-	-
Egg grooming	LM	$F(1,54) = 0.24$	0.8784	-	-	-
b) Effects of clutch attendance on mothers						
Hemocyte number	GLM	LR $\chi^2(2) = 0.48$	0.7881	-	-	-
Fresh weight	LM	$F(2,72) = 8.31$	**0.0006**	0.9803	**0.0014**	**0.0042**

Table 2. Effect of treatment (own eggs, foreign eggs, or no eggs) on egg development, hatching success and nymph weight at hatching. Significant p-values are in bold.

	Treatment			Post-hoc tests (Tukey)		
	Model	Statistical values	P-values	Related vs Unrelated	Related vs No mother	Unrelated vs No mother
Egg development time	LM	$F(2,50) = 0.41$	0.6647	-	-	-
Hatching success	GLM	LR χ^2 (2) = 43.16	**< 0.0001**	0.7125	**< 0.0001**	**< 0.0001**
Nymph weight at hatching	LM	$F(2,50) = 0.04$	0.9654	-	-	-