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The costs and benefits of maternal egg care in the earwig *Forficula pubescens*

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ABSTRACT

Maternal egg care is generally considered to be ubiquitous among the 1,700 species of free-living Dermaptera. However, the forms, costs, and benefits of egg care have only been studied in a handful of species. In this study, we examined for the first time egg care in the earwig *Forficula pubescens*. Under standard laboratory conditions, we set up 94 families containing mothers with either no eggs, a reduced, normal or increased clutch size, or eggs without mother. We first demonstrate that *F. pubescens* mothers indeed express multiple forms of egg care including egg grooming, egg guarding, and active defences against predators, some of which vary with clutch size. However, maternal presence had contrasting effects on the eggs’ fate. On one hand, it reduced the survival of eggs during their first 30 days of development, which suggests that mothers eat part of their clutch during egg development and, contrary to other Dermapterans, that abandoned eggs can resist fungal development. On the other hand, maternal presence was necessary to allow the remaining eggs to hatch on day 53, indicating that mothers enhance late embryonic development and/or facilitate the hatching process. Finally, our results did not shed light on the costs of egg care for mothers in terms of premature death, reduced expression of self-grooming, or increased weight loss. Overall, our study emphasizes that investigating the costs and benefits of egg care in poorly known species can provide novel insights into our understanding of the evolution of maternal care within and across animal taxa.

Keywords: Brood development; Egg cannibalism; Family life; Parental care

INTRODUCTION

Egg care is a taxonomically widespread phenomenon in animals. It is found in taxa ranging from arthropods to fish, birds and mammals, where it can be expressed by one or both parents, or even adult siblings, either during critical periods or throughout the entire development of the eggs (Smiseth et al. 2012). Across species and taxa, parental egg care typically encompasses a great diversity of forms ranging from mildly beneficial to essential for egg development (Klug and Bonsall 2014; Meunier et al. 2022). For instance, a common form of parental egg care is to guard the eggs, which allows parents to passively deter potential predators or to actively protect eggs during predator attacks as reported in the flagfish *Jordanella floridae* (Klug et al. 2005), the harvestman *Acutisoma proximum* (Buzatto et al. 2007), and the lizard *Eutropis longicaudata* (Huang et al. 2013). Similarly, parental egg care may involve sitting on eggs to ensure optimal temperature for embryonic development, an incubation behaviour that is particularly common in birds (Cones and Crowley 2020). Finally, another example of parental egg care is egg cleaning, which helps to remove dirt and pathogens that could otherwise accelerate desiccation or damage the eggs and infect the embryo or newly hatched juveniles, as in the fringed darter fish *Etheostoma crossopterygum* (Knouft et al. 2003) and the European earwig *Forficula auricularia* (Buxton and Madge 1974).

While egg care typically provides benefits to the eggs, it often imposes costs on the parents that can reduce their longevity and/or impede their reproduction (Trivers, 1972; Alonso-Alvarez & Velando, 2012). This is because parents use part of their resources to express egg care, which prevents them from investing these resources in other critical fitness traits (Klug and Bonsall 2014). For example, a high parental investment in egg care has been shown to reduce their investments in the search for new food resources, in future reproductive events, and in the development of effective immune responses in several vertebrate and arthropod species (Buzatto et al. 2007; Alonso - Alvarez and Velando 2012; Cones and Crowley 2020; Hongliang et al. 2022). As a result, the evolution and maintenance of egg care rely on the net benefits it provides to parents, which involves both the benefits for current offspring and the costs for parents in terms of future reproduction and may greatly vary between species and taxonomic groups (Clutton-Brock 1991; Gross 2005; Kramer and Meunier 2019). Improving our general understanding of the evolutionary drivers of egg care therefore requires developing an overview of the diversity of its forms, costs and benefits for each partner, with particular attention to taxonomic groups with an as yet poorly studied (breeding) biology.

In this study, we investigated the forms of maternal egg care as well as its costs and benefits for mothers and eggs in the earwig *Forficula pubescens* Gené (formerly *Guanchia pubescens*). *F. pubescens* belongs to the order Dermaptera, which includes about 1,700 free-living species for which the biology is generally poorly known – even if maternal egg care is often presented to be common (Matzke and Lass 2005; Haas 2018). To the best of our knowledge, the costs and benefits of egg care have only been quantified in two earwig species in which, somewhat surprisingly, egg care appears to entail clear benefits for eggs but no costs for mothers. In the maritime earwig *Anisolabis maritima*, egg care typically lasts 21 days and helps to reduce fungal growth on eggshells and to limit the risk of egg cannibalism by conspecifics (Miller et al. 2011; Greer et al. 2020). Whereas unattended eggs are rapidly overtaken and killed by fungi (Greer et al. 2020), *A. maritima* mothers experimentally prevented from or allowed to tend their eggs showed no differences in mortality and investment in future reproduction (Miller and Zink 2012) - even if a recent study suggests that a 50% reduction in clutch size subsequently leads to the production of a larger second clutch (Suzuki 2021). Similarly, in the European earwig *F. auricularia*, mothers tend their eggs for about 40 days, during which they regularly groom them to remove fungal spores (Boos et al. 2014), show fierce behaviours to deter predators from the clutch (Meunier et al. 2012), deposit chemical compounds on the eggs to (possibly) limit the risk of desiccation (Boos et al. 2014), and relocate

eggs to reach optimal temperatures for development (Tourneur et al. 2022). However, just as for *A. maritima*, preventing egg care does not improve the survival and investment in immune functions and future reproduction of *F. auricularia* mothers (Van Meyel et al. 2019).

Contrary to the two earwig species described above, the biology and social life of the earwig *F. pubescens* are poorly known. This species is omnivorous and commonly found in southern European orchards where it lives in sympatry with the European earwig (Romeu-Dalmau et al. 2012; Lordan et al. 2015). Whereas *F. pubescens* females have been observed to remain with their eggs and newly hatched juveniles (Matzke and Lass 2005), the nature and duration of egg care, its potential costs for mothers and benefits for eggs remained unknown. To fill this knowledge gap, we maintained 94 *F. pubescens* females under standard laboratory conditions (in absence of predators and pathogens) and examined the expression of maternal egg care by measuring the durations of egg grooming and egg guarding, the level of egg defence, the delay of maternal return after an experimental clutch abandonment, and the likelihood to gather eggs two and eight hours after they had been experimentally scattered. In addition to these five forms of egg care, we measured three important traits in mothers that could be negatively affected by maternal investment in egg care (i.e., the expression of self-grooming, the amount of weight loss and maternal survival during the period of egg care), as well as four traits of the eggs and resulting juveniles that could be positively affected by maternal investment in egg care (i.e., egg survival rate over 30 days, hatching rate, egg development time, and the mean weight of the newly hatched juveniles). To investigate whether the potential costs of egg care for mothers and benefits for eggs depend on the number of eggs to be cared for, we manipulated clutch sizes to obtain mothers with either no eggs, a reduced clutch size, a normal (unmanipulated) clutch size, or an increased clutch size, as well as eggs isolated from mothers. If egg care is costly to mothers, we predicted that mothers with more eggs invest less in the expression of self-grooming, lose more weight and are more likely to die compared to mothers with less or no eggs. If egg care is beneficial to eggs, we predicted that eggs without attending mothers show a lower survival rate over 30 days, a lower hatching rate, a longer development time, and produce juveniles with a smaller weight compared to eggs with a mother.

MATERIAL AND METHODS

Animal sampling and rearing

We field-sampled 94 *F. pubescens* females and an equal number of males using wood traps in peach orchards near Valence, France (Lat 44.9772790, Long 4.9286990) in July 2021. Just after field sampling, we set up males and females in plastic containers (balanced sex ratio) lined with moistened sand and containing egg cardboard to serve as a shelter for individuals. Each container received *ad libitum* homemade food typically used to rear the European earwig *F. auricularia* and consisting mainly of a mixture of pollen, cat food, carrots, and bird seeds (details in Kramer et al. 2015). We then maintained the containers under a 12:12 light:dark cycle at 20:18°C, respectively. This setup allowed for uncontrolled matings. When we observed the first oviposition in the entire experimental population (i.e. five months later), we isolated each female in a Petri dish (diameter 5.0 cm) lined with moistened sand and then maintained all Petri dishes under constant darkness with the temperature being lowered from 18°C to 10°C in reductions of 2°C every week. Each Petri dish received *ad libitum* homemade food every week until oviposition. We checked each female twice a week to record the date of oviposition. Females did not receive food from oviposition to egg hatching, as previous observations suggested that they stop their foraging activity during the period of egg care (J. Meunier, pers. obs) and because this absence of foraging behaviour during egg care was already reported for other earwig species (Kölliker 2007).

Experimental setup

Three days after the first egg observation, we weighed females, counted their eggs, and then randomly allocated females that laid at least 15 eggs ($n = 92$, two females produced 8 eggs) to five experimental treatments. These treatments consisted of either 1) reducing the size of the clutch by removing half the eggs (“Reduced clutch” treatment), 2) increasing clutch size by adding a number of eggs equal to half the initial clutch size (“Increased clutch”), 3) removing all eggs and moving the mother to a new Petri dish (“No eggs”), 4) keeping all eggs and removing the mother (“Eggs without mother”) and finally 5) letting the mother with her initial clutch (“Control clutch”). Overall, this provided five treatments with 23 replicates each and no difference in the number of eggs before the manipulation of clutch size ($F_{4,110} = 1.74$, $P = 0.147$). For all treatments, mothers were removed from the Petri dish while the egg manipulation occurred (eggs handling occurred even in the Control clutch treatment) and then gently returned to the Petri dish. We set up the treatments “No eggs” and “Eggs without mother” with the same initial clutches. Eggs added to the “Increased clutch” treatment were from unrelated clutches produced on the same day as the recipient clutch. We assumed that like *F. auricularia* and *Anisolabis maritima*, *F. pubescens*, mothers would not be able to discriminate between their own and foreign eggs (Van Meyel et al. 2019; Suzuki 2021). We then maintained the resulting experimental clutches under constant darkness at 10°C to conduct the following tests.

Expression of maternal egg care

Thirty-three days after oviposition (i.e., 30 days after egg manipulation), we measured the effects of clutch size manipulation on five forms of egg care: the durations of egg grooming and egg guarding, the level of egg defence, the delay of maternal return after clutch abandonment, and the likelihood to gather eggs within eight hours after they had been experimentally scattered. All these measurements followed standard protocols developed to investigate egg care in other earwig species (Thesing et al. 2015; Van Meyel et al. 2019; Meunier et al. 2020; Merleau et al. 2022). We first measured the duration of (1) egg grooming and (2) egg guarding by gently depositing each Petri dish with a mother and its eggs on an experimental plate under infrared light, and then video recording their behaviour through the transparent lid for 12 min (Camera: BASLER BCA 1300, Germany; Media Recorder v4.0, Noldus Information Systems, Netherland). We analyzed the videos using the software Boris v7.13.3 (Friard and Gamba 2016) in which we defined egg grooming as the total amount of time during which each mother actively touched eggs with her mouthpieces, and egg guarding as the total time during which each mother was on the eggs or within one body length of them without interacting with the eggs. (3) We measured the level of egg defence just after the video recording. Egg defence represents the mother's endurance in defending her clutch and herself against predators (Van Meyel et al. 2021). This was measured by gently opening each Petri dish, standardly poking the pronotum of the mother with a glass capillary (1 poke per second) and then recording the number of pokes required for her to move more than one body length away from its initial position. We started poking when females were motionless. (4) We measured the delay of maternal return to the clutch just after measuring egg defence by recording the time it took the female to touch her first egg. We fixed the maximum delay of maternal return at 10 minutes. Beyond this delay, we indicated that the mother took more than 10 minutes to return to her clutch. Finally, (5) we measured the likelihood for mothers to gather their eggs just after measuring the delay of maternal return. We gently removed the mother and eggs from the Petri dish, evened the sand with a clean finger, scattered the eggs over the entire surface of the Petri dish, and then returned the mother. The resulting Petri dish was then immediately placed in darkness at 13°C. Two and eight hours later, we checked each Petri dish and assigned them a binary score indicating whether the clutch was gathered (i.e. 95% of the eggs were contained within a circle of 0.2 cm diameter) or not. The five forms of maternal egg care were taken in

the three treatments containing mothers and eggs, i.e. the “Increased clutch”, “Control clutch” and “Reduced clutch” treatments.

Potential costs of egg care for mothers

We investigated the potential costs of egg care for mothers by testing its impacts on mothers’ (1) expression of self-grooming – an important behaviour in insects (including earwigs) through which individuals remove dirt and pathogens and apply self-secreted chemicals on the cuticle to enhance protection against desiccation and parasites (Weiß et al. 2014; Meunier et al. 2020), (2) weight lost during the period of egg care and (3) mothers’ survival during that time. We expected a number of maternal deaths during the egg care period, as it is very long, females typically stop feeding and it usually occurs in winter, i.e., when conditions are particularly harsh. We measured the total duration of mothers’ self-grooming using the 12 min videos recorded 33 days after oviposition (see above). We defined self-grooming as the total amount of time each mother spent cleaning herself with her mouthpieces. To measure the relative amount of weight lost by each mother during the period of egg care, we divided the difference between the fresh weight of each female on the day of egg hatching and the day of oviposition, by the fresh weight of the female on the day of oviposition. When we maintained females without eggs (“No eggs” treatment) or when there were no remaining eggs in the Petri dish, we defined the day of egg hatching as the day at which 50% of the other same-age mothers had their eggs hatched. This method has been previously used to measure the level of maternal investment in egg care in the European earwig (Koch and Meunier 2014). Finally, we recorded whether mothers were still alive on the day of egg hatching. Overall, we investigated these potential costs of egg care for mothers using the treatments “Reduced clutch”, “Increased clutch”, “No eggs” and “Control clutch”.

Potential benefits of egg care for eggs and newly hatched juveniles

We investigated the effects of egg care on the fate of eggs by measuring (1) egg survival rate 30 days after our manipulation, (2) hatching rate, (3) egg development time, and (4) the mean weight of the newly hatched juveniles. We measured egg survival rate during the first 33 days of development by counting the number of eggs still present in the Petri dish at day 30 after our manipulation. We defined egg development time as the number of days between oviposition and the day of the first egg hatching (Meunier et al. 2012). We defined the hatching rate as the number of newly produced juveniles (called nymphs) one day after egg hatching divided by the number of eggs after treatment. We measured the mean nymph weight at hatching by weighing a random group of 10 nymphs (or all nymphs if fewer were available) one day after hatching and then dividing this value by the number of weighted nymphs. Just as for mother weight, we conducted all weighing to the nearest 0.01 mg. All these traits have been measured in the “Reduced clutch”, “Increased clutch”, “Eggs without mother” and “Control clutch” treatments.

Statistical analysis

We performed all statistical analyses using the R software v4.1.1 (<https://www.r-project.org/>) loaded with the packages *car* (Fox and Weisberg 2019), *DHARMA* (Hartig 2020), *emmeans* (Lenth 2022) and *survival* (Therneau 2020). We first analysed the expression of egg care using a series of three Linear models (LM), three Generalized linear models (GLM) and one 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), in which we entered clutch size after manipulation (categorical, i.e., reduced, normal or increased), the initial number of eggs produced (continuous) and their interaction as explanatory variables. In these models, the

response variable was either the overall duration of egg grooming (LM), the duration of egg grooming per egg (LM), the duration of egg guarding (GLM with a Poisson error distribution corrected for overdispersion), the level of egg defence (LM with the variable a log+1 transformed), the delay of maternal return after clutch abandonment (Cox model) and the likelihood to gather eggs 2hr and 8hr after our experimental scattering (two GLMs with Binomial error distributions). While we implemented the interactions between the number of eggs before and after the manipulation in each model, we removed them from all models following model simplification via AIC comparison (for information: all $P > 0.098$).

We analysed the potential costs of egg care for the mother using two LMs and one GLM, in which we entered the treatment as an explanatory factor (no eggs, reduced, normal or increased clutch size) and either the relative weight gained by the mother (LM), the total duration of self-grooming (LM) or whether mothers died before egg hatching (GLM with Binomial error distribution) as the response variable. We tested whether mothers of each treatment lost or gained weight during the period of egg care by conducting four Mann-Whitney Rank tests, each comparing the relative weight gain of mothers from a given treatment to the value of zero.

We analysed the eggs' fate using one GLM and three LMs. In these models, we entered the treatment as an explanatory factor (eggs with no mother, as well as reduced, normal, or increased clutch size) and either the egg survival rate 30 days after our manipulation (GLM with binomial error distribution corrected for overdispersion), the hatching rate (LM), the egg development time (LM), or the mean weight of the newly hatched juveniles (LM) as the response variable.

Overall, we checked that all model assumptions were met using the *DHARMA* R package and transformed the response variable in the two cases where it was required (log+1 transformation for the egg defence variable, and arcsin square-root transformation for the hatching rate). We conducted pairwise comparisons using the estimated marginal means of the models using the *emmeans* R package.

Table 1 – Overview of the life-history traits associated with egg production measured across all females, and for each of the three treatments of clutch size manipulation. SE = Standard Error.

	Overall		Reduced clutches		Normal clutches (control)		Increased clutches	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Date of oviposition (days after 29 Nov)	26.28	1.09	26.48	1.96	26.17	1.96	26.17	1.85
No. eggs produced	35.36	1.15	38.35	2.19	35.91	2.02	31.83	1.51
Mother weight at oviposition (mg)	21.76	0.37	22.45	0.64	21.48	0.65	21.39	0.64
Egg development time (days)	52.92	0.73	53.7	1.80	53.00	1.01	52.33	1.09
No. nymphs produced	9.81	1.68	4.78	1.65	10.42	2.77	13.57	3.48
Nymph weight at hatching (mg)	0.64	0.02	0.66	0.08	0.63	0.03	0.63	0.02
Mother weight at hatching (mg)	20.92	0.29	20.95	0.45	20.54	0.52	21.21	0.54

RESULTS

In the treatment where mothers remained with their initial number of eggs (i.e., control), they produced 35.91 ± 2.02 (mean \pm SE) eggs with a mean laying date occurring in the last week of December (Table 1). These eggs developed in about 53 days and led to the production of 10.42 ± 2.77 nymphs per clutch on average. The mean weight of the newly hatched nymphs was 0.63 ± 0.03 mg. The values for each treatment are presented in Table 1.

Between oviposition and egg hatching, most *F. pubescens* mothers expressed the five forms of egg care we have measured (Figure 1). Clutch size manipulation affected both the duration of egg grooming (Figure 1A; $F_{2,52} = 5.59$, $P = 0.006$) and the delay of return after clutch abandonment (Figure 1B; Likelihood Ratio $\chi^2_2 = 5.85$, $P = 0.054$). Mothers with reduced clutches spent overall less time grooming the eggs and returned to their clutches more slowly than both females with normal ($t_{53} = -2.49$, $P = 0.042$; Log-rank test $P = 0.028$, respectively) and increased ($t_{53} = -2.52$, $P = 0.038$; Log-rank test $P = 0.044$, respectively) clutches. By contrast, there was no difference in egg grooming and delay of maternal return between females with normal and increased clutches ($t_{53} = -0.52$, $P = 1.000$; Log-rank test $P = 0.876$, respectively). These effects did not reflect a reduction in the duration of egg grooming per egg, as this duration was independent of the clutch size manipulation ($F_{2,52} = 2.82$, $P = 0.069$). Moreover, tending clutches with a manipulated size had no effect on the duration of egg guarding (LR $\chi^2_2 = 4.36$, $P = 0.113$), the level of egg defence ($F_{2,58} = 1.99$, $P = 0.147$), and the likelihood to gather scattered eggs after two (LR $\chi^2_2 = 1.56$, $P = 0.458$) and eight hours (LR $\chi^2_2 = 2.18$, $P = 0.335$). Independent of clutch size manipulation, the initial number of eggs produced by a female did not influence the expression of any of the five forms of care measured, whether it was the duration of maternal egg grooming (overall: $F_{1,52} = 2.75$, $P = 0.104$; per egg: $F_{1,52} = 1.58$, $P = 0.214$), the delay of maternal return (LR $\chi^2_1 = 0.05$, $P = 0.815$), the duration of egg guarding (LR $\chi^2_1 = 1.72$, $P = 0.190$), the level of egg defence ($F_{1,58} = 1.01$, $P = 0.318$) and the likelihood to gather eggs after two (LR $\chi^2_1 = 0.99$, $P = 0.320$) and eight (LR $\chi^2_1 = 2.19$, $P = 0.139$) hours.

The presence of eggs and the manipulation of clutch size came with no apparent cost to *F. pubescens* mothers. On the contrary, mothers lost weight during the period of egg care when they were maintained without eggs (Figure 1A; $V = 6$, $P = 0.0002$), as well as with a reduced ($V = 15$, $P = 0.004$) and normal clutch size ($V = 37$, $P = 0.064$), but not when maintained with increased clutch size ($V = 93$, $P = 0.674$). This pattern is also present when testing the effect of clutch size on the relative weight loss of mothers during this period (Figure 2A; $F_{3,66} = 5.32$, $P = 0.002$). Mothers maintained in absence of eggs lost more weight than mothers maintained with increased clutch size ($t_{66} = -3.98$, $P = 0.001$), while the relative weight lost by mothers in the other treatments shows intermediate values (all $P > 0.112$). Contrary to these effects, we did not find an effect of egg presence or variation in clutch size on the total duration of self-grooming expressed by mothers (Figure 2B; $F_{3,71} = 0.82$, $P = 0.489$), nor on the likelihood of mothers dying during the period of egg care (Figure 2C; LR $\chi^2_3 = 2.76$, $P = 0.430$).

For the eggs, the presence of a mother affected both their survival rate after 30 days (Figure 3A; LR $\chi^2_3 = 15.05$, $P = 0.002$) and their hatching rate (Figure 3B; $F_{3,77} = 7.65$, $P = 0.0002$). However, these effects were in opposite directions. Eggs survived better during the first 30 days in the absence compared to the presence of a mother, regardless of the clutch size (No mother vs Reduced clutch, $P = 0.036$; No mother vs Normal clutch, $P = 0.008$; No mother vs Increased clutch, $P = 0.007$; all other pairwise comparisons $P > 0.998$). By contrast, none of the eggs hatched in the absence of the mothers, while the hatching rate of the tended eggs did not differ between clutch sizes (No mother vs Reduced clutch, $P = 0.0058$; No mother vs Normal clutch, $P = 0.0013$; No mother vs Increased clutch, $P = 0.0006$; all other pairwise comparisons $P > 0.952$). In the three treatments with a mother, the number of eggs that failed to hatch (i.e. that disappeared from the Petri dish) was positively correlated with the absolute

weight gained by the mothers (Spearman's rank correlation test; $S = 8917.9$, $P = 0.0006$, $Rho = 0.48$), while we did not detect an effect of clutch size on the egg development time (Figure 3C; $F_{2,33} = 0.29$, $P = 0.753$) and the mean weight of newly hatched juveniles (Figure 3D; $F_{2,32} = 0.12$, $P = 0.892$).

Figure 1 – Effect of clutch size manipulation on the expression of five forms of maternal egg care. Boxplots depict median and interquartile ranges, with whiskers extending to 1.5 times the interquartile range and dots representing jittered experimental values. Different letters refer to $P < 0.05$. ns $P > 0.05$

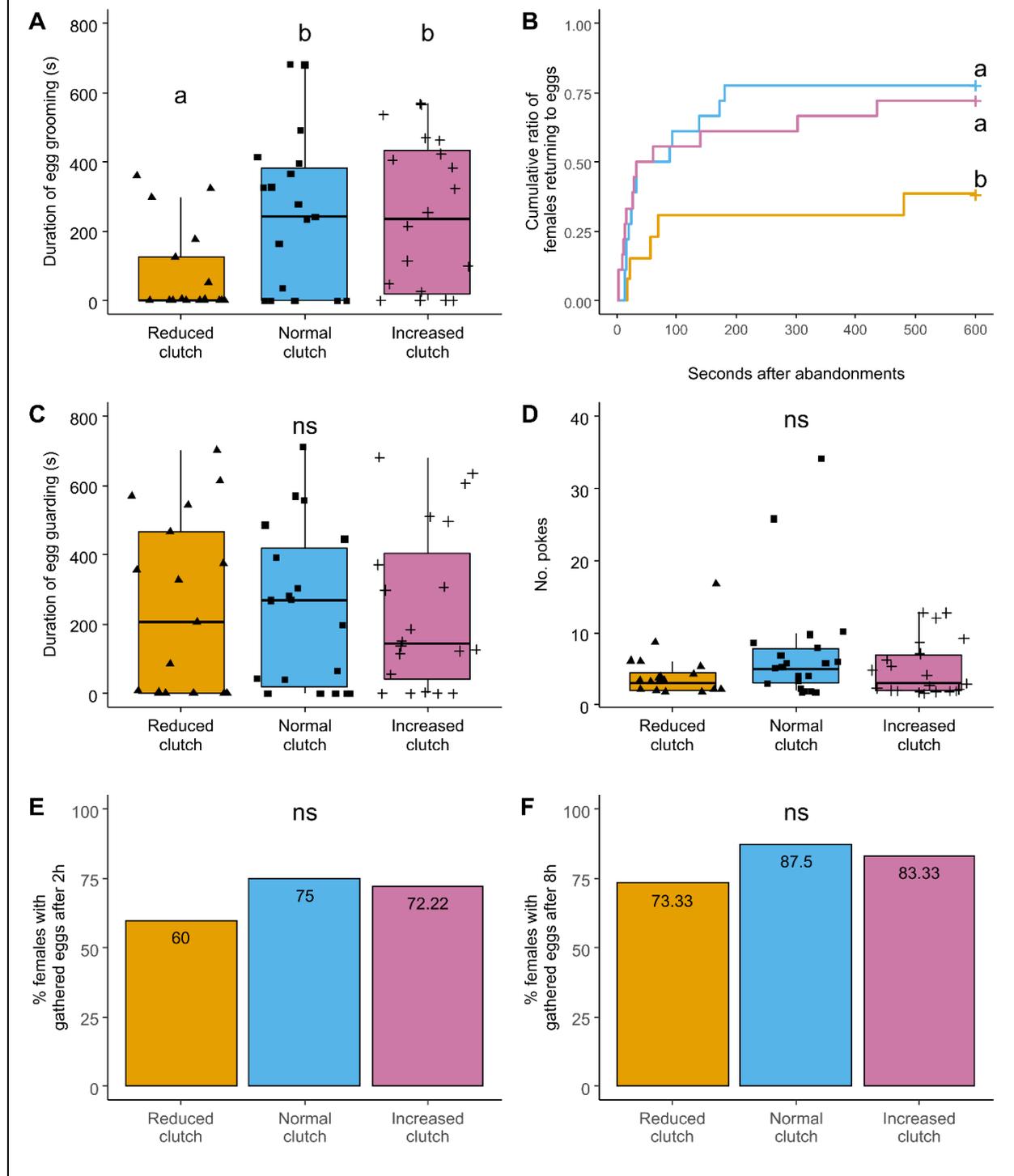


Figure 2 – Effects of egg presence and clutch size manipulation on three potential costs of egg care for mothers. Boxplots depict median and interquartile ranges, with whiskers extending to 1.5 times the interquartile range and dots representing jittered experimental values. Different letters refer to $P < 0.05$. ^{ns} $P > 0.05$. Red stars illustrate comparisons with zero weight loss (horizontal dashed red line). *** $P < 0.001$, ** $P < 0.01$

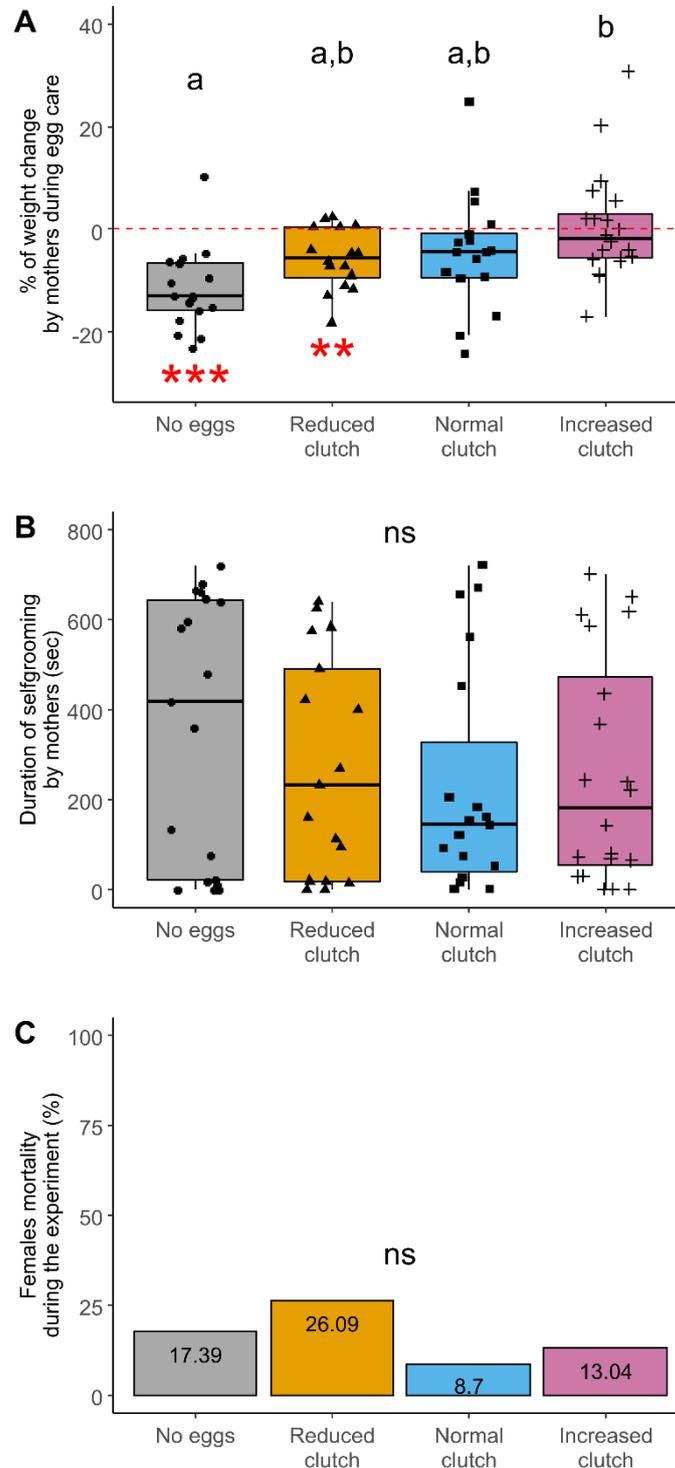
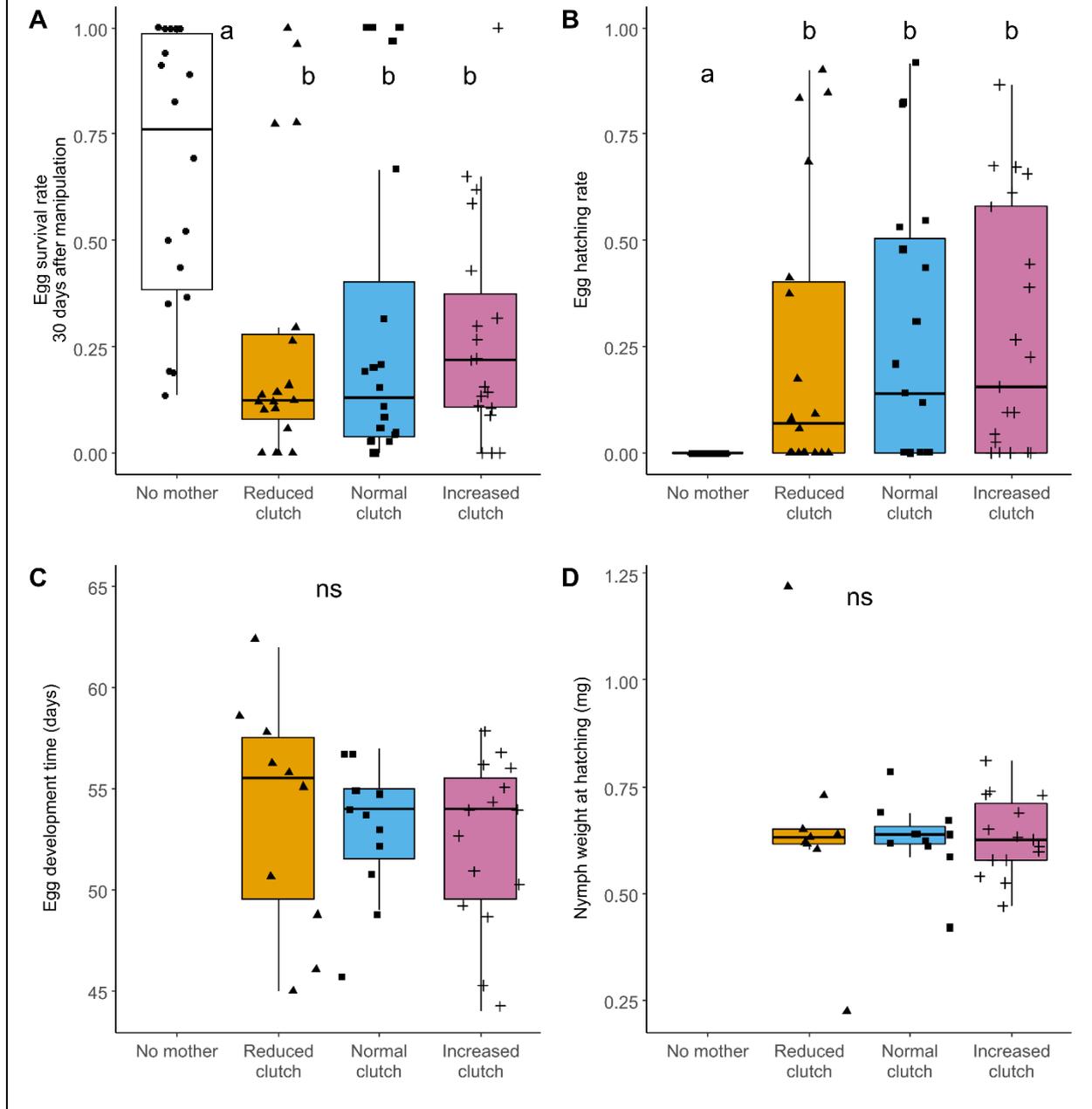


Figure 3 – Effects of mother presence and clutch size manipulation on the eggs' fate. Boxplots depict median and interquartile ranges, with whiskers extending to 1.5 times the interquartile range and dots representing jittered experimental values. Different letters refer to $P < 0.05$. ^{ns} $P > 0.05$.



DISCUSSION

Broadening the taxonomic diversity of our knowledge on the potential costs and benefits of egg care is of major importance to improve our general understanding of the evolution of this crucial behaviour in animals (Clutton-Brock 1991; Gross 2005; Kramer and Meunier 2019). In this study, we conducted a series of experiments under standard laboratory conditions to investigate for the first time the diversity of forms, costs and benefits of maternal egg care in *F. pubescens*, a member of Dermaptera, in which egg care has been studied in only a handful of its 1,700 free-living species (Matzke and Lass 2005; Haas 2018). Our results first reveal that *F. pubescens* mothers express the five forms of egg care we have measured. The expression of two of these

forms decreased when we experimentally reduced the clutch size (egg grooming and delay of maternal return) but did not augment when we increased it. The expression of the three other forms was independent of clutch size. Our data then revealed that tending eggs did not increase the risk of premature death in mothers, nor reduce the expression of self-grooming. Somewhat surprisingly, mothers even lost less weight in the presence compared to the absence of eggs. Finally, our results show that maternal presence had contrasting effects on the eggs' fate. Egg survival rate during the 33 days following oviposition was lower in the presence compared to the absence of mothers, whereas maternal presence was necessary for eggs to hatch. Egg development time and expression of the three other forms of egg care were independent of clutch size manipulation.

Our findings first reveal that *F. pubescens* mothers provide extended egg care in multiple forms, including egg grooming, egg guarding, egg defence against (simulated) predator attacks, and egg retrieval when the clutch has been unexpectedly dispersed. Whereas our study does not test the function of these forms of care in *F. pubescens*, the literature on arthropods and birds suggests they could be of particular importance in presence of egg predators (Klug et al. 2005; Buzatto et al. 2007; Huang et al. 2013; Klug and Bonsall 2014). For instance, in the few earwig species where it has been studied (i.e., the short-winged earwig *Apterygida media*, the European earwig *F. auricularia* and the woodland earwig *Chelidurella guentheri*), egg defence and egg guarding allow mothers to use their forceps to harm or kill intruders, and to spray chemical secretions onto intruders (via the dorsal glands) which effectively repel most predators, whether ants or frogs (Eisner 1960; Gasch et al. 2013). Hence, our findings call for future studies manipulating the presence of predators near the nest (e.g. spiders, scolopendra and pseudoscorpions) and measuring the impact of maternal presence and care on egg survival and development.

Whereas *F. pubescens* mothers express multiple forms of egg care, our data show that expressing this set of behaviours did not entail apparent costs for mothers in terms of self-grooming, weight loss and probability of dying during the first 50 days after egg laying. Although such an apparent lack of costs is consistent with results from two other earwig species (Miller and Zink 2012; Van Meyel et al. 2019)(but see Suzuki 2021), it is still surprising compared to available data on birds and other arthropods (Klug et al. 2012; Klug and Bonsall 2014). This is particularly true in *F. pubescens*, as mothers appear to cease their foraging activity during the 50 days of egg care and can thus only rely on the limited resources they have stored before oviposition to both express egg care and ensure their survival during seven weeks. We propose three non-mutually exclusive explanations for this apparent absence of trade-offs between egg care and the other measured traits. First, the costs of care may not appear until after the eggs have hatched in *F. pubescens*. Such long-term costs have been reported, for instance, in the treehoppers *Publilia concava* (Zink 2003) and the lace bug *Gargaphia solani* (Tallamy and Denno 1982) where egg guarding reduces the number and sizes of future broods. However, such a trade-off is absent in the European earwig *F. auricularia* (Meunier et al. 2012; Ratz et al. 2016) and it is still unclear whether it may occur in *F. pubescens* as we do not yet know whether females produce multiple clutches (we did not manage to obtain second clutches under laboratory conditions). The second hypothesis is that mothers store sufficient resources before oviposition to mask the effects of investment trade-offs during egg care (Stearns 1992; Edward and Chapman 2011). This hypothesis could (at least partially) explain our results as we reared our field-sampled females with an *ad libitum* amount of food before egg laying, and the nature of food resources can affect second clutch production in the European earwig (Berleur et al. 2001). Finally, the third hypothesis is that mothers find other energy resources during the period of egg care to mitigate the costs of care. In line with this hypothesis, we found that mothers gained more weight when more of their eggs disappeared from the nest, suggesting that they did eat part of their clutch during the 50 days of egg development and that this consumption is a resource input. Filial egg cannibalism is a common phenomenon in oviparous

animals (Manica 2002; Klug and Bonsall 2007) - including other earwig species (Knabke and Grigarick 1971; Butnariu et al. 2013; Van Meyel and Meunier 2020) -, where it can be a non-adaptive response to stress or an adaptive behaviour allowing mothers to reallocate resources to future reproduction and/or a higher quality of care to current clutches (Sargent 1992; Rohwer 2002). Whether filial egg cannibalism is an adaptive behaviour in *F. pubescens* and thus whether egg cannibalism can help mothers offset the cost of care on their longevity or future clutches production remain open questions in *F. pubescens*.

Somewhat surprisingly, our results show contrasting benefits of care for *F. pubescens* eggs. Without predators, pathogens and other harsh environmental conditions, these eggs survived for up to three weeks in the absence of the mothers, their survival rate during this period was surprisingly higher in the absence than in the presence of the mothers, but no eggs hatched in the absence of the mothers. These three points contrast with results obtained in other Dermapteran species. In particular, abandoned eggs typically die within a few days due to fungal development (even under standard laboratory conditions) in the ring-legged earwig *Euborellia annulipes* (Klostermeyer 1942), the maritime earwig *A. maritima* (Miller and Zink 2012) and the European earwig *F. auricularia* (Boos et al. 2014), and earwig eggs always show a higher survival rate in the presence compared to the absence of a mother - even in case of filial egg cannibalism (e.g. Boos et al. 2014; Van Meyel and Meunier 2020). These intriguing results suggest that, contrary to the other earwig species, *F. pubescens* eggs exhibit long-term resistance against the development of fungi and other pathogens (under standard laboratory conditions) but require the presence of mothers to terminate their development and/or successfully hatch. This need may be due to specific actions of mothers that enhance late embryonic development and/or facilitate the hatching process. Such processes have been reported in a few earwig species from ancestral lineages, e.g. *Marava arachidis* (Spongiphoridae) and *Labidura riparia* (Labiduridae) (Caussanel 1966; Patel and Habib 1978), where mothers bite the eggs at the time of hatching to help the emergence of juveniles. However, this phenomenon is absent in most of the other earwig species where it has been investigated (Matzke and Lass 2005; Tourneur et al. 2020). Further studies are thus required to analyse the behaviour of *F. pubescens* mothers during egg hatching and get new insights into how the dependence on mothers for hatching evolved among Dermapterans.

To conclude, our results confirm the presence of egg care and reveal the extended diversity of its forms in the earwig *F. pubescens* (Matzke and Lass 2005; Haas 2018). They then reveal that the benefits of maternal presence for the eggs are not the same in *F. pubescens* as in the maritime earwig *A. maritima* (Greer et al. 2020) and the European earwig *F. auricularia* (Boos et al. 2014). While *A. maritima* and *F. auricularia* eggs cannot survive the absence of their mothers for more than a few days, *F. pubescens* eggs survive better in the absence than in the presence of mothers during the first 30 days post-oviposition (under standard laboratory conditions) and need the presence of a mother later on produce juveniles. Overall, our study emphasizes the importance to study the diversity, costs and benefits of egg care in poorly studied taxonomic groups to improve our general understanding of the evolution of egg care and its potential cheating strategies (Clutton-Brock 1991; Gross 2005; Kramer and Meunier 2019).

STATEMENTS AND DECLARATIONS

The authors declare no competing interests.

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AUTHOR CONTRIBUTION

CL and JM: Conceptualization, methodology and validation. NM: Data acquisition. NM, JM: Formal analysis. NM and JM: Manuscript writing — original draft. NM, CL, JM: Manuscript reviewing and editing.

DATA ACCESSIBILITY

The dataset analysed in this study and the associated R script are available as supplementary files.

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