

**PROCEEDINGS OF  
THE ROYAL SOCIETY B**

BIOLOGICAL SCIENCES

---

**Residual correlation shows that European earwigs do not  
trade off clutch and egg size.**

Journal:	<i>Proceedings B</i>
Manuscript ID	Draft
Article Type:	Research
Subject:	Evolution < BIOLOGY
Keywords:	trade off, clutch size, egg size, resource allocation, life history, insect
Proceedings B category:	Evolution

**SCHOLARONE™**  
Manuscripts

**Author-supplied statements**

Relevant information will appear here if provided.

**Ethics**

*Does your article include research that required ethical approval or permits?:*

*Statement (if applicable):*

No permits were required for this work.

**Data**

*It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:*

*Statement (if applicable):*

CUST\_IF\_YES\_DATA :No data available.

If yes, please tell us how your data or code can be accessed and provide a link to your data if it is in a repository for the editors and reviewers to use.

<https://doi.org/10.17605/OSF.IO/KWCS8>

CUST\_REPOSITORY\_LINKS :No data available.

***Conflict of interest***

I/we declare we have no competing interests.

*Statement (if applicable):*

CUST\_STATE\_CONFLICT :No data available.

***Use of AI***

*Please provide a statement of any use of AI technology in the preparation of the paper.*

No, we have not used AI-assisted technologies in creating this article

CUST\_IF\_YES\_DECLARATION\_OF\_AI\_USE :No data available.

## 1   **Abstract**

2   Life history theory predicts that clutch and egg size trade off because both traits compete for the  
3   same limited resource pool. Tests of this prediction often show a positive phenotypic correlation,  
4   probably because some females acquire more resources than others and can produce more and  
5   larger eggs. To accurately assess whether a trade-off exists, it is necessary to examine within-  
6   individual correlations, since phenotypic correlations can be misleading. I addressed this issue  
7   using a multivariate mixed model to decompose the phenotypic correlation between egg number  
8   and size in European earwigs (*Forficula auricularia*) into among-female and within-female  
9   (residual) components. I found that earwigs do not trade off clutch and egg size; instead, these  
10   traits are positively correlated. This unexpected result is likely due to changes in ovarian structure  
11   after laying the first clutch, combined with how limited resources are allocated to fewer  
12   developing oocytes in the second clutch. Contrary to expectation, evidence suggests that the  
13   among-female correlation is negative. Additionally, I found that second clutches have greater  
14   variation in egg size than first clutches, although the average variation in egg size among females  
15   is similar across clutches. Further research is needed to clarify the proximate reasons for the  
16   tendency of second clutches to have fewer and smaller eggs than first clutches, as well as to  
17   identify the proximate and ultimate causes of the greater variation in egg size in second clutches.

18

19

20

21

22

23 **Introduction**

24 Maternal investment is allocated between offspring fitness and quantity, with larger eggs  
25 generally enhancing offspring fitness [1]. A limited pool of reproductive resources, therefore,  
26 requires females to balance investment between the number and quality of eggs produced during  
27 a reproductive cycle [2–4, see also 5]. However, these traits do not always trade off against each  
28 other [3,4,6–9]. Or at least, they do not appear to trade off. Positive correlations between traits  
29 that should otherwise covary negatively could be due to how individuals acquire resources and  
30 subsequently allocate them among competing traits [10]. Van Noordwijk and DeJong [11, see also  
31 10] explained that whether we observe positive or negative correlations between fitness-related  
32 traits (e.g., egg number or egg size) depends on whether some individuals in a population can  
33 acquire more resources than others and thus possess a larger resource pool that can be partitioned  
34 to competing traits. Consequently, such variation in acquisition can lead to a positive correlation  
35 between traits (e.g., egg number vs. egg size) when measured across individuals within a  
36 population, while masking allocation trade-offs within individuals (assuming that all individuals  
37 follow a similar allocation strategy) [i.e Simpson's Paradox, 12]. This means that females that  
38 acquire more reproductive resources can produce more and larger eggs, but must nevertheless  
39 trade off size and number.

40 Careau and Wilson [13] argue that revealing a trade-off when contrasting processes occur at the  
41 among- and within-individual levels requires partitioning the phenotypic correlation between two

42 competing traits into its among- and within-individual components. This can be achieved by  
43 repeatedly measuring traits of interest (i.e. egg number and size) for a group of individuals and  
44 then using multivariate mixed models to estimate the among- and within-individual correlations.  
45 To my knowledge, no study has yet adopted this approach to show that females indeed trade off  
46 egg number and size, despite these traits positively correlating across a population of females. I  
47 use the approach of Careau and Wilson [13] here to test the hypothesis that European earwigs  
48 (*Forficula auricularia*) trade off clutch and egg size. *F. auricularia* is an ideal insect for testing  
49 this hypothesis because females lay a single clutch of eggs in a subterranean burrow within a  
50 short period of time (i.e. hours) [14]. Females care for eggs and the nymphs for up to 2 weeks  
51 post-hatching [14,15]. Earwigs in Quebec, Canada, are semelparous because the harsh  
52 environmental conditions extend the incubation and egg-care period beyond the point at which a  
53 second clutch is possible [16]. However, females can be induced to lay a second clutch under  
54 optimal laboratory conditions. I use this system to test the prediction that if resource allocation to  
55 clutches is greater among than within individuals, then the phenotypic and among-individual  
56 correlations between egg size and number will be positive, but the within-individual correlation  
57 will be negative because individual females trade off egg number for size. Second, I compare the  
58 average number and size of eggs across clutches to test whether fitness gains are optimised at a  
59 specific egg quantity or quality [e.g., 2]. If so, one trait should not differ between clutches (e.g.,  
60 egg number), whereas the other (e.g., egg size) is adjusted accordingly [17]. Alternatively,  
61 females laying a second clutch may recognise their low residual reproductive value and,  
62 consequently, terminally invest in current reproduction by producing either more or larger eggs in

63 this clutch [18]. Finally, I explore whether eggs in first and second clutches differ in their size  
64 variation at the among- and within-female (clutch) levels [e.g. 9].

## 65 **Methods**

66 I collected adult female earwigs in September and October 2024 in an urban parks (Parc  
67 Outremont) in Montréal, Canada. All earwigs were brought into the laboratory, assigned a unique  
68 ID, and individually placed in a 90-mm-diameter Petri dish containing a thin layer of moist sand.

69 Females were provided a cotton-plugged water vial and fed TetraMin Tropical fish flakes ad  
70 libitum. Females were maintained in an incubator (Percival) at 10°C in constant darkness.

71 Females were checked daily for oviposition. When a female laid eggs, I recorded the date and  
72 collected all eggs from the sand and placed them on filter paper in a new Petri dish. The eggs  
73 were then photographed under a Leica S6D stereo microscope (Leica Microsystems Inc.,  
74 Concord, ON, Canada) at 0.68x magnification using Enersight software (Leica Microsystems  
75 Inc., Concord, ON, Canada), which automatically adds a scale bar to the photo. Eggs were then  
76 discarded.

77 To stimulate females to lay a second clutch of eggs, I recreated a brief period of spring where  
78 they were allowed to accumulate resources for egg production and replenish their sperm stores.  
79 To achieve this, females that had recently oviposited were placed in a new Petri dish containing a  
80 cotton-plugged water vial, TetraMin Tropical fish flakes, and a shelter consisting of four 4 cm-  
81 long pieces of paper straw (Blowholes, Markham, Canada) glued together. These Petri dishes  
82 were placed in a 23 °C incubator with a 12L:12D light: dark cycle. Females were maintained  
83 under these conditions for two weeks, at which time a haphazardly chosen stock male from our

84 colony was placed with her. The pair was kept together for a week, after which a new stock male  
85 replaced the original male, and that pair was kept together for another week. Females were then  
86 transferred to the 10 °C incubator and treated as previously until they laid their second clutch, at  
87 which point their eggs were photographed. Females were euthanised by freezing after laying their  
88 second clutch, and their pronotum was photographed as described above. Females were then  
89 weighed to the nearest 0.01 mg using a Sartorius Secura 224-1S analytical balance. Females were  
90 weighed three times, with each weighing bout separated by four days. I used Fiji image analysis  
91 software [19] to measure the length of the female pronotum and the perimeter of each egg to the  
92 nearest 0.001 mm. Both traits were measured three times, with each measurement separated by 4  
93 days.

#### 94 **Statistical analysis**

95 I calculated the repeatability of the body mass, pronotum length and egg perimeter measurements  
96 using the R package *rptR* [20]. I entered the trait of interest as the response variable, female ID as  
97 a random effect, and assumed a Gaussian distribution. Each analysis was based on 1000 bootstrap  
98 samples. Because the measurements of my three traits were highly repeatable (pronotum length:  
99  $R$  [95% CI] = 0.98 [0.97, 0.99]; body mass:  $R$  [95% CI] = 0.99 [0.988, 0.996]; egg perimeter in  
100 the first brood:  $R$  [95% CI] = 0.977 [0.976, 0.979] and in the second brood:  $R$  [95% CI] = 0.93  
101 [0.926, 0.937]). I used each female's mean value for each trait in all subsequent analyses.  
  
102 I reduced the two measurements representing body size (pronotum length and body mass) to a  
103 single value (PC1) by performing a principal components analysis (PCA) on the correlation  
104 matrix of standardized measurements using the *prcomp* function in the stats package in R [21].

105 The first PC accounted for 60.8% of the variation. I also standardised female body mass relative  
106 to body size using the scaled mass index procedure of Peig and Green [22,23,see also 24].

107 I tested the prediction that egg number and egg size trade off within females using a Bayesian  
108 multivariate linear mixed-effects model (*brms* package, [25]). Egg number and egg perimeter  
109 were entered as scaled response variables, and *res\_cor* was set to TRUE to estimate the within-  
110 individual (residual) correlation ( $r_{\text{within}}$ ) between egg number and egg size. I assumed a Gaussian  
111 error distribution for both traits to permit the calculation of within-female residuals. Clutch  
112 number (first or second) was entered as a fixed effect to test whether the two clutches differed in  
113 egg number or egg size. This model also included female scaled mass as a continuous covariate  
114 because body size generally correlates with fecundity in insects [26]. Female ID was included as  
115 a random effect via the term (1|a|id), ensuring that random effects were correlated within each  
116 female. I assessed which of the four measures of female body size (pronotum length, body mass,  
117 PC1, or scaled mass) provided the greatest explanatory power by running three models, each with  
118 a different measure, and then comparing them, in addition to a null model without a size measure,  
119 using leave-one-out cross-validation (LOO) [27]. Pronotum length, body mass, and scaled mass  
120 were scaled (mean = 0, sd = 1) before analysis. The model that included pronotum length as a  
121 continuous covariate provided the best fit (Expected Log Predictive Density (ELPD) = -6749.35).  
122 I report the among- ( $r_{\text{among}}$ ) and within- (residual,  $r_{\text{within}}$ ) female correlations and associated 95%  
123 credible intervals (CrIs) from the model and sum these two values to estimate the phenotypic  
124 correlation ( $r_p$ ) and its associated 95% CrI.

125 I examined whether the first and second clutches of eggs differed in egg size variation among  
126 ( $V_{\text{among}}$ ) and within ( $V_{\text{within}}$ ) females by constructing a univariate hierarchical linear mixed-effects

127 model with scaled mean egg perimeter as the response variable, clutch (first or second) as a fixed  
128 effect, and female body mass as a continuous covariate. I also included, as random effects, a  
129 random slope for each clutch for each female. In the dispersion part of the model, I included  
130 clutch as a fixed effect to estimate the within-individual (i.e. residual) variance in egg size for  
131 each clutch. I then tested whether the first and second clutch differed in egg size at the among-  
132 and within-female levels.

133 Bayesian mixed models were run for 10000 iterations (3000 warm-up iterations) across 6 chains,  
134 with a thinning interval of 2 (total post-warm-up samples = 21,000). I used weakly informative  
135 normal priors ( $N(0,10)$ ) for fixed effects and positively bound exponential (1) priors for random  
136 effects in multivariate models. The univariate hierarchical mixed models were run using default  
137 priors. I performed posterior predictive checks to ensure adequate model fits, while trace plots  
138 confirmed that models converged with low among-chain variability ( $Rhat = 1.00$ ). I report  
139 posterior means with 95% credible intervals (CrIs) for all parameter estimates, where inference  
140 was based on CrIs that did not include zero.

## 141 **Results**

142 I did not support the prediction that egg number and egg size positively correlate either  
143 phenotypically ( $r_p$  [95% CrI] = -0.08 [-0.36, 0.22]; [Figure 1](#)) or among females ( $r_{\text{among}}$  [95% CrI]  
144 = -0.13 [-0.41, 0.17]). Contrary to prediction, egg number and size were positively, rather than  
145 negatively, correlated at the within-individual level ( $r_{\text{within}}$  [95% CrI] = 0.06 [0.03, 0.09]).

146 I found that second clutches ( $\bar{x} = 34.14 \pm 17.17$  eggs, range: 1 - 69 eggs,  $n = 42$  clutches) were,  
147 on average, smaller than first clutches ( $\bar{x} = 51.55 \pm 16.13$  eggs, range: 21 - 86 eggs,  $n = 42$

148 clutches; multivariate mixed model: Estimate [95% CrI] = -0.68 [-0.73, -0.63]). Similarly, egg  
149 size was smaller, on average, in second clutches ( $\bar{x} = 3.41 \pm 0.20$  mm, range: 3.11 - 4.11 mm)  
150 versus first clutches ( $\bar{x} = 3.54 \pm 0.21$  mm, range: 3.10 - 3.93 mm; Estimate [95% CrI] = -0.92 [-  
151 0.96, -0.88]). These findings suggest that larger clutches had, on average, larger eggs, which  
152 supports the aforementioned positive within-female correlation. Female pronotum length (body  
153 size) was not correlated with either clutch (Estimate [95% CrI] = 0.06 [-0.18, 0.30]) or egg  
154 (Estimate [95% CrI] = -0.03 [-0.24, 0.16]) size. ### Egg size exhibited significant repeatability  
155 across female broods ( $R$  [95% CI] = 0.40 [0.21, 0.57]) while clutch size did not ( $R$  = 0.03 [0.0,  
156 0.32]).###

157 There was no difference in egg size variation between first and second clutches among females (   
158  $\Delta V_{\text{among}}$  [95% CrI] = 0.11 [-0.39, 0.65]; Figure 2) but within-clutch egg size variation was smaller  
159 in first than in second clutches ( $\Delta V_{\text{within}}$  [95% CrI] = -0.15 [-0.18, -0.12]; Figure 2). Within-clutch  
160 egg size variation (i.e. standard deviation of egg size per clutch) was related to clutch size in first  
161 ( $\rho = 0.36$ ,  $p=0.020$ ) but not in second ( $\rho = -0.14$ ,  $p=0.401$ ) clutches.

## 162 Discussion

163 My multivariate repeated-measures analysis of clutch and egg size found no evidence that female  
164 European earwigs trade off egg number and egg size. Despite failing to support general life  
165 history theory [3,8] and contradicting the results of a previous study in this species [28], it is the  
166 first, to my knowledge, to partition the phenotypic correlation between egg number and size into  
167 its among- and within-individual components. Although many studies have supported the  
168 prediction that egg number and size trade off, some have not [3,4]. Because these previous

169 studies relied on phenotypic correlations to examine the relationship between egg number and  
170 size, it is not possible to assess the extent to which this prediction is empirically supported across  
171 taxa, given the propensity for phenotypic correlations to generate spurious and misleading  
172 associations. For example, Koch and Meunier [- 28] showed that, in an Italian population of *F.*  
173 *auricularia*, residual egg number and residual egg size (adjusted for female body mass) are  
174 negatively correlated at the phenotypic level. However, these findings must be treated with  
175 caution; they are based on pseudo-replicated data (both clutches for each female were pooled and  
176 treated as independent), a situation that can lead to Simpson's Paradox [12] and spurious  
177 correlations because within-individual relationships are masked by among-individual variation.  
178 Indeed, I also observed a negative, albeit weaker, correlation at the phenotypic level. However,  
179 by partitioning the variance into its among- and within-individual components, I found that  
180 females do not make the predicted trade-off. Rather, I found evidence that egg number and size  
181 are positively correlated within females.

182 My study revealed that second clutches comprised, on average, fewer and smaller eggs than first  
183 clutches, which can be explained at both the proximate and ultimate levels of causation. My  
184 findings are consistent with those of another study on a Montreal population [29] and with one  
185 involving an Italian population [28]. Tourneur and Gingras [29] proximally attributed the fewer,  
186 smaller eggs in second clutches to ovarian structure and function in *F. auricularia*. Specifically,  
187 they suggested that second clutches are smaller than first ones because some (or all) ovarioles  
188 become non-functional and thus produce no eggs after the first clutch. This reduction in ovariole  
189 number might explain the smaller second clutches that I observed here, but why did females not  
190 produce larger eggs and thus exhibit the expected number-size trade-off? One possibility is that

191 females had a shallower resource pool from which to build eggs for the second clutch, for  
192 example, because they had less time to accumulate reproductive resources for the second clutch  
193 than for the first. Females in the wild presumably spent from mid-spring to mid-fall acquiring  
194 resources for reproduction, while they had only about a month in the laboratory to do so for the  
195 second one. Hence, by partitioning their fewer resources equally to each functional ovariole  
196 during their second bout of oogenesis, females produced fewer and smaller eggs than in their first  
197 clutches. This proximate explanation assumes that females use a resource-allocation strategy for  
198 eggs that does not vary across their clutches.

199 Producing fewer but smaller eggs seems like a costly fitness decision since, in most animal taxa,  
200 larger eggs generally have a higher probability of hatching and producing larger offspring, which,  
201 in turn, have a higher probability of surviving to adulthood [e.g. birds: 30,amphibians:  
202 31,reptiles: 32,fish: 33]. Although this does not appear to be the typical case in insects [34],  
203 larger eggs are more likely to hatch and to produce larger nymphs in *F. auricularia* [28], so egg  
204 size appears to ultimately have some positive fitness effects for the mother and offspring in this  
205 species. Therefore, the smaller earwig eggs in the second clutch by female *F. auricularia* might  
206 have reduced fitness, except for two extenuating factors. First, maternal care in this species likely  
207 improves the survival chances of smaller eggs [e.g., 35,36], and the poor outcomes commonly  
208 associated with smaller nymphs might be mitigated by maternal provisioning [15]. Second,  
209 smaller eggs tend to hatch faster as development time is positively related to egg size across  
210 animal species [37]. This would be advantageous if a second clutch is produced later in the  
211 reproductive season, such as mid-winter, because it would mean the eggs would hatch at a time  
212 of year (e.g., late-winter) that allows nymphs to emerge at an optimal time in spring. Empirical

213 evidence, however, suggests that time-to-hatch is unrelated to egg mass in at least one (Italian)  
214 population of *F. auricularia* [28]. This latter population, however, is from a more temperate  
215 locale than Montreal, which experiences a milder climate and thus perhaps less intense selection  
216 on reduced development time. I did not find the predicted positive among-female correlation  
217 between clutch and egg size. Rather, the weak negative among-individual correlation between  
218 clutch and egg size suggests that variance in resource allocation may exceed variance in resource  
219 acquisition in this population of earwigs [see 13]. In other words, some female earwigs in my  
220 study population might prioritise investment in egg number versus egg size and vice versa. Taken  
221 together, my results resemble Careau and Wilson's [13] "sink or swim" scenario, which is  
222 generally reserved for performance trade-offs. That is, females in my population of earwigs might  
223 ultimately produce an among-female (albeit weak) trade-off due to differences among females in  
224 how they allocate resources to clutch and egg size, with some females prioritising egg number  
225 over size, while also producing a positive residual correlation due to a combination of ovary  
226 (dis)function, and the equal apportionment of fewer resources to eggs. Further research is needed  
227 to identify the proximate mechanisms underlying the observed multilevel correlation patterns.

228 Among-female variation in average egg size was similar in both clutches, meaning that females  
229 exhibited similar levels of individuality in average egg size in both clutches. The repeatability of  
230 average egg size between clutches could indicate that egg size is a significantly heritable trait  
231 [e.g. 38]. This would not be surprising as egg size has been demonstrated to be significantly  
232 heritable in a variety of insect species, including *Callosobruchus chinensis* seed beetles [39],  
233 *Parnara guttata guttata* butterflies [40], *Lobesia botrana* moths [41], and spruce budworm  
234 (*Choristoneura fumiferana*) [42]. Moreover, the lack of between-female variation in average egg

235 size between first and second clutches suggests that the food-acquisition environment (i.e. wild  
236 vs. lab) had little effect on average egg size.

237 In contrast, I found evidence that variation in egg size within a clutch was greater in second  
238 clutches than in first clutches, the opposite of the pattern observed in birds. [e.g., 43]. Empiricists  
239 have argued that lower variation in egg size within a clutch is probably linked to environmental  
240 factors and food availability. For example, desert finches (*Rhodopsiza obsoleta*) produced  
241 similar-sized eggs when environmental conditions were stable [43], collared flycatchers  
242 (*Ficedula albicollis*) produced larger eggs with the laying sequence in favourable conditions [9],  
243 and blue tits (*Parus caeruleus*) in better nutritional condition had clutches with less variation in  
244 egg size [44]. Although information on intraclutch egg-size variation and its proximal drivers is  
245 scarce in insects, the same principles may apply, given that female earwigs in my study had less  
246 time to accumulate resources and maximise their body condition before producing their second  
247 clutch. If true, then females might have allocated resources maximally to the eggs in their first  
248 clutch, following an individual allocation strategy based on intrinsic factors such as body  
249 condition. This strategy would produce individual-specific egg sizes that are consistent across  
250 eggs within a clutch. In second clutches, by contrast, females might have allocated an optimal  
251 (but smaller) amount of resources to each oocyte until the last few oocytes, when they had fewer  
252 resources remaining and thus produced a few significantly smaller eggs. I did not record laying  
253 order in this study and therefore cannot assess whether larger eggs were laid first or last. Within-  
254 clutch variation in egg size is adaptive in birds. For example, larger eggs later in the egg-laying  
255 sequence may be a brood-survival strategy that counteracts the effects of hatching asynchrony,  
256 whereas smaller eggs later in the laying sequence may be a brood-reduction strategy [45].

257 However, it is unknown whether variation in egg size has an equivalent adaptive function in  
258 insects expressing maternal care.

259 In conclusion, by partitioning variance into its among- and within-individual components, I found  
260 that female European earwigs do not trade off clutch and egg size. Instead, I found a positive  
261 correlation between egg number and size and some evidence for an among-female trade-off. I  
262 also discovered that second clutches consist of eggs with more variable size than first clutches,  
263 but the among-female variation in average egg size was similar between the two clutches.

264

## 265      **References**

- 266      1. Clutton-Brock TH. 1991 *The Evolution of Parental Care*. Princeton University Press.
- 267      2. Smith CC, Fretwell SD. 1974 The optimal balance between size and number of offspring.  
268      *Am Nat* **108**, 499–506.
- 269      3. Roff D. 1992 *Evolution of Life Histories: Theory and Analysis*. New York, NY: Chapman  
270      & Hall, Inc.
- 271      4. Fox CW, Czesak ME. 2000 Evolutionary ecology of progeny size in arthropods. *Annu  
272      Rev Entomol* **45**, 341–369.
- 273      5. Parker GA. 1982 Why are there so many tiny sperm? Sperm competition and the  
274      maintenance of two sexes. *J Theor Biol* **96**, 281–294.
- 275      6. Cavaleiro FI, Santos MJ. 2014 Egg number-egg size: An important trade-off in parasite  
276      life history strategies. *Int J Parasitol* **44**, 173–182.
- 277      7. Bernardo J. 1996 The particular maternal effect of propagule size, especially egg size:  
278      Patterns, models, quality of evidence and interpretations. *Am Zool* **36**, 216–236.
- 279      8. Stearns SC. 1992 *The Evolution of Life Histories*. Oxford University Press.
- 280      9. Hargitai R, Török J, Tóth L, Hegyi G, Rosivall B, Szigeti B, Szöllösi E. 2005 Effects of  
281      environmental conditions and parental quality on inter-and intraclutch egg-size variation in the  
282      collared flycatcher (*ficedula albicollis*). *The Auk* **122**, 509–522.
- 283      10. Reznick D, Nunney L, Tessier A. 2000 Big houses, big cars, superfleas and the costs of  
284      reproduction. *Trends Ecol Evol* **15**, 421–425.
- 285      11. Van Noordwijk AJ, Jong G de. 1986 Acquisition and allocation of resources: Their  
286      influence on variation in life history tactics. *Am Nat* **128**, 137–142.
- 287      12. Simpson EH. 1951 The interpretation of interaction in contingency tables. *Journal of the  
288      Royal Statistical Society: Series B (Methodological)* **13**, 238–241.
- 289      13. Careau V, Wilson R. 2017 Of uberfleas and krakens: Detecting trade-offs using mixed  
290      models. *Integr Comp Biol* **57**, 362–371.
- 291      14. Meunier J. 2024 The biology and social life of earwigs (dermaptera). *Annu Rev Entomol*  
292      **69**, 259–276.
- 293      15. Staerkle M, Kölliker M. 2008 Maternal food regurgitation to nymphs in earwigs (*forficula  
294      auricularia*). *Ethology* **114**, 844–850.
- 295      16. Tourneur J-C. 2018 Factors affecting the egg-laying pattern of *forficula auricularia*  
296      (dermaptera: Forficulidae) in three climatologically different zones of north america. *The  
297      Canadian Entomologist* **150**, 511–519.

- 298 17. Winkler DW, Wallin K. 1987 Offspring size and number: A life history model linking  
299 effort per offspring and total effort. *Am Nat* **129**, 708–720.
- 300 18. Clutton-Brock TH. 1984 Reproductive effort and terminal investment in iteroparous  
301 animals. *Am Nat* **123**, 212–229.
- 302 19. Schindelin J *et al.* 2012 Fiji: An open-source platform for biological-image analysis. *Nat  
303 Methods* **9**, 676–682.
- 304 20. Stoffel MA, Nakagawa S, Schielzeth H. 2017 RptR: Repeatability estimation and  
305 variance decomposition by generalized linear mixed-effects models. *Methods Ecol Evol* **8**, 1639–  
306 1644.
- 307 21. R Core Team. 2025 R: A language and environment for statistical computing.
- 308 22. Peig J, Green AJ. 2009 New perspectives for estimating body condition from mass/length  
309 data: The scaled mass index as an alternative method. *Oikos* **118**, 1883–1891.
- 310 23. Peig J, Green AJ. 2010 The paradigm of body condition: A critical reappraisal of current  
311 methods based on mass and length. *Funct Ecol* **24**, 1323–1332.
- 312 24. Kelly CD, Tawes B, Worthington A. 2014 Evaluating indices of body condition in two  
313 cricket species. *Ecology and Evolution* **4**, 4476–4487.
- 314 25. Bürkner P-C. 2017 brms: An R package for Bayesian multilevel models using Stan.  
315 *Journal of Statistical Software* **80**, 4308.
- 316 26. Honek A. 1993 Intraspecific variation in body size and fecundity in insects: A general  
317 relationship. *Oikos*, 483–492.
- 318 27. Vehtari A, Gelman A, Gabry J. 2017 Practical Bayesian model evaluation using leave-  
319 one-out cross-validation and WAIC. *Statistics and Computing* **27**, 1413–1432.
- 320 28. Koch LK, Meunier J. 2014 Mother and offspring fitness in an insect with maternal care:  
321 Phenotypic trade-offs between egg number, egg mass and egg care. *BMC Evol Biol* **14**, 125.
- 322 29. Tourneur J-C, Gingras J. 1992 Egg laying in a northeastern North American (montréal,  
323 québec) population of *forficula auricularia* l. (Dermaptera: Forficulidae). *The Canadian  
324 Entomologist* **124**, 1055–1061.
- 325 30. Williams TD. 1994 Intraspecific variation in egg size and egg composition in birds:  
326 Effects on offspring fitness. *Biol Rev Camb Philos Soc* **69**, 35–59.
- 327 31. Ficetola GF, De Bernardi F. 2009 Offspring size and survival in the frog *rana latastei*:  
328 From among-population to within-clutch variation. *Biol J Linn Soc* **97**, 845–853.

- 329 32. Nelson NJ, Thompson MB, Pledger S, Keall SN, Daugherty CH. 2004 Egg mass  
330 determines hatchling size, and incubation temperature influences post-hatching growth, of tuatara  
331 sphenodon punctatus. *J Zool* **263**, 77–87.
- 332 33. Einum S, Fleming IA. 2000 Highly fecund mothers sacrifice offspring survival to  
333 maximize fitness. *Nature* **405**, 565–567.
- 334 34. Church SH, Donoughe S, Medeiros BAS de, Extavour CG. 2019 Insect egg size and  
335 shape evolve with ecology but not developmental rate. *Nature* **571**, 58–62.
- 336 35. Kölliker M. 2007 Benefits and costs of earwig (*forficula auricularia*) family life. *Behav*  
337 *Ecol Sociobiol* **61**, 1489–1497.
- 338 36. Boos S, Meunier J, Pichon S, Kölliker M. 2014 Maternal care provides antifungal  
339 protection to eggs in the european earwig. *Behav Ecol* **25**, 754–761.
- 340 37. Shine R. 1978 Propagule size and parental care: The ‘safe harbor’ hypothesis. *J Theor*  
341 *Biol* **75**, 417–424.
- 342 38. Falconer DS, MacKay TFC. 1996 *An Introduction Quantitative Genetics*. Essex, England:  
343 Pearson Education Limited.
- 344 39. Yanagi S, Oikawa T, Miyatake T. 2006 Heritability and genetic correlation estimates for  
345 egg size and number in callosobruchus chinensis (coleoptera: bruchidae). *Ann Entomol Soc Am*  
346 **99**, 364–368.
- 347 40. Seko T, Miyatake T, Fujioka S, Nakasuji F. 2006 Genetic and environmental sources of  
348 egg size, fecundity and body size in the migrant skipper, parnara guttata guttata (lepidoptera:  
349 hesperiidae). *Popul Ecol* **48**, 225–232.
- 350 41. Torres-Vila L, Cruces-Calderá E, Rodríguez-Molina M, Cauterruccio L. 2012 Host plant  
351 selects for egg size in the moth lobesia botrana: Integrating reproductive and ecological trade-offs  
352 is not a simple matter. In *Moths: Types, ecological significance and control methods* (ed L  
353 Cauterruccio), pp. 145–167. New York, NY: Nova Science Publishers.
- 354 42. Harvey GT. 1983 Environmental and genetic effects on mean egg weight in spruce  
355 budworm (lepidoptera: tortricidae). *The Canadian Entomologist* **115**, 1109–1117.
- 356 43. Yosef R, Zduniak P. 2008 Variation in clutch size, egg size variability and reproductive  
357 output in the desert finch (*rhodospiza obsoleta*). *J Arid Environ* **72**, 1631–1635.
- 358 44. Nilsson J-Å, Svensson E. 1993 Causes and consequences of egg mass variation between  
359 and within blue tit clutches. *J Zool* **230**, 469–481.
- 360 45. Slagsvold T, Sandvik J, Rofstad G, Lorentsen Ö, Husby M. 1984 On the adaptive value of  
361 intraclutch egg-size variation in birds. *The Auk* **101**, 685–697.
- 362

363

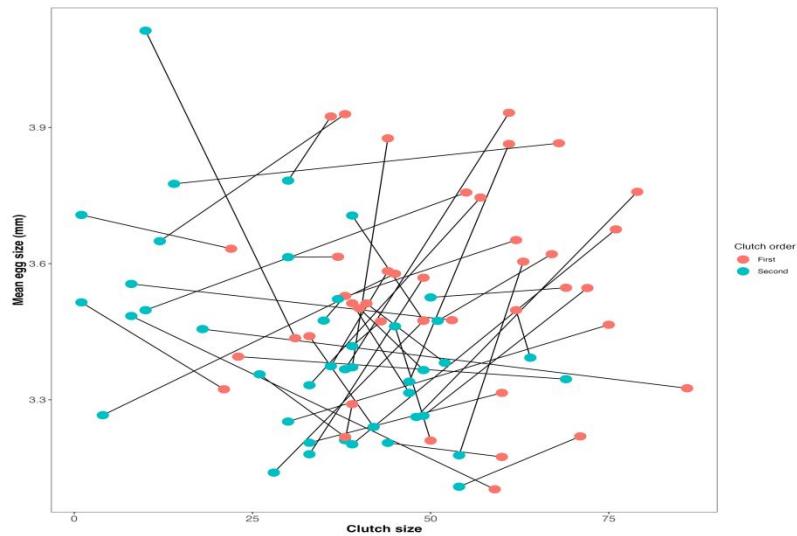


Figure 1: Mean egg perimeter (mm) plotted against clutch size for the first (salmon) and second (blue) clutches of  $n = 42$  female European earwigs (*F. auricularia*). Data are raw values.

364

365

366

367

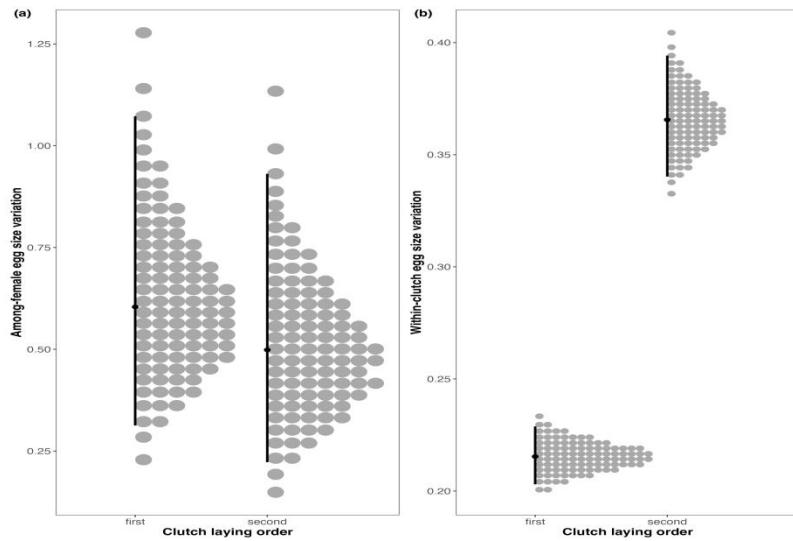
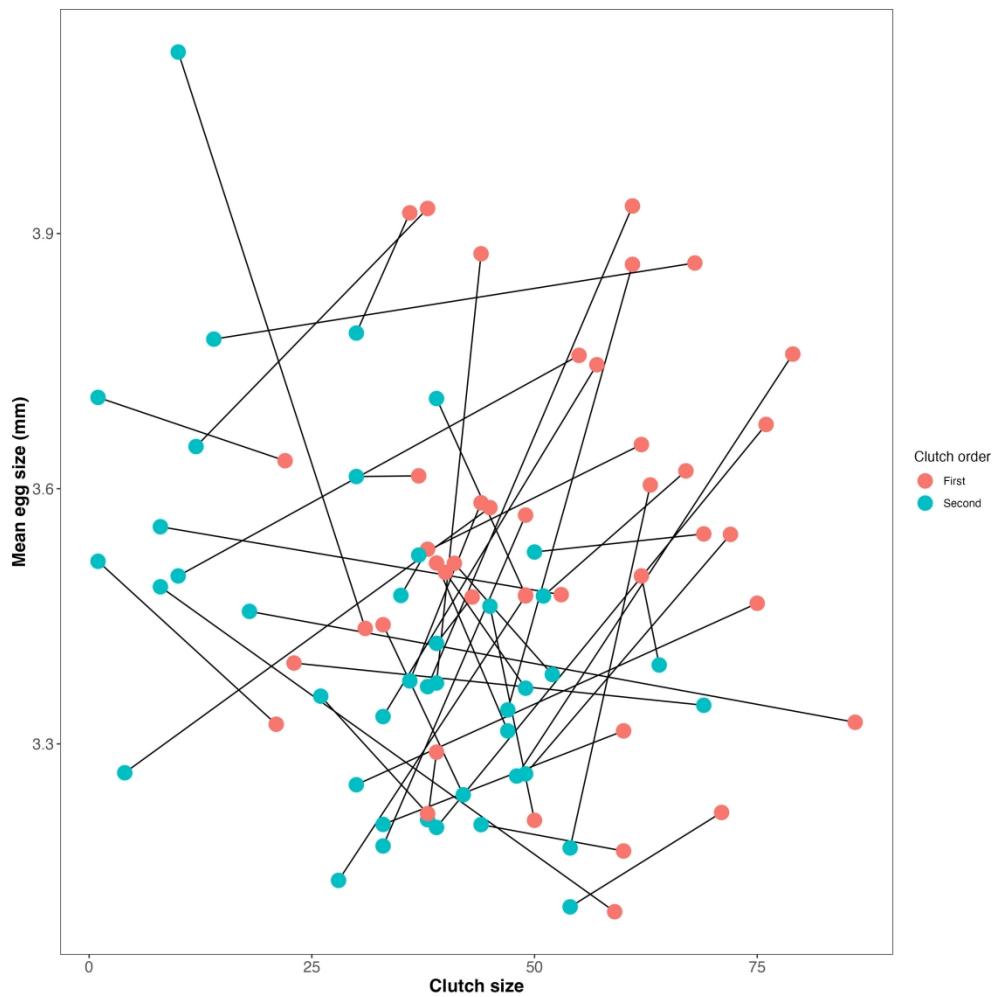
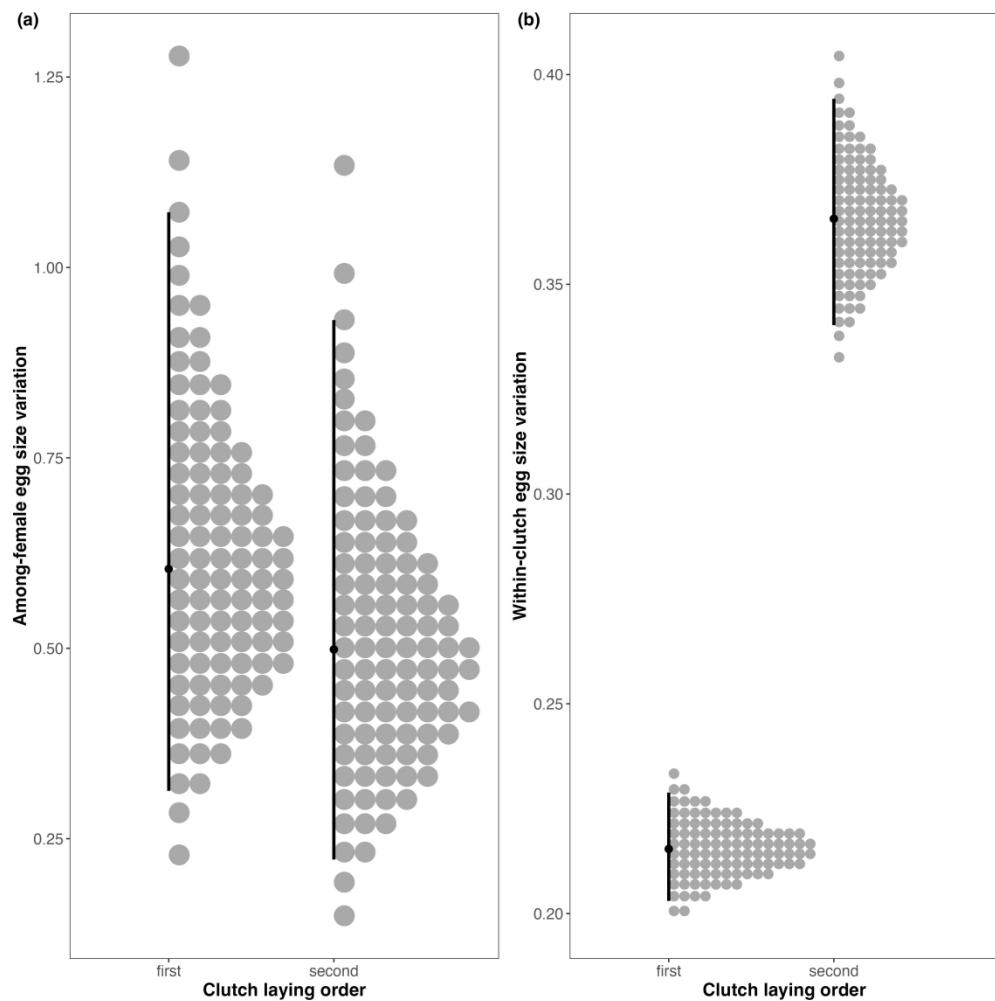


Figure 2: (a) Among and (b) within-female egg size variation in the first and second clutches of  $n = 42$  female European earwigs (*F. auricularia*).

368



1146x1146mm (72 x 72 DPI)



1146x1146mm (72 x 72 DPI)