

1 **Thermal regimes, but not mean temperatures, drive patterns of rapid**  
2 **climate adaptation at a continent-scale: evidence from the introduced**  
3 **European earwig across North America**

4 ***Running title:*** Climate adaptation in earwigs

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## ABSTRACT

13 The recent development of human societies has led to major, rapid and often inexorable  
14 changes in the environment of most animal species. Over the last decades, a growing number  
15 of studies formulated predictions on the modalities of animal adaptation to climate change,  
16 questioning how and at what speed animals should adapt to such changes, discussing the levels  
17 of risks imposed by changes in the mean and/or variance of temperatures on animal  
18 performance, and exploring the underlying roles of phenotypic plasticity and genetic  
19 inheritance in this adaption. These fundamental predictions, however, remain poorly tested  
20 using field data. Here, we tested these predictions using a unique continental-scale data set in  
21 the European earwig *Forficula auricularia* L, a univoltine insect introduced in North America  
22 one century ago. We conducted a common garden experiment, in which we measured 13 life-  
23 history traits in 4158 field-sampled earwigs originating from 19 populations across North  
24 America. Our results first demonstrate that in less than 100 generations, this species modified  
25 10 of the 13 measured life-history traits in response to the encountered thermal regimes, defined  
26 as a variation of temperatures between seasons or months (here winter-summer and autumn-  
27 spring temperatures). We found, however, no response to the overall mean monthly  
28 temperatures of the invaded locations. Our use of a common garden setup also suggests that  
29 the observed changes in earwigs' life-history traits first emerged as a plastic response to the  
30 thermal constraints of the different localities, then diverged between populations through  
31 canalization, and ultimately became inherited traits. Overall, these findings provide continent-  
32 scale support to the claims that adaptation to thermal changes occurs quickly, even in insects  
33 with long life cycles, and emphasize the importance of thermal regimes over mean population  
34 temperatures in climate adaptation.

35 **Keywords:** Temperature, Adaptation, Reproductive strategy, Climate change, Invasion,  
36 Dermaptera

## INTRODUCTION

37 The Earth's climate has changed several times throughout history, leading to gradual  
38 modifications of both its natural environments and multiple traits of its resident organisms,  
39 such as their reproduction, survival, abundance and geographic range (Parmesan 2006, Merilä  
40 and Hendry 2014). The dramatic acceleration of climate change observed over the last decades,  
41 however, challenges the ability of resident organisms to track these changes and adapt their life  
42 histories accordingly (Meehl and Tebaldi 2004, Parmesan 2006, Williams et al. 2007), raising  
43 major issues in terms of biodiversity, conservation, ecosystems functioning and animal  
44 evolution (Bellard et al. 2012, Travis et al. 2013).

45 Over the last decades, modelling and theoretical approaches have been developed to  
46 better understand the nature and extent of animals' response to such a climate change  
47 (Parmesan 2006). These studies formulated key predictions on how and at what speed animals  
48 should adapt to such changes, on the respective importance of an increase in the overall mean  
49 temperature and/or seasonality of a population on animal performance, as well as on the  
50 underlying roles of phenotypic plasticity and genetic inheritance in adaption (Nylin and  
51 Gotthard 1998, Kingsolver et al. 2013, Paaijmans et al. 2013, Gilbert et al. 2014, Merilä and  
52 Hendry 2014, Levis and Pfennig 2016, Williams et al. 2017, Corl et al. 2018, Fox et al. 2019,  
53 Rohner et al. 2019). For instance, these studies suggest that a rapid adaptation to climate change  
54 should be facilitated in organisms with fast development and short life-cycles, as found in many  
55 arthropods, whereas it should be more difficult in organisms exhibiting slow development and  
56 long life-cycle, as found in many vertebrates. Species should also be less sensitive to changes  
57 in seasonality compared to changes in overall mean temperatures when there are endotherms  
58 and/or when their entire life-cycle occur within a single season, whereas the opposite pattern  
59 is expected when they are ectotherms and/or have a life-cycle encompassing several seasons.  
60 Finally, phenotypic plasticity is often considered a keystone of rapid adaptation to

61 environmental changes, whereas fixed and inherited patterns of adaptation are often thought to  
62 secondarily derive from the canalization of ancestral plastic variation.

63 Although central in our current understanding of animal's responses to climate change,  
64 these fundamental predictions remain poorly tested in the field (Janion-Scheepers et al. 2017,  
65 Blanckenhorn et al. 2018). This is probably because such field data are difficult to collect, as  
66 it typically requires measuring variation in life-history traits across multiple natural  
67 populations, over several years, and under different levels of climate change. However, a  
68 powerful alternative consists in using field data of introduced species that quickly invaded large  
69 geographic areas exhibiting a broad diversity of thermal constraints (Huey et al. 2000, Bellard  
70 et al. 2016). In this study, we present and analyze such a unique field data set in one of these  
71 species, the European earwig *Forficula auricularia* Linnaeus (Dermaptera: Forficulidae), after  
72 its introduction in North America. This insect exhibits a broad native range extending across  
73 Europe, Asia and northern Africa (Lamb and Wellington 1975) from which it has been  
74 introduced to Australia, New Zealand, East Africa, East Indies, Tasmania and America (Frank  
75 1918, Guillet et al. 2000, Quarrell et al. 2018, Hill et al. 2019). Its presence in North America  
76 was first reported on the Pacific coast in Seattle (WA) in 1907 (Fulton 1924), and then on the  
77 Atlantic coast in Newport (RI) in 1911 (Jones 1917) and in Vancouver (BC) in 1919 (Treherne  
78 1923). From these introductory foci, *F. auricularia* first spread along the coasts to cover areas  
79 ranging from British Columbia to California and from Newfoundland to South Carolina, and  
80 then reached the interior of the continent in both United States of America (Crumb et al. 1941)  
81 and Canada (Wilson 1971, Cantrall 1972, Tourneur 2017). Given that this species produces  
82 only one generation per year (Tourneur and Gingras 1992, Meunier et al. 2012), these historical  
83 records reveal that its successful colonization of North America and thus its adaptation to a  
84 broad diversity of thermal environments occurred in less than 100 generations.

85           Because the univoltine life cycle of the European earwig lasts up to 2 years and  
86 encompasses all seasons and temperatures (Lamb 1976, Meunier et al. 2012), it has long been  
87 thought that annual mean temperatures and/or temperature seasonality could be major  
88 constraints in the success of *F. auricularia* invasions (Vancassel 1984, Hill et al. 2019).  
89 However, it remains unclear whether this species can mitigate these thermal constraints, and  
90 whether it does so by adapting its life cycle and life-history traits (Ratz et al. 2016, Tourneur  
91 2018). The life cycle of the European earwig generally starts with the emergence of new adults  
92 in late spring to early July, with variation among populations. These adults form groups of up  
93 to several hundred individuals, in which both males and females typically mate with several  
94 partners (Weiß et al. 2014, Sandrin et al. 2015, Tourneur 2017). Females then burrow in the  
95 ground from mid fall to early winter and build a nest where they lay their first clutch of eggs.  
96 After egg laying, females stop their foraging activity and provide extensive forms of egg care  
97 until hatching (Gingras and Tourneur 2001, Boos et al. 2014, Koch and Meunier 2014, Thesing  
98 et al. 2015, Diehl and Meunier 2018, Körner et al. 2018). The eggs of this first clutch hatch in  
99 spring and mothers remain with their newly hatched larvae for several weeks, during which  
100 mothers provide larvae with multiple forms of care (Gingras and Tourneur 2001, Kölliker et  
101 al. 2015, Kramer et al. 2015) and larvae exhibit forms of sibling cooperation (Falk et al. 2014,  
102 Kramer et al. 2015, Kramer and Meunier 2016, Körner et al. 2016). A few weeks later, the  
103 family unit is naturally disrupted. While larvae continue their development to adults in new  
104 social groups, some females produce a second clutch of eggs (i.e. iteroparous as compared to  
105 semelparous females), which will also receive pre- and post-hatching care and will hatch in  
106 late spring (Lamb and Wellington 1975, Meunier et al. 2012, Ratz et al. 2016). All females  
107 generally die during the following summer (Albouy and Caussanel 1990).

108           In this study, we used a common garden experiment to explore how *F. auricularia*  
109 responded to the different thermal environments encountered during their North American

110 invasion over the last century, i.e. in less than 100 generations. In particular, we 1) tested  
111 whether and how individuals altered their life history traits in response to the thermal  
112 constraints of the invaded locations, 2) identified to which thermal constraints they adapted to  
113 and 3) investigated the role of phenotypic plasticity in this adaptation. From 1988 to 1995, we  
114 field-sampled individuals originating from 19 populations located from the East to the West  
115 coasts, maintained them under standard laboratory conditions and measured the properties of  
116 the 1<sup>st</sup> and 2<sup>nd</sup> clutches produced by each female in terms of egg laying date, egg number, egg  
117 development time and number of newly hatched larvae. We also recorded the reproductive  
118 strategy of the females (iteroparity versus semelparity), their reproductive outcome (total  
119 number of eggs and larvae produced over lifetime), as well as the experimental survival  
120 duration of the field-sampled males and females. To identify which thermal constraints the  
121 tested earwigs adapted to, we tested whether our measurements could be explained by the  
122 results of a principal component analyses (PCA) of the mean monthly temperatures of each  
123 population. This process characterizes patterns of variation among populations' temperatures  
124 without a priori definitions of their associations, i.e. without predetermining the focus on  
125 overall mean temperatures and/or specific thermal regimes (defined as variation of  
126 temperatures between seasons or months). If *F. auricularia* individuals adapted their life-cycle  
127 and life-history traits to the mean temperatures and/or thermal regimes of the population in  
128 which they have been sampled (and if this adaptation is determined by their genetic background  
129 and/or early life experience), we predict these traits to covary with the overall mean  
130 temperatures and/or variation in seasonal temperatures of their population (i.e. all sampled  
131 populations should show different performance in the common garden). Conversely, if earwig  
132 life-history traits are independent of the thermal environment of the population in which they  
133 have been sampled (i.e. no adaptation) and/or are plastic to their current thermal environment,  
134 we predict no apparent association between the traits measured in our field-sampled individuals

135 and the thermal regimes of their populations (i.e. all sampled populations should show similar  
136 performance in the common garden).

## MATERIAL AND METHODS

### 137 Earwig sampling and laboratory rearing

138 All *F. auricularia* individuals were collected over 7 years among 19 natural populations located  
139 across North America (Figure 1, Table 1). These individuals were mostly collected as adults  
140 using wooden traps (Tourneur 2018) between July and August, and were immediately setup in  
141 glass containers (Mason Jars Company, Erie, Pennsylvania, United States of America) in  
142 groups of 20 to 30 individuals. These containers received two sheets of creased toilet paper as  
143 resting places for earwigs, and were then transported to our laboratory in Montreal, Canada.

144 Upon their arrival, containers were deposited in a shelf covered by a shelter and maintained  
145 under the natural outdoor conditions of Montreal. During their transport and outdoor  
146 maintenance, containers received an *ad libitum* amount of carrots and pollen as a food source  
147 for earwigs, and were supplied with water by means of a cotton pad regularly soaked in water.  
148 This setup allowed earwigs to continue their development, while performing non-controlled  
149 mating and expressing social interactions (Weiß et al. 2014, Sandrin et al. 2015, Kohlmeier et  
150 al. 2016, Körner et al. 2018).

151 One to two months later (between the 7<sup>th</sup> and the 19<sup>th</sup> day of October of each year), we  
152 used 4158 of these field-sampled individuals to set up 2079 mating pairs (from 17 to 356 pairs  
153 per population, see Table 1), in which we subsequently measured 13 life-history traits (see  
154 below). These pairs were set up in Petri dishes (diameter 10 cm) lined with a thin layer of moist  
155 sand, and in which food was changed and substrate humidified once a week. Each Petri dish  
156 was then transferred in a climate chamber and then maintained at  $10 \pm 1$  °C, a temperature

157 close to the overall median temperature of the 19 sampled populations (i.e. 9.5°C, see Table  
158 S1). Food was removed at egg laying to mimic the natural end of earwigs' foraging activity  
159 (Kölliker 2007). At egg hatching, we discarded all newly emerged larvae from the experiments  
160 to trigger a novel ovarian cycle in the mothers and allow their production of a subsequent clutch  
161 (Vancassel and Foraste 1980, Meunier et al. 2012). We then maintained the pairs under the  
162 rearing conditions described above until our experiment ended, i.e. either one year after the  
163 beginning of our laboratory setup or at the death of the adult males and females. Overall, 3927  
164 of the 4158 (94.4%) tested individuals died within the year following the beginning of our  
165 experiments, a value in line with previous data on *F. auricularia* lifespan (Albouy and  
166 Caussanel 1990). Note that recent studies revealed that North American *F. auricularia* L.  
167 encompasses two genetic subspecies with no apparent mixing of their populations (Wirth et al.  
168 1998, Quarrell et al. 2018, Tourneur 2018). Although these subspecies were not considered in  
169 our analyses (our data were collected before the publication of these genetic analyses), the  
170 continuous distribution (unimodal data) of the life history traits measured across populations  
171 (Figures 2 to 4) suggests an absence of species-specific values regarding these measurements.  
172 The potential co-occurrence of the two subspecies in our data set is thus unlikely to bias our  
173 study and its main conclusions.

#### 174 **Measurements of the life-history traits**

175 For each mating pair, we measured 13 life-history traits encompassing the properties of the  
176 resulting 1<sup>st</sup> and 2<sup>nd</sup> clutches (when present), the reproductive strategy and reproductive  
177 outcomes of each female, as well as the experimental survival duration of both field-sampled  
178 males and females. These properties were obtained by recording the date of egg production,  
179 counting the number of eggs produced, calculating the duration of egg development until  
180 hatching (in days) and finally counting the number of larvae at egg hatching in both 1<sup>st</sup> and 2<sup>nd</sup>  
181 clutches (when present). The reproductive strategies and reproductive outcomes of females

182 were obtained by recording whether they were semelparous or iteroparous (i.e. produced one  
183 or two clutches in their lifetime, respectively), and by counting the total number of eggs and  
184 larvae produced per female during their lifetime. Finally, we measured the experimental  
185 survival duration of adult's by counting the number of days each male and female survived  
186 after October 1<sup>st</sup> of the year of field sampling. Although our measurement of survival duration  
187 does not necessarily reflect adults' longevity, as individuals could have different age at field  
188 sampling (see discussion), it nevertheless provides important insights into the period at which  
189 males and females of each population die during the year. Note that 8.1% and 5.4% females  
190 from Santa Cruz and Asheville, respectively, produced a third clutch. This third clutch was not  
191 considered in the present study, as our experiment ended before their hatching.

#### 192 **Extraction of mean temperatures and thermal regimes of each population**

193 We extracted the mean monthly temperature of the 19 studied populations using their GPS  
194 coordinates (Table 1) and the Worldclim database v2.0 (<http://www.worldclim.org/>) with a  
195 spatial resolution of 30 seconds. The mean temperatures provided by the Worldclim database  
196 are calculated over 30 years, from 1970 to 2000. To reduce dimensionality of co-varying  
197 temperatures in our data set while characterizing potential thermal regimes of each population  
198 without a priori definitions of their composition, we then conducted a Principal Component  
199 Analysis (PCA) on the set of 12 mean monthly temperatures per population (Table S1). This  
200 analysis provided us with 12 orthogonal principal components (PCs), out of which we retained  
201 the first three PCs (total variance explained = 98.6%, Table 2). The first components (PC1)  
202 was positively loaded by almost all monthly temperatures, therefore positively reflecting the  
203 overall mean temperature of a population. The second component (PC2) revealed variation in  
204 seasonality between February on one hand, and June, July, and August on the other hand. In  
205 particular, high values of PC2 reflected populations with cold February (winter) and warm  
206 summer, whereas small values of PC2 reflected populations with warm February (winter) and

207 cold summer. Finally, the third component (PC3) captured variation in seasonality between  
208 October and November on one hand, and April and May on the other hand. High values of PC3  
209 therefore characterized populations with cold autumn and warm spring, whereas small values  
210 of PC3 reflected populations with warm autumn and cold spring.

### 211 **Statistical analyses**

212 To test whether *F. auricularia* adapt their life-cycle and life-history traits to North American  
213 temperatures, we conducted a series of 12 linear models (LM in R) and one generalized linear  
214 model (GLM in R) – see Table 3. In the 12 LMs, the three selected PCs and their interactions  
215 were entered as explanatory variables (PC1, PC2 and PC3), whereas the response variable was  
216 either egg laying date, egg number, egg development time and larvae number for the 1<sup>st</sup> or 2<sup>nd</sup>  
217 clutches (a total of 8 LMs), the total number of eggs or larvae produced, or the survival duration  
218 of males or females. Note that both egg laying date and adult's survival duration were  
219 calculated using October 1<sup>st</sup> as day 0. In the GLM, the response variable was the ratio of  
220 iteroparous females per population, which was entered using the command *cbind* in R (to  
221 weight each ratio by the sample size of its population) and fitted to a binomial error distribution  
222 corrected for overdispersion. In all our statistical models, the response variables were the mean  
223 values of each measured trait per population. They were also checked for homoscedasticity and  
224 normality of residuals, as well as simplified stepwise by removing all non-significant  
225 interaction terms (all P > 0.05). To correct for inflated Type-I errors due to multiple testing  
226 (and provide an experiment-wide Type I error rate of 5%), all *P*-values were adjusted using  
227 False Discovery Rate (FDR) correction (Benjamini and Hochberg 1995). All analyses were  
228 conducted using the software R v3.5.1 loaded with the packages *raster*, *FactoMineR*, *rsq* and  
229 *rcompanion*.

## RESULTS

230 The 19 studied populations greatly varied in their mean temperatures and thermal regimes  
231 (Table S1), as well as in the mean values of the 13 traits measured in their sampled individuals  
232 (Figures 2 to 4; Tables S2 to S4). Mean monthly temperatures overall ranged from 22.9°C (July  
233 in Saluda) to -10.1°C (January in Montreal), while thermal amplitudes over a year ranged from  
234 30.7°C (Montreal) to 7.9°C (Santa Cruz). For the traits measured in the 1<sup>st</sup> clutches, the mean  
235 dates of egg production ranged from 47.8 to 132.6 days after the 1<sup>st</sup> of October, the mean  
236 number of eggs per clutch from 23.2 to 66.0, the mean egg development time from 42.2 to 71.4  
237 days and the mean number of larvae per clutch from 11.6 to 44.8. For the 2<sup>nd</sup> clutches, the mean  
238 dates of egg production ranged from 142.0 to 248.2 days after the 1<sup>st</sup> of October, the mean  
239 number of eggs from 14.0 to 38.4, the mean egg development time from 10.0 to 63.7 days and  
240 the mean number of larvae from 0 to 17.7. Finally, the total number of eggs produced ranged  
241 from 28.1 to 83.4, the total number of larvae produced from 13.0 to 46.3, the proportion of  
242 iteroparous females from 0 to 70.8%, the survival duration of males from 82.0 to 299.8 days  
243 after the 1<sup>st</sup> of October and the survival duration of females from 146.0 to 322.5 days after the  
244 1<sup>st</sup> of October.

245 Of the 13 measured traits, 10 varied together with the thermal regimes of the population  
246 of origin (Table 3). Five of these 10 traits were exclusively associated with PC2 (February-  
247 summer temperatures), two traits were exclusively associated with PC3 (autumn-spring  
248 temperatures), and three traits were associated with both PC2 and PC3. By contrast, no traits  
249 were associated with PC1 (overall mean temperatures). The associations with PC2 revealed  
250 that populations with cold February and warm summers (high PC2 values) had females that  
251 produced their 1<sup>st</sup> clutch of eggs earlier and these eggs had longer development time compared  
252 to populations exhibiting warm February and cold summers (low PC2 values, Figure 2).  
253 Similarly, females from the former populations were less likely to produce a second clutch (i.e.

254 to be iteroparous, Figure 3) and when they did so, their 2<sup>nd</sup> clutches eggs were less numerous  
255 (Figure 3) and showed longer development time (Figure 3). Moreover, females and males from  
256 populations with cold February and warm summers lived less long compared to adults from  
257 warm February and cold summers (Figure 4). On the other hand, the effects of PC3 reveal that  
258 populations exhibiting cold autumn and warm spring (high PC3 values) had females that  
259 produced their 1<sup>st</sup> clutch of eggs later in the season and these eggs were less numerous  
260 compared to females from populations with warm autumn and cold spring (low PC3 values,  
261 Figure 2). Females from the former populations also had 2<sup>nd</sup> clutch eggs that exhibited a shorter  
262 developmental time (Figure 3), they produced an overall lower number of eggs (Figure 4) and  
263 had males with a longer survival duration (Figure 4). By contrast, PC1, PC2 and PC3 did not  
264 shape the number of 1<sup>st</sup> clutch larvae, as well as their total number and the dates of 2<sup>nd</sup> clutch  
265 egg laying (Figures 2, 3 and 4; Table 3).

## DISCUSSION

266 Shedding light on how species successfully adapt to a broad set of environmental constraints  
267 is of major importance to improve our general understanding of the mechanisms underlying  
268 animal adaptations to climate change. In this study, we demonstrate that the successful invasion  
269 of the European earwig across North America came with multiple changes in their life-history  
270 traits in response to the thermal regimes (sets of winter-summer and autumn-spring  
271 temperatures), but not to the overall mean temperature of the invaded areas. In particular, our  
272 data from 19 populations revealed that females changed their timing of first reproduction, their  
273 reproductive strategy and investment into egg production when facing different thermal  
274 regimes, while both males and females experimental survival duration varied accordingly. By  
275 contrast, we found no association between thermal regimes and both the timing of second  
276 reproduction and the total number of larvae produced per female.

277 We showed that females produced their first clutch of eggs earlier when they came from  
278 populations facing warm summers and/or warm autumns (PC2 and PC3, respectively), and  
279 were less likely to produce a second clutch in populations with cold February. A plastic  
280 response to warm temperatures on egg laying date would not be surprising: adult earwigs  
281 typically develop and mate during summer and autumn, so that warm temperatures during these  
282 seasons could accelerate their reproductive physiology (as shown in other insect species, Singh  
283 et al., 2018) and thus accelerate egg laying (Tourneur 2018). Similarly, cold Februaries might  
284 slow down the development of 1<sup>st</sup> clutch eggs and thus extend the corresponding period of egg  
285 care. This, in turn, might inhibit females' physiological transformation to produce a second  
286 clutch (Vancassel 1984, Tourneur 2018). Such an apparent plasticity is in line with previous  
287 results showing that cold winters increase the duration of egg development time in *F.*  
288 *auricularia* (Gingras and Tourneur 2001, Körner et al. 2018). It is also in line with other results  
289 demonstrating that tending eggs inhibits vitellogenic activity and the production of juvenile  
290 hormone in the earwig *Labidura riparia* Pallas, two parameters required to activate ovary  
291 development and allow egg production (Vancassel et al. 1984). However, our results were  
292 obtained under common garden conditions, revealing that the observed effects of thermal  
293 regime on egg laying dates are not the outcome of plasticity, but are either due to canalization  
294 (i.e. the same phenotype results regardless of environmental variation) or to the effect of early  
295 life environments faced before field sampling (Nylin and Gotthard 1998). It has been suggested  
296 that traits tightly linked to fitness are more strongly canalized due to past stabilizing selection  
297 (Falconer 1990). Our findings therefore suggest that the observed changes in the timing of first  
298 reproduction and females' reproductive strategy may have first emerged as a plastic response  
299 to the thermal constraints of the different localities, then diverged between populations through  
300 canalization to ultimately become inherited traits – all this in a maximum of 100 generations.

Field Code Changed

301 Our data also reveals that thermal regimes are associated with lifetime egg production,  
302 but not with lifetime larvae production. In particular, the total number of eggs produced per  
303 female decreased with decreasing autumn temperatures, whereas this association vanished with  
304 larvae number. This apparent discrepancy suggests that females from populations with the  
305 warmest autumns lost a larger number of eggs during egg development. A first explanation  
306 could be that these females produced eggs of lower quality and/or were less efficient in egg  
307 care, a process that is essential to ensure egg development until hatching in earwigs (Boos et  
308 al. 2014, Van Meyel et al. 2019). Whereas both effects should be tested in future studies,  
309 previous results may suggest that the second effect is unlikely, as maternal investment in post-  
310 hatching care is not population-specific, at least in Europe (Ratz et al. 2016). Another  
311 explanation is that females consumed a larger part of their clutch in populations with the  
312 warmest compared to the coldest autumns. Filial egg consumption is a common phenomenon  
313 in insects (Elgar and Crespi 1992) and it has been recently reported in several Dermapteran  
314 species, such as the European earwig *F. auricularia* (Koch and Meunier 2014, Van Meyel et  
315 al. 2019) and the maritime earwig *Anisolabis maritima* Bonelli (Miller and Zink 2012). In the  
316 European earwig, this phenomenon has been proposed to reflect an adaptive strategy to limit  
317 female weight loss during the period of egg care (i.e. when they stop all other foraging  
318 activities) and by doing so, to reallocate resources into post-hatching care and/or into a 2<sup>nd</sup>  
319 oogenesis cycle (Koch and Meunier 2014, Tourneur 2018). Given that females lay eggs earlier  
320 in populations with the warmest autumns, this increased egg consumption could be an adaptive  
321 strategy to limit the cost of tending newly hatched offspring earlier in the season (middle of  
322 winter) when food sources are scarce or absent. If this hypothesis holds true, it would suggest  
323 that filial egg cannibalism could be a strategy that *F. auricularia* females have evolved to better  
324 cope with warmer autumns.

325 Furthermore, we found that the survival duration of both males and females were  
326 associated with the thermal regime of the population of origin. In particular, female's and  
327 male's survival duration decreased together with warm summers (and cold Februaries), while  
328 male's survival duration also decreased with warm autumns (and cold springs). The first results  
329 may be a by-product of the effect of temperature on their date of egg laying and/or egg hatching.  
330 In particular, we showed that females from populations facing warm summers are the first to  
331 lay their eggs. Individuals from these populations might thus have been the oldest at the date  
332 of our field sampling, therefore leading to the shortest survival duration in our subsequent  
333 experiment. Surprisingly, there was a sex-specific effect of spring (and autumn) temperatures  
334 on adult's survival duration: males lived up to two times longer in populations with warm  
335 compared to cold springs (as well as cold compared to warm autumns), whereas this effect was  
336 absent in females. This finding may reflect sex-specific sensitivity to high temperatures in  
337 terms of, for instance, physiology or expression of costly behaviors. Whereas some  
338 physiological traits are known to be sex-specific in this species (Kohlmeier et al. 2016,  
339 Vogelweith et al. 2017), further studies should explore the effects of temperature on the  
340 observed differences. Notwithstanding its underlying mechanisms, the long survival duration  
341 of males in warm spring populations opens scope for these males to mate with females of the  
342 subsequent generation, as well as for a possible involvement of fathers into larva care — a  
343 phenomenon reported in other insect species (Smiseth 2014). These two processes remain  
344 unknown in this species, but they could be of central importance in their successful adaptation  
345 to climate change. Hence, follow-up studies should investigate the (re)mating strategies of  
346 earwig males, as well as the expression of paternal care across these populations.

347 Common garden experiments are powerful tools to disentangle the effects of  
348 phenotypic plasticity and genetic background on adaptation (Franks et al. 2014, Stoks et al.  
349 2014, Blanckenhorn et al. 2018). Individuals reared under a common environment are expected

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350 to exhibit homogenized life-history traits if adaptation is the outcome of phenotypic plasticity,  
351 whereas they should exhibit population-specific traits otherwise. Our results are in line with  
352 the latter process for the great majority of the measured life-history traits (10 out of 13),  
353 therefore suggesting that the observed associations between thermal regimes and life-history  
354 traits do not stem from phenotypic plasticity. Further studies are now needed to disentangle  
355 whether the observed associations are the outcome of earwigs' genetic background or early-  
356 life experience. Our tested individuals were mostly collected as adults in the field, so that we  
357 cannot rule out that population-specific constraints occurring during their early developmental  
358 stages have had long-lasting effects on their life-history traits (English et al. 2016). In line with  
359 this hypothesis, food restriction and poor food quality during juvenile stage has been shown to  
360 have negative effects on females' body weight and egg production in *F. auricularia* (Berleur  
361 et al. 2001, Wong and Kölliker 2014). Future studies using field-collected eggs and/or F1  
362 generation individuals should help disentangling among these two processes. Common garden  
363 experiments also do not preclude the possibility of genotype-by-environment interactions on  
364 the measured life-history traits, which can in turn affect the strength and nature of the reported  
365 patterns of adaptation (Merilä and Hendry 2014). Because our common garden experiment was  
366 set up under a single temperature, future studies may repeat our protocol with multiple  
367 temperatures to test the impact of rearing conditions on the strength and nature of the observed  
368 associations between life-history traits and populations' thermal regimes in *F. auricularia*.

369 To conclude, our results demonstrate that the spread of the European earwigs across  
370 North America came with important changes in their life-history traits and life cycle, and that  
371 these changes emerged in a maximum of 100 generations. Whereas we show that some of these  
372 changes are by-products of novel thermal constraints (timing of first reproduction and female  
373 iteroparity), we reveal that others are likely to reflect adaptive strategies to cope with different  
374 autumn temperatures (egg production and the possibility of egg cannibalism). Overall, these

375 findings emphasize that adaptation of an insect with a relatively long life-cycle does not  
376 necessarily operate in response to the overall mean temperatures of the invaded environments,  
377 but to their thermal regimes – i.e. to seasonality and/or mean temperature at specific time of  
378 their life-cycle. Whether the reported adaptations are the product of population-differences in  
379 energetic/metabolic constraints experienced by adults during their early development (Wong  
380 and Kölliker 2014, English et al. 2016), and/or the product of an inherited genetic basis that  
381 varies with thermal regimes (Levis and Pfennig 2016; Corl et al. 2018; Fox et al. 2019), as well  
382 as whether these adaptations are similar across its worldwide distribution (Frank 1918, Guillet  
383 et al. 2000, Huey et al. 2000, Quarrell et al. 2018, Hill et al. 2019) will be investigated in future  
384 studies. On a more general level, our findings emphasize that studying invasive species can  
385 provide unique data sets to empirically and comprehensively test general predictions on  
386 animals' responses to climate change (Gilbert et al. 2014, Merilä and Hendry 2014, Levis and  
387 Pfennig 2016, Hulme 2017, Fox et al. 2019, Rohner et al. 2019), and therefore call for their  
388 open access to the entire research community - a timely task to which the present study  
389 contributes.

#### **AUTHOR CONTRIBUTION STATEMENT**

390 JCT designed the experiment, conducted field samplings, and run the experiments. JM analysed  
391 the data and wrote the first version of the manuscript. The final manuscript was commented  
392 and corrected by all authors.

#### **DATA AVAILABILITY**

393 The complete data set and R script are archived in the open data repository  
394 Zenodo (<https://doi.org/10.5281/zenodo.2652192>).

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## CONFLICT OF INTEREST

401 [The authors of this preprint declare that they have no financial conflict of interest with the](#)  
402 [content of this article. J Meunier is one of the PCI Evol Biol recommenders.](#)

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- 542

543 **Table 1 – Details of the 19 sampled populations.** The table shows the name and location of  
 544 each population, their GPS coordinates (Latitude, Longitude), samplings years, total number  
 545 of mating pair setup across years (N. pairs), and thermal regimes (defined as PC1, PC2 and  
 546 PC3).

Populations	Country	State (USA)/Province (CDN)	Latitude	Longitude	Samplings	N. pairs	PC1	PC2	PC3
<a href="#">Asheville</a>	USA	North Carolina	35.612	-82.566	1994-95	80	4.60	0.73	0.74
Charlestown	USA	Rhode Island	41.383	-71.642	1990	42	1.37	0.73	-0.84
Deschutes	USA	Oregon	44.157	-121.256	1990	17	-1.54	-2.32	-0.27
Enderby	CDN	British Columbia	50.551	-119.14	1989-90	121	-1.68	-0.02	1.14
Ennis lake	USA	Montana	45.447	-111.695	1990	36	-2.86	-0.36	0.02
Kimberley	CDN	British Columbia	49.635	-115.998	1990	94	-5.27	-0.95	0.73
Kingston	USA	Rhode Island	41.486	-71.531	1991	137	1.00	0.76	-0.75
Montreal	CDN	Quebec	45.542	-73.893	1988,1990-95	356	-2.78	2.32	-0.07
Pointe Pelée	CDN	Ontario	41.963	-82.518	1992	47	1.25	2.31	-0.37
Revelstoke	CDN	British Columbia	50.998	-118.196	1989-90	100	-2.69	-0.11	0.95
Rocky knob	USA	Virginia	36.832	-80.345	1993-94	304	1.44	-0.07	0.48
Saluda	USA	North Carolina	35.198	-82.353	1993-95	117	5.03	0.69	0.77
Santa Cruz*	USA	California	36.926	-121.845	1991	130	5.04	-4.50	-0.57
Selkirk	CDN	Ontario	42.834	-79.932	1992-94	233	-0.69	1.35	-0.67
Selinsgrove	USA	Pennsylvania	40.832	-76.872	1993-94	134	1.76	1.83	0.27
Truro	CDN	Nova Scotia	45.372	-63.264	1988	39	-3.46	-0.13	-1.42
Vancouver	CDN	British Columbia	49.252	-123.24	1989,1991	84	0.23	-2.89	-0.05
Waterrock knob	USA	North Carolina	35.464	-83.138	1991-94	167	-1.88	-1.69	0.22
Wheatley	CDN	Ontario	42.094	-82.445	1992	52	1.13	2.31	-0.31

547 \* This population was called San Francisco in (Tourneur 2018).

548

549 **Table 2 – Loadings of the four first principal components (PCs) reflecting combinations**  
 550 **of the 12 mean monthly temperatures across populations.** The traits having significant  
 551 loadings on each PC are in bold.

	PC1	PC2	PC3	PC4
Jan	<b>0.800</b>	-0.589	-0.066	0.083
Feb	0.716	<b>-0.668</b>	0.131	0.139
Mar	<b>0.844</b>	-0.486	0.216	0.048
Apr	<b>0.949</b>	-0.140	<b>0.267</b>	-0.082
May	<b>0.890</b>	0.321	<b>0.286</b>	<b>-0.145</b>
Jun	0.731	<b>0.665</b>	0.123	-0.060
Jul	0.547	<b>0.823</b>	-0.006	<b>0.143</b>
Aug	0.641	<b>0.746</b>	-0.013	<b>0.175</b>
Sep	<b>0.905</b>	0.380	-0.175	-0.019
Oct	<b>0.951</b>	0.019	<b>-0.292</b>	-0.064
Nov	<b>0.931</b>	-0.174	<b>-0.296</b>	-0.112
Dec	<b>0.872</b>	-0.469	-0.113	0.041
<b>Eigenvalues</b>	<b>8.153</b>	<b>3.224</b>	<b>0.453</b>	<b>0.130</b>
Variance explained (%)	<b>67.9</b>	26.9	3.8	1.1
Cumulative variance explained (%)	67.9	94.8	98.6	99.7

552

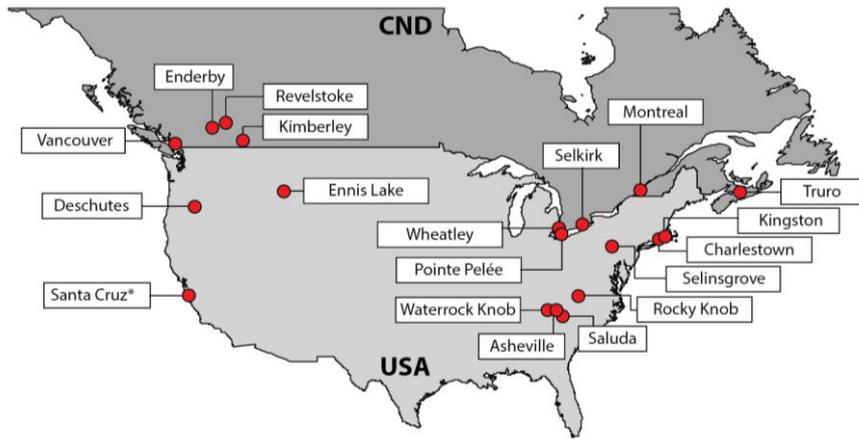
553 **Table 3 –Results of the statistical models on the 13 measured life-history traits.** PC1 positively reflects the overall mean temperature of a  
554 population. High values of PC2 reflect populations with cold February (winter) and warm summer, and vice-versa. High values of PC3 reflect  
555 populations with warm spring and cold autumn, and vice-versa. P-values significant after FDR correction (adj-P) are in bold. Note that FDR  
556 correction transforms each P-value in function of its rank of statistical significance in the data set, which can lead to similar corrected p-values.  
557 Model estimates (estim).

558

	PC1				PC2				PC3			
	estim.	SE	P	adj-P	estim.	SE	P	adj-P	estim.	SE	P	adj-P
<b>First clutch</b>												
Egg laying date	-1.55	1.47	0.307	0.665	-8.92	2.34	0.002	<b>0.011</b>	20.37	6.23	0.005	<b>0.014</b>
Egg number	-0.32	0.82	0.705	0.896	1.87	1.30	0.171	0.234	-11.77	3.47	0.004	<b>0.014</b>
Egg development time	-0.31	0.53	0.575	0.896	2.16	0.85	0.022	<b>0.041</b>	-4.57	2.26	0.061	0.132
Larvae number	-1.28	0.72	0.098	0.425	1.53	1.08	0.180	0.234	-3.85	3.39	0.275	0.357
<b>Second clutch</b>												
Egg laying date	0.79	2.01	0.700	0.896	-3.28	3.26	0.331	0.391	13.13	8.46	0.143	0.233
Egg number	0.08	0.44	0.855	0.896	-1.97	0.72	0.016	<b>0.041</b>	0.27	1.86	0.887	0.887
Egg development time	1.92	0.92	0.059	0.381	3.93	1.48	0.021	<b>0.041</b>	-19.02	4.04	0.001	<b>0.005</b>
Larvae number	-0.05	0.38	0.896	0.896	-1.70	0.59	0.012	<b>0.041</b>	2.96	1.78	0.121	0.224
<b>General</b>												
Total egg number	0.17	1.01	0.866	0.896	-0.15	1.60	0.929	0.929	-13.93	4.26	0.005	<b>0.014</b>
Total larvae number	-1.04	0.77	0.198	0.642	0.60	1.16	0.615	0.666	-3.45	3.61	0.355	0.419
Ratio of iteroparous females	0.01	0.09	0.896	0.896	-0.35	0.13	0.022	<b>0.041</b>	-0.48	0.40	0.254	0.357
Male longevity	-10.26	3.63	0.013	0.165	-23.93	5.77	0.001	<b>0.011</b>	65.49	15.39	0.001	<b>0.005</b>
Female longevity	-4.30	3.74	0.268	0.665	-14.80	5.94	0.025	<b>0.041</b>	13.63	15.86	0.404	0.437

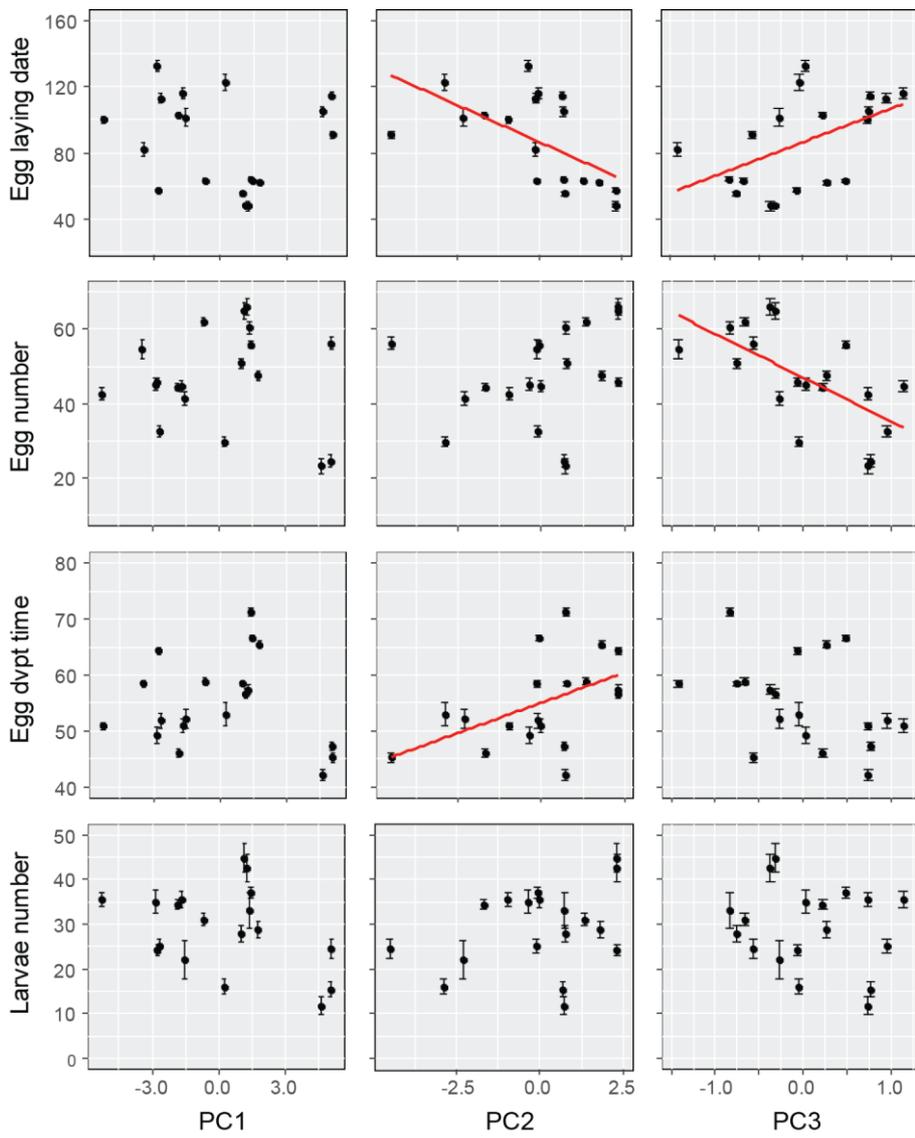
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560 **Figure 1 – Map showing the 19 sampled populations across Canada (CND) and United**  
561 **States of America (USA).** \* This population was called San Francisco in Tourneur (2018).



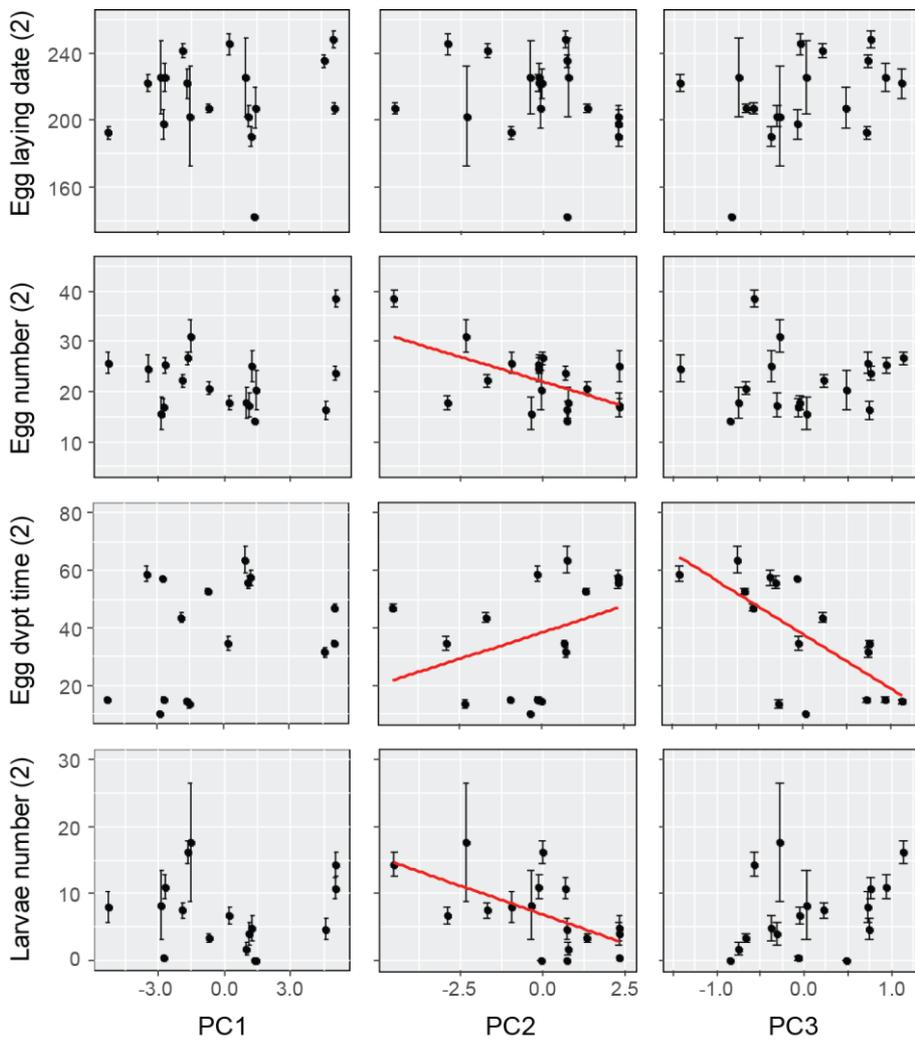
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563 **Figure 2** – Associations between the thermal regimes (PC1, PC2, PC3) of the 19 populations  
564 of origin and 1<sup>st</sup> clutch parameters. The red lines represent correlations that are significant after  
565 FDR correction. Mean values  $\pm$  SE. Egg laying date was calculated using October 1<sup>st</sup> as a  
566 reference (i.e. as day 0).



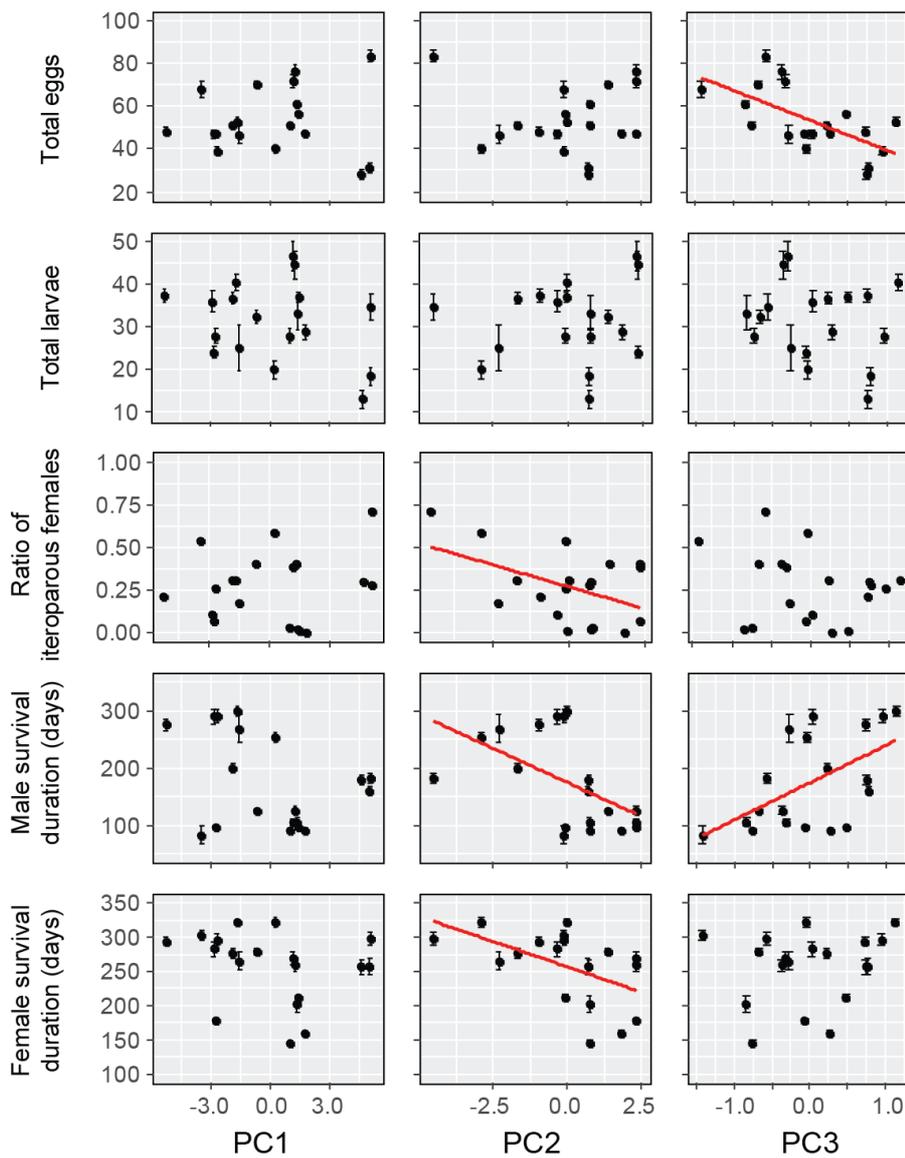
567

568 **Figure 3** – Associations between the thermal regimes (PC1, PC2, PC3) of the 19 populations  
 569 of origin and 2<sup>nd</sup> clutch parameters (when produced). The red lines represent correlations that  
 570 are significant after FDR correction. Mean values  $\pm$  SE. Egg laying date was calculated using  
 571 October 1<sup>st</sup> as a reference (i.e. as day 0).



572

573 **Figure 4** – Associations between the thermal regimes (PC1, PC2, PC3) of the 19 populations  
574 of origin and females' reproductive strategies and outcomes, as well as adult's survival  
575 duration. The red lines represent correlations that are significant after FDR correction. Mean  
576 values  $\pm$  SE.



577