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Variations in seasonal (not mean) temperatures drive rapid adaptations to novel environments at a continent-scale

Running title: Climate adaptation in earwigs

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ABSTRACT

The recent development of human societies has led to major, rapid and often inexorable changes in the environment of most animal species. Over the last decades, a growing number of studies formulated predictions on the modalities of animal adaptation to novel or changing environments, questioning how and at what speed animals should adapt to such changes, discussing the levels of risks imposed by changes in the mean and/or variance of temperatures on animal performance, and exploring the underlying roles of phenotypic plasticity and genetic inheritance. These fundamental predictions, however, remain poorly tested using field data. Here, we tested these predictions using a unique continental-scale data set in the European earwig *Forficula auricularia* L, a univoltine insect introduced in North America one century ago. We conducted a common garden experiment, in which we measured 13 life-history traits in 4158 field-sampled earwigs originating from 19 populations across North America. Our results first demonstrate that 10 of the 13 measured life-history traits are associated with two sets of variations in seasonal temperatures, i.e. winter-summer and autumn-spring. We found, however, no association with the overall mean monthly temperatures of the invaded locations. Furthermore, our use of a common garden setup reveals that the observed patterns of variation in earwigs' life-history traits are not mere plastic responses to their current environment, but are either due to their genetic background and/or to the environmental conditions they experienced during early life development. Overall, these findings provide continent-scale support to the claims that adaptation to thermal changes can occur quickly (in less than 100 generations), even in insects with long life cycles, and emphasize the importance of variation in seasonal temperature over mean population temperatures in climate adaptation.

Keywords: Temperature, Adaptation, Reproductive strategy, Climate change, Invasion, Dermaptera

INTRODUCTION

Adaptation to novel and changing environments is a keystone in our current understanding of species distribution, abundance and evolution (Holt 1990). Over the last century, the development of human activities has led to rapid and often inexorable changes in the environment of many living organisms (Parmesan 2006). These changes occur, for instance, due to human trade and transit, which increasingly favours the transport (invasion) of a large number of animal and plant species out of their native area (Hulme 2009), and possibly bring them to novel environments with unfamiliar biotic and/or abiotic properties (Jeschke and Strayer 2005). These changes can also occur in the native area of these organisms due to the global climate change, a phenomenon that has accelerated over the last decades and now reaches an unprecedented speed (Meehl and Tebaldi 2004, Williams et al. 2007). Because the extent and multiplicity of these rapid environmental changes challenge the ability of resident populations to track them and adapt their life histories accordingly, understanding the nature of animals' adaptation to novel and changing environment is considered a critical, ongoing and challenging question in ecology (Parmesan 2006, Hill et al. 2016, 2019, Courchamp et al. 2017).

Among the multiple parameters that can vary when a species is exposed to a novel or changing environment, the mean and seasonal temperatures can be particularly critical. This is because the severity and duration of changes in the temperatures experienced by an individual during its entire or a specific period of its life cycle can alter a great number of its life history traits and ultimately modify its own fitness. For instance, extended winter durations or exposure to warmer environmental conditions can shape the size and time of first reproduction (Fretwell 1972, Altizer et al. 2006), the duration of foetal development and levels of immune activity (Körner et al. 2018, Zhang et al. 2019), as well as the mobility, morphology and metabolism of individuals (Adamczewski et al. 1993, Danks 2000, Polidori et al. 2019).

Over the last decades, a great number of modelling and theoretical approaches have been developed to better understand the nature and extent of animals' adaptation to novel temperatures (Parmesan 2006). These studies formulated key predictions on how and at what speed animals should adapt to such changes, on the respective importance of an increase in the overall mean temperature and/or seasonality of a population on animal performance, as well as on the underlying roles of phenotypic plasticity and genetic inheritance in adaption (Nylin and Gotthard 1998, Kingsolver et al. 2013, Paaijmans et al. 2013, Gilbert et al. 2014, Merilä and Hendry 2014, Levis and Pfennig 2016, Williams et al. 2017, Corl et al. 2018, Fox et al. 2019, Rohner et al. 2019). For instance, these studies suggest that adaptation to climate change should be rapid in organisms with fast development and short life-cycles, as found in many arthropods, whereas it should be slower in organisms exhibiting delayed development and long life-cycles, as found in many vertebrates. Species should also be less sensitive to changes in seasonality compared to changes in overall mean temperatures when they are endotherms and/or when their entire life-cycle occur within a single season, whereas the opposite pattern is expected when they are ectotherms and/or have a life-cycle encompassing several seasons. Finally, phenotypic plasticity is often considered a keystone of rapid adaptation to environmental changes, whereas fixed and inherited patterns of adaptation are often thought to secondarily derive from the canalization of ancestral plastic variation (Chevin et al. 2010).

Although central in our current understanding of animal's adaptation to novel temperatures, these fundamental predictions remain poorly tested in the field (Janion-Scheepers et al. 2017, Blanckenhorn et al. 2018). This is probably because such field data are difficult to collect, as it typically requires measuring variation in life-history traits across multiple natural populations, over several years, and under different climates. A powerful alternative consists in using field data of introduced species that recently invaded large geographic areas exhibiting a broad diversity of thermal constraints (Huey et al. 2000, Bellard

et al. 2016). The European earwig *Forficula auricularia* Linnaeus (Dermaptera: Forficulidae) is one of these species. This insect exhibits a broad native range extending across Europe, Asia and northern Africa (Lamb and Wellington 1975) from which it has been introduced to Australia, New Zealand, East Africa, East Indies, Tasmania and North America (Frank 1918, Guillet et al. 2000, Quarrell et al. 2018, Hill et al. 2019). Its presence in North America was first reported on the Pacific coast in Seattle (WA) in 1907, and then on the Atlantic coast in Newport (RI) in 1911 and in Vancouver (BC) in 1919 (Crumb et al. 1941). From these introductory foci (Figure 1), historical data suggests that *F. auricularia* first spread along the coasts to cover areas ranging from British Columbia to California and from Newfoundland to South Carolina, and then spread to the interior of the continent in both United States of America and Canada (Crumb et al. 1941, Tourneur 2017)(Historical records are detailed in Appendix S1: Table S1). Given that this species produces only one generation per year (Tourneur and Gingras 1992, Meunier et al. 2012), these data reveal that its successful colonization of North America and thus its adaptation to a broad diversity of thermal environments occurred in less than 100 generations.

In this study, we conducted a common garden experiment to explore how *F. auricularia* responded to the different thermal environments encountered during their North American invasion over the last century, i.e. in less than 100 generations. Because the univoltine life cycle of the European earwig encompasses all seasons and temperatures (Lamb 1976, Meunier et al. 2012), it has long been thought that annual mean temperatures and/or seasonality could be major constraints in its invasive success (Vancassel 1984, Hill et al. 2019). However, it remains unclear whether this species can mitigate these thermal constraints, and whether it does so by adapting its life cycle and life-history traits (Ratz et al. 2016, Tourneur 2018).

Here, we 1) tested whether and how thermal constraints of the invaded locations selected for specific developmental, reproductive and fitness traits (later called life history

traits), 2) identified the thermal constraints to which they adapted and 3) investigated the role of phenotypic plasticity in this adaptation. From 1988 to 1995, we field-sampled individuals originating from 19 populations located from the East to the West coasts, maintained them under standard laboratory conditions and measured the properties of the 1st and 2nd (generally terminal) clutches produced by each female in terms of egg laying date, egg number, egg development time and number of newly hatched larvae. We also recorded the reproductive strategy of the females (iteroparity versus semelparity), their reproductive outcome (total number of eggs and larvae produced over lifetime), as well as the experimental survival duration of the field-sampled males and females. To identify which thermal constraints the tested earwigs adapted to, we tested whether our measurements could be explained by the results of a principal component analyses (PCA) of the mean monthly temperatures of each population. This process characterizes patterns of variation among populations' temperatures without *a priori* definitions of their associations, i.e. without predetermining the focus on overall mean temperatures and/or variation of temperatures between seasons or months. Generating these temperature predictor variables without a priori definitions of their composition was important, as both temperatures' average and seasonal variability can shape animal life histories (Kingsolver et al. 2013). If *F. auricularia* individuals adapted their life-cycle and life-history traits to the mean temperatures and/or seasonal temperature variation of the population in which they have been sampled (and if this adaptation is determined by their genetic background and/or early life experience), we predict these traits to covary with the overall mean temperatures and/or variation in seasonal temperatures of their population (i.e. all sampled populations should show different performance in the common garden). Conversely, if earwig life-history traits are independent of the thermal environment of the population in which they have been sampled (i.e. no adaptation) and/or are plastic to their current thermal environment, we predict no apparent association between the traits measured in our field-

sampled individuals and the seasonal temperature variation of their populations (i.e. all sampled populations should show similar performance in the common garden).

MATERIAL AND METHODS

Earwig biology

The life cycle of the European earwig generally starts with the emergence of new adults in late spring to early July (with variation among populations). These adults form groups of up to several hundred individuals, in which both males and females typically mate with several partners (Weiß et al. 2014, Sandrin et al. 2015, Tourneur 2017). Females then burrow in the ground from mid fall to early winter and build a nest where they lay their first clutch of eggs. After egg laying, females stop their foraging activity and provide extensive forms of egg care until hatching (Gingras and Tourneur 2001, Boos et al. 2014, Koch and Meunier 2014, Thesing et al. 2015, Diehl and Meunier 2018, Körner et al. 2018). The eggs of this first clutch hatch in spring and mothers remain with their newly hatched larvae for several weeks, during which mothers provide larvae with multiple forms of care (Gingras and Tourneur 2001, Kölliker et al. 2015, Kramer et al. 2015) and larvae exhibit forms of sibling cooperation (Falk et al. 2014, Kramer et al. 2015, Kramer and Meunier 2016, Körner et al. 2016). A few weeks later, the family unit is naturally disrupted. While larvae continue their development to adults in new social groups, some females produce a second clutch of eggs (i.e. iteroparous as compared to semelparous females), which will also receive pre- and post-hatching care and will hatch in late spring (Lamb and Wellington 1975, Meunier et al. 2012, Ratz et al. 2016). All females generally die during the following summer (Albouy and Caussanel 1990).

Whereas the European earwig is often considered a pest control in its native range (Moerkens et al. 2012), it has been described as an agricultural pest and a nuisance of human

159 habitations in its newly colonized area (Crumb et al. 1941, Lamb and Wellington 1975, Walker
160 et al. 1993, Quarrell et al. 2016, 2018). Moreover, this species has been suggested to have partly
161 drove the decline of threatened and endangered invertebrates in America, such as the El
162 Segundo Blue Butterfly *Euphilotes bernardino allyni* and the Valley Elder-berry Longhorn
163 Beetle *Desmocerus californicus dimorphus* (Quarrell et al. 2018).

164 **Earwig sampling and laboratory rearing**

165 All *F. auricularia* individuals were collected over 7 years among 19 natural populations located
166 across North America (Figure 1, Table 1). These individuals were mostly collected as adults
167 using wooden traps (Tourneur 2018) between July and August, and were immediately setup in
168 glass containers (Mason Jars Company, Erie, Pennsylvania, United States of America) in
169 groups of 20 to 30 individuals. These containers received two sheets of creased toilet paper as
170 resting places for earwigs, and were then transported to the laboratory in Montreal, Canada.
171 Upon their arrival, containers were deposited in a shelf covered by a shelter and maintained
172 under the natural outdoor conditions of Montreal. During their transport and outdoor
173 maintenance, containers received an *ad libitum* amount of carrots and pollen as a food source
174 for earwigs, and were supplied with water by means of a cotton pad regularly soaked in water.
175 This setup allowed earwigs to perform non-controlled mating and to live in groups, which is
176 similar to their natural living conditions (Weiß et al. 2014, Sandrin et al. 2015, Kohlmeier et
177 al. 2016, Körner et al. 2018).

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

184 close to the overall median temperature of the 19 sampled populations (i.e. 9.5°C, see Appendix
185 S1: Table S2). Food was removed at egg laying to mimic the natural end of earwigs' foraging
186 activity (Kölliker 2007). At egg hatching, we discarded all newly emerged larvae from the
187 experiments to trigger a novel ovarian cycle in the mothers and allow their production of a
188 subsequent clutch (Vancassel and Foraste 1980, Meunier et al. 2012). We then maintained the
189 pairs under the rearing conditions described above until our experiment ended, i.e. either one
190 year after the beginning of our laboratory setup or at the death of the adult males and females.
191 Overall, 3927 of the 4158 (94.4%) tested individuals died within the year following the
192 beginning of our experiments, a value in line with previous data on *F. auricularia* lifespan
193 (Albouy and Caussanel 1990). Note that recent studies revealed that North American *F.*
194 *auricularia* encompasses two genetic subspecies with no apparent mixing of their populations
195 (Wirth et al. 1998, Quarrell et al. 2018, Tourneur 2018). Although these subspecies were not
196 considered in our analyses (our data were collected before the publication of these genetic
197 analyses), the continuous distribution (unimodal data) of the life history traits measured across
198 populations (Figures 2 to 4) suggests an absence of subspecies-specific values regarding these
199 measurements. The potential co-occurrence of the two subspecies in our data set is thus
200 unlikely to bias our study and its main conclusions.

201 **Measurements of the life-history traits**

202 For each mating pair, we measured 13 life-history traits encompassing the properties of the
203 resulting 1st and 2nd clutches (when present), the reproductive strategy and reproductive
204 outcomes of each female, as well as the experimental survival duration of both field-sampled
205 males and females. These properties were obtained by recording the date of egg production,
206 counting the number of eggs produced, calculating the duration of egg development until
207 hatching (in days) and finally counting the number of larvae at egg hatching in both 1st and 2nd
208 clutches (when present). The reproductive strategies and reproductive outcomes of females

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

Extraction of mean and seasonal temperatures of each population

We extracted the mean monthly temperature of the 19 studied populations using their GPS coordinates (Table 1) and the Worldclim database v2.0 (http://www.worldclim.org/) with a spatial resolution of 30 seconds. The mean temperatures provided by the Worldclim database are calculated over 30 years, from 1970 to 2000. To reduce dimensionality of co-varying temperatures in our data set while characterizing the variation in seasonal temperature of each population without *a priori* definitions of their composition, we then conducted a Principal Component Analysis (PCA) on the set of 12 mean monthly temperatures per population (Appendix S1: Table S2). This analysis provided us with 12 orthogonal principal components (PCs), out of which we retained the first three PCs (total variance explained = 98.6%, Table 2). The first component (PC1) was positively loaded by almost all monthly temperatures, therefore positively reflecting the overall mean temperature of a population. The second component (PC2) revealed variation in seasonality between February on one hand, and June, July, and August on the other hand. In particular, high values of PC2 reflected populations with cold February (winter) and warm summer, whereas small values of PC2 reflected populations with

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

Statistical analyses

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

RESULTS

The 19 study sites greatly varied in their mean and seasonal variation of temperature (Appendix S1: Table S2), as well as in the mean values of the 13 traits measured in their sampled individuals (Figures 2 to 4; Appendix S1: Tables S3 to S5). Mean monthly temperatures overall ranged from 22.9°C (July in Saluda) to -10.1°C (January in Montreal), while thermal amplitudes over a year ranged from 30.7°C (Montreal) to 7.9°C (Santa Cruz). For the traits measured in the 1st clutches, the mean ± SE dates of egg production ranged from 47.8 ± 0.8 to 132.6 ± 3.3 days after the 1st of October, the mean ± SE number of eggs per clutch from 23.2 ± 1.9 to 66.0 ± 2.3, the mean ± SE egg development time from 42.2 ± 1.0 to 71.4 ± 0.8 days and the mean ± SE number of larvae per clutch from 11.6 ± 2.0 to 44.8 ± 3.2. For the 2nd clutches, the mean ± SE dates of egg production ranged from 142.0 to 248.2 ± 5.3 days after the 1st of October, the mean ± SE number of eggs from 14.0 to 38.4 ± 1.7, the mean ± SE egg development time from 10.0 ± 3.0 to 63.7 ± 4.6 days and the mean ± SE number of larvae from 0 to 17.7 ± 8.8. Finally, the total number of eggs ± SE produced ranged from 28.1 ± 2.6 to 83.4 ± 2.9, the total number of larvae ± SE produced from 13.0 ± 2.2 to 46.3 ± 3.5, the proportion of iteroparous females from 0 to 70.8%, and the mean survival duration ± SE of males and females from 82.0 ± 15.4 to 299.8 ± 8.6 days and from 146.0 ± 4.7 to 322.5 ± 7.6 days after the 1st of October, respectively.

Of the 13 measured traits, 10 varied together with the seasonal temperature variation of the population of origin (Table 3). Five of these 10 traits were exclusively associated with PC2 (February-summer temperatures), two traits were exclusively associated with PC3 (autumn-spring temperatures), and three traits were associated with both PC2 and PC3. By contrast, no traits were associated with PC1 (overall mean temperatures). The associations with PC2 revealed that populations with cold February and warm summers (high PC2 values) had females that produced their 1st clutch of eggs earlier and these eggs had longer development

283 time compared to populations exhibiting warm February and cold summers (low PC2 values,
284 Figure 2). Similarly, females from the former populations were less likely to produce a second
285 clutch (i.e. to be iteroparous, Figure 3) and when they did so, their 2nd clutch eggs were less
286 numerous (Figure 3) and showed longer development time (Figure 3). Moreover, females and
287 males from populations with cold February and warm summers lived fewer days compared to
288 adults from warm February and cold summers (Figure 4). On the other hand, the effects of PC3
289 reveal that populations exhibiting cold autumns and warm springs (high PC3 values) had
290 females that produced their 1st clutch of eggs later in the season and these eggs were less
291 numerous compared to females from populations with warm autumns and cold springs (low
292 PC3 values, Figure 2). Females from populations with high PC3 values also had 2nd clutch eggs
293 that exhibited a shorter developmental time (Figure 3), they produced an overall lower number
294 of eggs (Figure 4) and had males with a longer survival duration (Figure 4). By contrast, PC1,
295 PC2 and PC3 did not shape the number of 1st clutch larvae, as well as their total number and
296 the dates of 2nd clutch egg laying (Figures 2, 3 and 4; Table 3).

297 **DISCUSSION**

298 In this study, we demonstrate that the successful invasion of the European earwig across North
299 America came with multiple changes in their life-history traits, and that these changes are
300 associated with seasonal variation in the temperatures - but not with overall mean temperatures
301 - of the invaded areas. In particular, our data from 19 populations revealed an association
302 between seasonal temperature variation and females' timing of first reproduction, reproductive
303 strategy and investment into egg production, as well as between seasonal temperature variation
304 and the experimental survival duration of both males and females. By contrast, we found no
305 association between seasonal temperature variation and both the timing of second clutch
306 reproduction and the total number of larvae produced per female.

307 Our data first showed that females produced their first clutch of eggs earlier when they
308 came from populations facing warm summers and/or warm autumns (PC2 and PC3,
309 respectively), and were less likely to produce a second clutch in populations with cold
310 February. A plastic response to warm temperatures on egg laying date could be expected in
311 nature: adult earwigs typically develop and mate during summer and autumn, so that warm
312 temperatures during these seasons could accelerate their reproductive physiology (as shown in
313 other insect species, Singh et al., 2018) and thus accelerate egg laying (Tourneur 2018).
314 Similarly, cold Februaries might slow down the development of 1st clutch eggs and thus extend
315 the corresponding period of egg care. This, in turn, might inhibit females' physiological
316 transformation to produce a second clutch (Vancassel 1984, Gingras and Tourneur 2001,
317 Tourneur 2018, Körner et al. 2018). However, our results were obtained under common garden
318 conditions, which reveals that the observed effects of the variation in seasonal temperature on
319 egg laying dates are not a plastic response to their current environment, but are either due to
320 the environment experienced during their early life development (i.e. before field sampling),
321 or due to an inherited basis that possibly emerged through canalization (Nylin and Gotthard
322 1998, Van Buskrik and Steiner 2009). It has been proposed that traits tightly linked to fitness
323 are more strongly canalized due to past stabilizing selection (Falconer 1990). Our findings may
324 therefore suggest that the observed patterns in the timing of first reproduction and females'
325 reproductive strategy may have first emerged as a plastic response to the thermal constraints of
326 the different localities, then diverged between populations through canalization and ultimately
327 become inherited traits – all this in a maximum of 100 generations. Further experiments with
328 naïve individuals would be required to rule out an effect of early life experience.

329 Our data also reveal that seasonal temperature variation is associated with lifetime egg
330 production, but not with lifetime larvae production. In particular, the total number of eggs
331 produced per female decreased with decreasing autumn temperatures, whereas this association

vanished with larvae number. This apparent discrepancy suggests that eggs from populations with the warmest autumns suffered higher mortality during development. A first explanation of this phenomenon could be that these eggs are of a lower quality and/or that their mothers were less efficient in egg care, a process that is essential to ensure egg development until hatching in earwigs (Boos et al. 2014, Van Meyel et al. 2019). Whereas both effects should be tested in future studies, previous results may suggest that a population-specific efficiency in egg care is unlikely in this species, as a previous study showed that maternal investment in post-hatching care is not population-specific, at least in Europe (Ratz et al. 2016). Another explanation is that females consumed a larger proportion of their clutch in populations with the warmest compared to the coldest autumns. Filial egg consumption is a common phenomenon in insects (Elgar and Crespi 1992) and it has been recently reported in several Dermapteran species, such as the species studied here (Koch and Meunier 2014, Van Meyel et al. 2019) and the maritime earwig *Anisolabis maritima* Bonelli (Miller and Zink 2012). In the European earwig, this phenomenon has been proposed to reflect an adaptive strategy to limit female weight loss during the period of egg care (i.e. when they stop all other foraging activities) and by doing so, to reallocate resources into post-hatching care and/or into a 2nd oogenesis cycle (Koch and Meunier 2014, Tourneur 2018). Given that females lay eggs earlier in populations with the warmest autumns, this increased egg consumption could be an adaptive strategy to limit the cost of tending newly hatched offspring earlier in the season (middle of winter) when food sources are scarce or absent. If this hypothesis holds true, it would suggest that filial egg cannibalism could be a strategy that *F. auricularia* females have evolved to better cope with warmer autumns.

In addition to the above findings, our results show that the survival duration of both males and females was associated with the seasonal temperature variation of the population of origin. In particular, females' and males' survival duration decreased together with warm

summers (and cold Februaries), while male's survival duration also decreased with warm autumns (and cold springs). The first results may be a by-product of the effect of temperature on their date of egg laying and/or egg hatching. We showed that females from populations facing warm summers are the first to lay their eggs. Individuals from these populations might thus have been the oldest at the date of our field sampling, therefore leading to the shortest survival duration in our subsequent experiment. Surprisingly, there was a sex-specific effect of spring (and autumn) temperatures on adult survival duration: males lived up to two times longer in populations with warm compared to cold springs (as well as cold compared to warm autumns), whereas this effect was absent in females. This finding may reflect sex-specific sensitivity to high temperatures in terms of, for instance, physiology or expression of costly behaviors. Whereas some physiological traits are known to be sex-specific in this species (Kohlmeier et al. 2016, Vogelweith et al. 2017), further studies should explore the effects of temperature on the observed differences. Notwithstanding its underlying mechanisms, the long survival duration of males in warm spring populations opens scope for these males to mate with females of the subsequent generation, as well as for a possible involvement of fathers into larva care – a phenomenon reported in other insect species (Smiseth 2014). These two processes remain unknown in the European earwig, but they could be of central importance in their successful adaptation to climate change.

All our results are based on a common garden experiment, a method that is often considered a powerful tool to disentangle the roles of phenotypic plasticity and genetic background on adaptation (Franks et al. 2014, Stoks et al. 2014, Blanckenhorn et al. 2018). Individuals reared under a common environment are typically expected to exhibit homogenized life-history traits if adaptation is the outcome of phenotypic plasticity, whereas they should exhibit population-specific traits otherwise. Our results are in line with the latter process for the great majority of the measured traits (10 out of 13), therefore suggesting that the observed

associations between variation in seasonal temperature and life-history traits do not stem from a plastic response to their current environment. Nevertheless, common garden experiments can also have some limits: they do not necessarily prevent maternal and grand maternal effects, they cannot preclude the possibility of genotype-by-environment interactions on the measured life-history traits, and they are poorly efficient at shedding light on the multiple facets of plasticity (e.g. some traits can be partially plastic, the plastic responses can vary in intensity and slope, and plasticity may become apparent only after certain thresholds)(Franks et al. 2014, Merilä and Hendry 2014, Stoks et al. 2014, Bodensteiner et al. 2019). Concluding on the absence or limited role of plasticity in earwigs' adaptation to seasonality therefore needs further empirical works. These works should, for instance, explore its pattern using lab-generations of each population to control for potential maternal effects, or investigate the multiple facets of adaptation under different common garden conditions (e.g. using different temperatures) (Bodensteiner et al. 2019) and if an apparent plasticity emerge, they should demonstrate its adaptive value.

To conclude, our results demonstrate that the spread of the European earwigs across North America came with important changes in their life-history traits and life cycle, and that these changes emerged in a maximum of 100 generations. Whereas we show that some of these changes are by-products of novel thermal constraints (timing of first reproduction and female iteroparity), we reveal that others are likely to reflect adaptive strategies to cope with different autumn temperatures (egg production and the possibility of egg cannibalism). Overall, these findings emphasize that adaptation of an insect with a relatively long life-cycle does not necessarily operate in response to the overall mean temperatures of the invaded environments, but in response to their seasonality and/or mean temperature at a specific time of their life-cycle. Whether the reported adaptations are the product of population-differences in energetic/metabolic constraints experienced by adults during their early development (Wong

and Kölliker 2014, English et al. 2016), and/or the product of an inherited genetic basis that varies with seasonal temperature variation (Levis and Pfennig 2016; Corl et al. 2018; Fox et al. 2019), as well as whether these adaptations are similar across its worldwide distribution (Frank 1918, Guillet et al. 2000, Huey et al. 2000, Quarrell et al. 2018, Hill et al. 2019) will be investigated in future studies. On a more general level, our findings emphasize that studying invasive species can provide unique data sets to empirically and comprehensively test general predictions on animals' responses to novel environmental conditions and climate change (Gilbert et al. 2014, Merilä and Hendry 2014, Levis and Pfennig 2016, Hulme 2017, Fox et al. 2019, Rohner et al. 2019), and therefore call for their open access to the entire research community - a timely task to which the present study contributes.

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DATA AVAILABILITY

The complete data set and R script are archived in the open data repository Zenodo: https://doi.org/10.5281/zenodo.2652192.

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

Populations	Country	State (USA)/Province (CDN)	Latitude	Longitude	Samplings	N. pairs	PC1	PC2	PC3
Asheville	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

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

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

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

643 **Table 3 –Results of the statistical models on the 13 measured life-history traits.** PC1 positively reflects the overall mean temperature of a
644 population. High values of PC2 reflect populations with cold February (winter) and warm summer, and vice-versa. High values of PC3 reflect
645 populations with warm spring and cold autumn, and vice-versa. P-values significant after FDR correction (adj-P) are in bold. Note that FDR
646 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.
647 Model estimates (estim).

	PC1				PC2				PC3			
	estim.	SE	P	adj-P	estim.	SE	P	adj-P	estim.	SE	P	adj-P
First clutch												
Egg laying date	-1.55	1.47	0.307	0.665	-8.92	2.34	0.002	**0.011**	20.37	6.23	0.005	**0.014**
Egg number	-0.32	0.82	0.705	0.896	1.87	1.30	0.171	0.234	-11.77	3.47	0.004	**0.014**
Egg development time	-0.31	0.53	0.575	0.896	2.16	0.85	0.022	**0.041**	-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
Second clutch												
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	**0.041**	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	**0.041**	-19.02	4.04	0.001	**0.005**
Larvae number	-0.05	0.38	0.896	0.896	-1.70	0.59	0.012	**0.041**	2.96	1.78	0.121	0.224
General												
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	**0.014**
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	**0.041**	-0.48	0.40	0.254	0.357
Male longevity	-10.26	3.63	0.013	0.165	-23.93	5.77	0.001	**0.011**	65.49	15.39	0.001	**0.005**
Female longevity	-4.30	3.74	0.268	0.665	-14.80	5.94	0.025	**0.041**	13.63	15.86	0.404	0.437

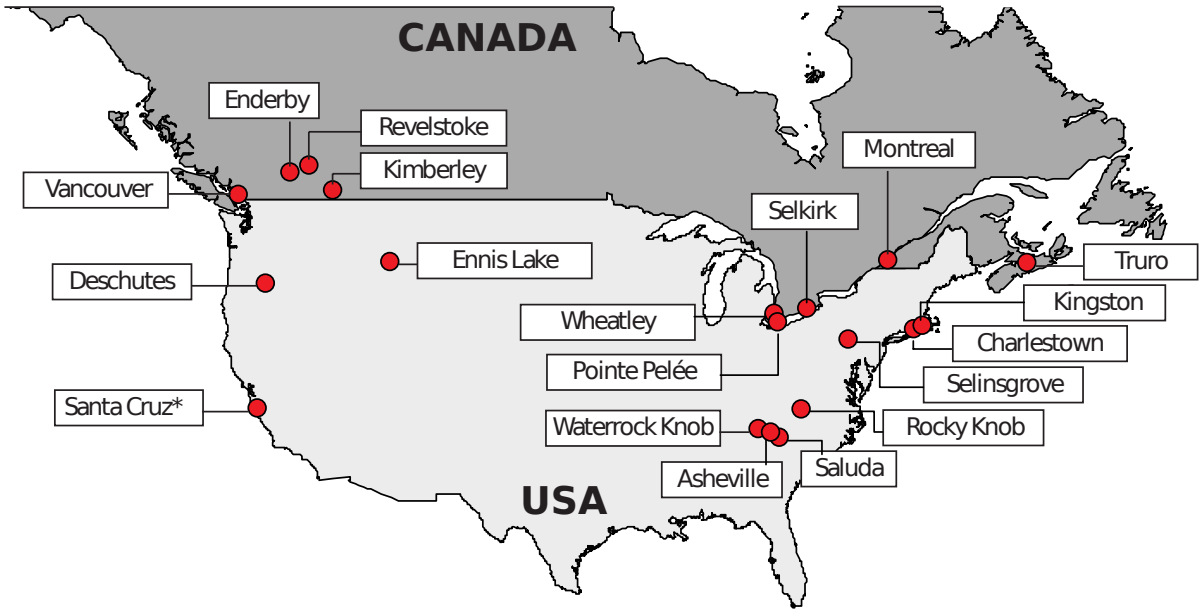
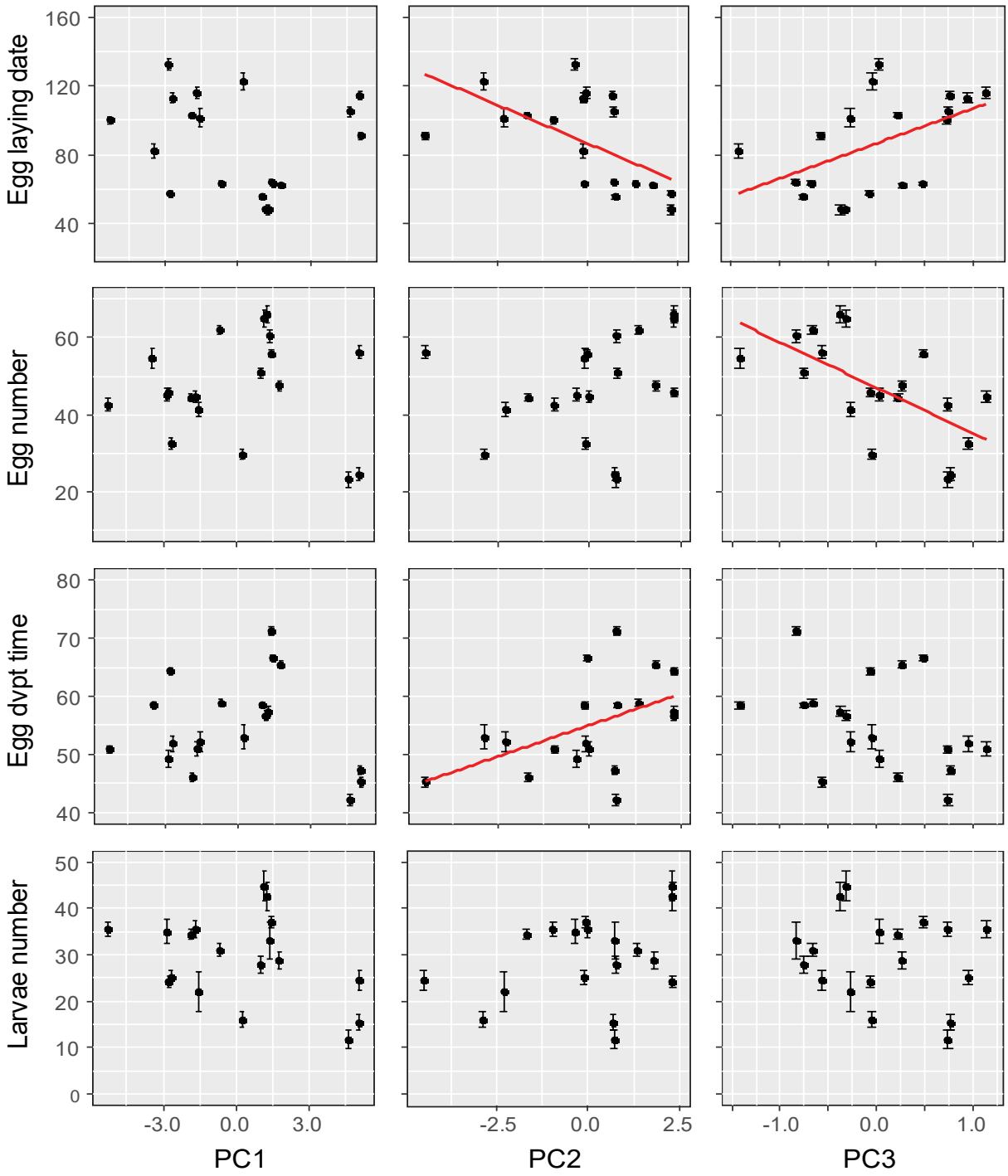
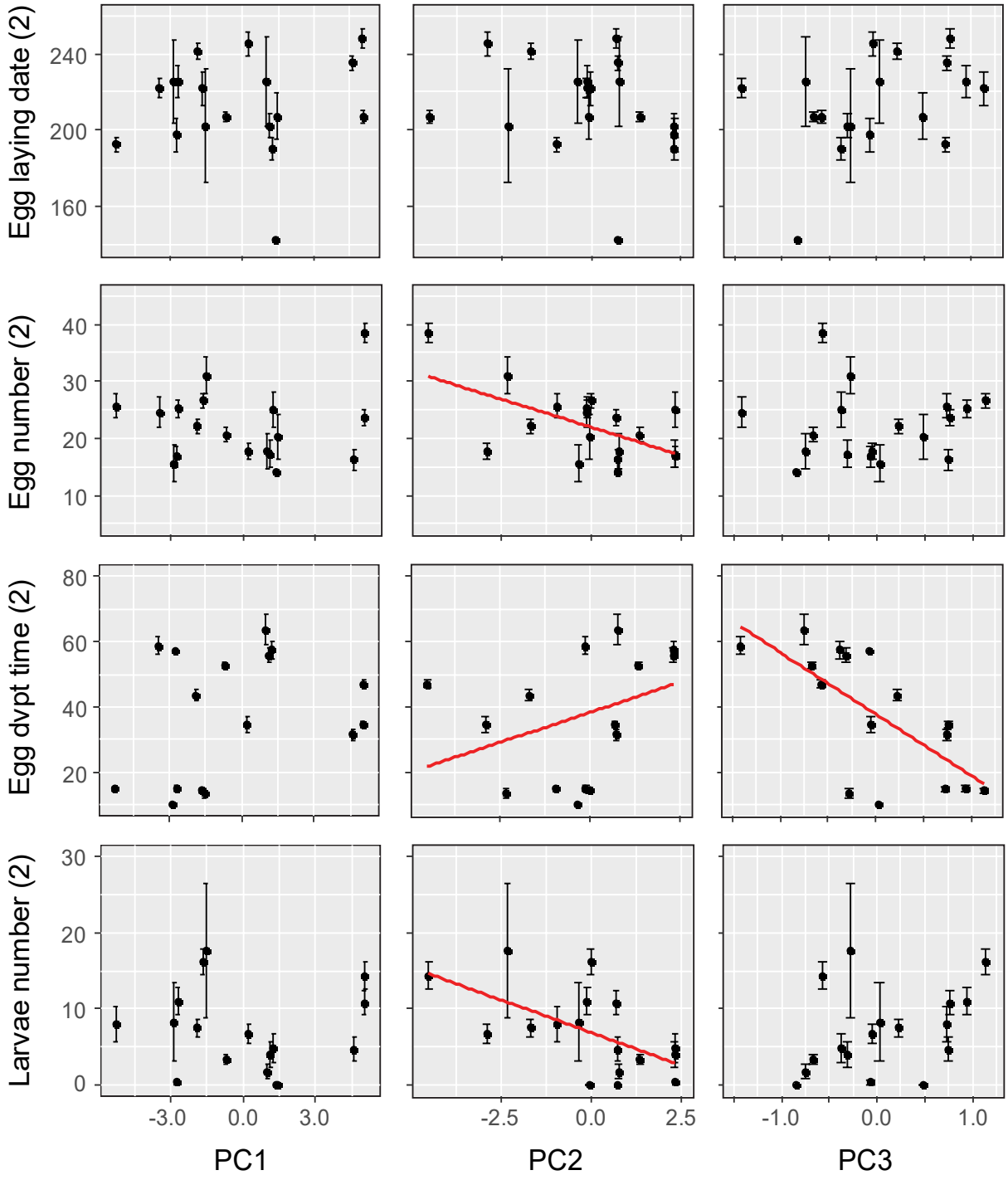


Figure 1 – Map showing the 19 sampled populations across Canada (CND) and United States of America (USA). * This population was called San Francisco in Tourneur (2018).



652 **Figure 2** – Associations between variation in seasonal temperatures (PC1, PC2, PC3) of the
653 19 populations of origin and 1st clutch parameters. Red lines represent correlations significant
654 after FDR correction. Mean values ± SE. Egg laying date was calculated using October 1st as a
655 reference (i.e. as day 0).
656



657

658 **Figure 3** – Associations between variation in seasonal temperatures (PC1, PC2, PC3) of the
659 19 populations of origin and 2nd clutch parameters (when produced). Red lines represent
660 correlations significant after FDR correction. Mean values ± SE. Egg laying date was
661 calculated using October 1st as a reference (i.e. as day 0).

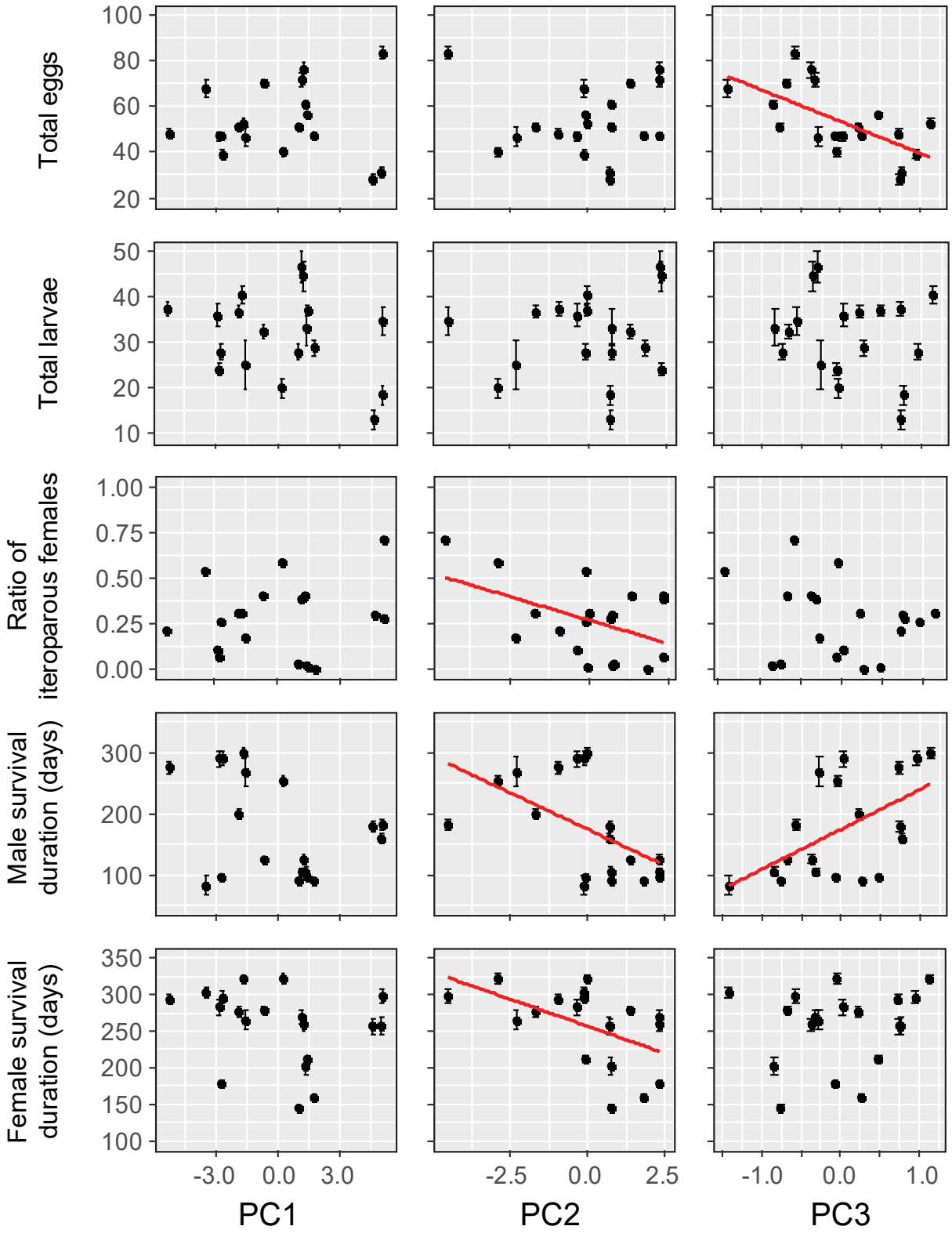


Figure 4 – Associations between variation in seasonal temperatures (PC1, PC2, PC3) of the 19 populations of origin and females' reproductive strategies and outcomes, as well as adult's survival duration. Red lines represent correlations significant after FDR correction. Mean values ± SE.