1   **The successful invasion of the European earwig across North America**

2   **reflects adaptations to thermal regimes but not mean temperatures.**

3   *Running title:* Climate adaptation in earwigs

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ABSTRACT

12   Understanding the mechanisms by which an introduced species adapt to newly encountered

13   habitats is a major question in ecology. A key method to address this question is to collect

14   data on introduced species that have successfully invaded a broad diversity of novel

15   environments, and analyze how their life-history traits changed with these new constraints.

16   Here, we present and analyze such a unique data set in the European earwig *Forficula*

17   *auricularia* L, an insect that invaded North America during the last century. We conducted a

18   common garden experiment, in which we measured 13 life-history traits in 4158 individuals

19   from 19 populations across North America. Our results demonstrate that the successful

20   invasion of this species came with changes in 10 of their life-history traits in response to

21   thermal regimes (winter-summer and autumn-spring temperatures), but with no change in

22   response to the overall mean temperatures of the invaded locations. Importantly, we show

23   that some of these changes are by-products of novel thermal regimes, whereas others reflect

24   adaptive strategies of females to these constraints. Overall, our findings reveal the importance

25   of thermal regimes over mean temperatures in climate adaptation, and emphasize that

26   studying adaptive capabilities is crucial to predict the limits of biological invasions.

27   **Keywords**: Temperature, Adaptation, Reproductive strategy, Climate change, Dermaptera

INTRODUCTION

28   Over the last centuries, the dramatic increase in human trade and transit has facilitated the

29   transport of a large number of animal and plant species out of their native area (Hulme 2009).

30   Although most of these species rapidly disappeared from their novel environment, a few of

31   them remained, adapted and became invasive (Jeschke and Strayer 2005). These biological

32   invasions are often considered a major threat for the maintenance of native biodiversity, and

33   have profound impacts on agriculture, economy and human health (Bradshaw et al. 2016).

34   Understanding what triggers and promotes biological invasions is therefore a major, ongoing

35   and challenging question in population biology, ecology and evolution (Hill et al. 2016;

36   Courchamp et al. 2017; Hill et al. 2019).

37   A key method to better understand the determinants of biological invasions is to

38   collect and analyze large biological data sets on introduced species that have successfully

39   invaded novel environments exhibiting a broad diversity of constraints (Bellard et al. 2016).

40   The European earwig *Forficula auricularia* L. is one of these species. This insect exhibits a

41   broad native range extending across Europe, Asia and northern Africa (Lamb and Wellington

42   1975) from which it has been introduced in Australia, New Zealand, East Africa, East Indies,

43   Tasmania and America (Frank 1918; Guillet et al. 2000; Quarrell et al. 2018; Hill et al. 2019).

44   Its presence in North America was first reported on the Pacific coast in Seattle (WA) in 1907

45   (Fulton 1924), on the Atlantic coast in Newport (RI) in 1911 (Jones 1917) and in Vancouver

46   (BC) in 1919 (Treherne 1923). From these introductory foci, *F. auricularia* first spread along

47   the coasts to cover areas ranging from British-Columbia to California and from

48   Newfoundland to South Carolina, and then reached the interior of the continent in both

49   United States of America (Crumb et al. 1941) and Canada (Wilson 1971; Cantrall 1972;

50   Tourneur 2017). Whereas the European earwig is often considered a pest control in its native

51   range (Moerkens et al. 2012), it has been described as an agricultural pest and a nuisance of

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52   human habitations in its newly colonized area (Crumb et al. 1941; Lamb and Wellington

53   1975; Walker et al. 1993; Quarrell et al. 2016; Quarrell et al. 2018). Moreover, this species

54   has been suggested to have partly drove the decline of threatened and endangered

55   invertebrates in America, such as the El Segundo Blue Butterfly *Euphilotes bernardino allyni*

56   and the Valley Elder-berry Longhorn Beetle *Desmocerus californicus dimorphus* (Quarrell et

57   al. 2018).

58   Because the univoltine life cycle of this species lasts up to 2 years and encompasses

59   all seasons and temperatures (Lamb 1976), it has long been thought that mean temperatures

60   and thermal regimes (defined as variation of temperatures between seasons or months) could

61   be major constraints in the success of *F. auricularia* invasions (Vancassel 1984; Hill et al.

62   2019). However, it remains unclear whether and how this species can mitigate such

63   constraints by adapting its life-cycle and life-history traits (Ratz et al. 2016; Tourneur 2018).

64   The life cycle of this species generally starts with the emergence of new adults in late spring

65   to early July (depending on the populations). These adults form groups of up to several

66   hundred individuals, in which both males and females typically mate with several partners

67   (Weiß et al. 2014; Sandrin et al. 2015; Tourneur 2017). Females then burrow in the ground

68   from mid fall to early winter and build a nest where they lay their first clutch of eggs. After

69   egg laying, females stop their foraging activity and provide extensive forms of egg care until

70   hatching (Gingras and Tourneur 2001; Boos et al. 2014; Koch and Meunier 2014; Thesing et

71   al. 2015; Diehl and Meunier 2018; Körner et al. 2018). The eggs of this first clutch hatch in

72   spring and mothers remain with their newly hatched larvae for several weeks to provide them

73   with multiple forms of care (Gingras and Tourneur 2001; Kölliker et al. 2015; Kramer et al.

74   2015). A few weeks later, the family unit is naturally disrupted. While larvae continue their

75   development to adults in new social groups, some females produce a second clutch of eggs

76   (i.e. iteroparous as compared to semelparous females), which will also receive pre- and post-

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77   hatching care and will hatch in late spring (Lamb and Wellington 1975; Meunier et al. 2012;

78   Ratz et al. 2016). All females generally die during the following summer (Albouy and

79   Caussanel 1990).

80   In this study, we used a common garden experiment to investigate whether and how

81   *F. auricularia* individuals altered their life history traits in response to the thermal constraints

82   encountered during their North American invasion. From 1988 to 1995, we field-sampled

83   individuals originating from 19 populations located from the East to the West coasts,

84   maintained them under standard conditions and measured the properties of the 1st and 2nd

85   clutches produced by each female in terms of egg laying date, egg number, egg development

86   time and number of newly hatched larvae. We also recorded the reproductive strategy of the

87   females (iteroparity versus semelparity), their reproductive outcome (total number of eggs

88   and larvae produced over lifetime), as well as the longevity of the field-sampled males and

89   females. If *F. auricularia* individuals adapted their life-cycle and life-history traits to the

90   mean temperatures and/or thermal regimes of their populations of origin, we predict these

91   traits to covary with the overall mean temperatures and/or variation in seasonal temperatures

92   of their population. Conversely, if earwig life-history traits are independent to their previous

93   thermal environments (i.e. no adaptation) and/or are plastic to their current thermal

94   environment, we predict no apparent association between the traits measured in our field-

95   sampled individuals and the thermal regimes of their populations of origins.

MATERIAL AND METHODS

96   **Earwig sampling and laboratory rearing**

97   A total of 4158 *F. auricularia* individuals were collected over 7 years among 19 natural

98   populations located across North America (Figure 1, Table 1). These individuals were

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99   collected as larvae or adults using wooden traps (Tourneur 2018) between July and August,

100   and were immediately setup in glass containers (Mason Jars Company, Erie, Pennsylvania,

101   United States of America) in groups of 20 to 30 individuals. These containers received two

102   sheets of creased toilet paper as resting places for earwigs, and were then transported to our

103   laboratory in Montreal, Canada. Upon their arrival, each container was maintained under a

104   standard climate condition (natural temperature and light-cycle of Montreal). During their

105   transport and laboratory maintenance, containers received an *ad libitum* amount of carrots

106   and pollen as a food source for earwigs, and were supplied with water by means of a cotton

107   pad regularly soaked in water. This experimental setup allowed earwigs to continue their

108   development, while performing non-controlled mating and expressing social interactions

109   (Weiß et al. 2014; Sandrin et al. 2015; Kohlmeier et al. 2016; Körner et al. 2018). Two to

110   three months later (between the 7th and the 19th day of October of each year), we used these

111   individuals to set up 2079 mating pairs (from 17 to 356 pairs per population, see Table 1), in

112   which we subsequently measured 13 life-history traits (see below). We maintained each of

113   these pairs at 10 ± 1 °C in a Petri dish (diameter 10 cm) grounded with a thin layer of moist

114   sand, and in which food was changed and substrate humidified once a week. Food was

115   removed at egg laying to mimic the natural end of earwigs' foraging activity (Kölliker 2007).

116   At egg hatching, we discarded all newly emerged larvae from the experiments to trigger a

117   novel ovarian cycle in the mothers and allow their production of a subsequent clutch

118   (Vancassel and Foraste 1980; Meunier et al. 2012). We then maintained these pairs under the

119   rearing conditions described above until our experiment ended, i.e. either one year after the

120   beginning of our laboratory setup or at the death of the adult males and females. Overall,

121   3927 of the 4158 (94.4%) tested individuals died within the year following the beginning of

122   our experiments, a value in line with previous data on *F. auricularia* lifespan (Albouy and

123   Caussanel 1990). Note that recent studies revealed that *F. auricularia* L. encompasses two

124   genetic subspecies which do not coexist within populations (Wirth et al. 1998; Tourneur

125   2018; Quarrell et al. 2018). Although these subspecies were not taken into account in our

126   analyses (our data were collected before the publication of these genetic analyses), the

127   homogeneous distribution of the life history traits measured across populations (Figures 2 to

128   4) suggests an absence of species-specific values regarding these measurements. The

129   potential co-occurrence of the two subspecies in our data set is thus unlikely to bias our study

130   and its main conclusions.

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

132   For each mating pair, we measured 13 life-history traits encompassing the properties of the

133   resulting 1st and 2nd clutches (when present), the reproductive strategy and reproductive

134   outcomes of each female, as well as the longevity of both field-sampled males and females.

135   These properties were obtained by recording the date of egg production, counting the number

136   of eggs produced, calculating the duration of egg development until hatching (in days) and

137   finally counting the number of larvae at egg hatching in both 1st and 2nd clutches (when

138   present). The reproductive strategies and outcomes of females were obtained by recording

139   whether females were semelparous or iteroparous (i.e. produced one or two clutches in their

140   lifetime, respectively), and by counting the total number of eggs and larvae produced per

141   female during their lifetime. Finally, we measured adult's longevity by counting the number

142   of days each male and female survived after October 1st of the year of field sampling. Note

143   that 8.1% and 5.4% females from Santa Cruz and Asheville, respectively, produced a third

144   clutch. This third clutch was not considered in the present study, as our experiment ended

145   before their hatching.

146   **Extraction of mean temperatures and thermal regimes of each population**

147   We extracted the mean monthly temperature of the 19 studied populations using their GPS

148   coordinates (Table 1) and the Worldclim database v2.0 (http://www.worldclim.org/) with a

149   spatial resolution of 30 seconds. These mean temperatures were calculated over 30 years,

150   from 1970 to 2000. To reduce dimensionality of co-varying temperatures in our data set and

151   to characterize the thermal regimes of each population, we then conducted a Principal

152   Component Analysis (PCA; an analysis without *a priori*) on the set of 12 mean monthly

153   temperatures per population (Table S1). This analysis provided us with 12 orthogonal

154   principal components (PCs), out of which we retained the first three PCs (total variance

155   explained = 98.6%, Table 2). The first components (PC1) was positively loaded by almost all

156   monthly temperatures, therefore positively reflecting the overall mean temperature of a

157   population. The second component (PC2) revealed a trade-off between the mean temperature

158   of February, and the mean temperatures of June, July, and August. In particular, high values

159   of PC2 reflected populations with cold February (winter) and warm summer, whereas small

160   values of PC2 reflected populations with warm February (winter) and cold summer. Finally,

161   the third component (PC3) showed a trade-off between October and November on one hand,

162   and April and May on the other hand. High values of PC3 therefore characterized populations

163   with cold autumn and warm spring, whereas small values of PC3 reflected populations with

164   warm autumn and cold spring.

165   **Statistical analyses**

166   To test whether *F. auricularia* adapt their life-cycle and life-history traits to North American

167   thermal regimes, we conducted a series of 12 general linear models (LM in R) and one

168   generalized linear model (GLM in R) – see Table 3. In the 12 LMs, the three selected PCs

169   and their interactions were entered as explanatory variables (PC1, PC2 and PC3), whereas the

170   response variable was either egg laying date, egg number, egg development time and larvae

171   number for the 1st or 2nd clutches (a total of 8 LMs), the total number of eggs or larvae

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172   produced, or the longevity of males or females. Note that both egg laying date and adult

173   longevity were calculated using October 1st as day 0. In the GLM, the response variable was

174   the ratio of iteroparous females per population, which was entered using the command *cbind*

175   in R and fitted to a binomial error distribution corrected for overdispersion. All statistical

176   models were based on the mean value of each response variable per population. They were

177   also checked for homoscedasticity and residuals normality, as well as simplified stepwise by

178   removing all non-significant interaction terms. To correct for inflated type-I errors due to

179   multiple testing, all *P*-values were adjusted using False Discovery Rate (FDR) correction

180   (Benjamini and Hochberg 1995). All analyses were conducted using the software R v3.5.1

181   loaded with the packages *raster*, *FactoMineR*, *rsq* and *rcompanion*.

RESULTS

182   The 19 studied populations greatly varied in their mean temperatures and thermal regimes

183   (Table S1), as well as in the mean values of the 13 traits measured in their sampled

184   individuals (Figures 2 to 4; Tables S2 to S4). Mean monthly temperatures overall ranged

185   from 22.9°C (July in Saluda) to -10.1°C (January in Montreal), while thermal amplitudes

186   over a year ranged from 30.7°C (Montreal) to 7.9°C (Santa Cruz). For the traits measured in

187   the 1st clutches, the mean dates of egg production ranged from 47.8 to 132.6 days after the 1st

188   of October, the mean number of eggs per clutch from 23.2 to 66.0, the mean egg development

189   time from 42.2 to 71.4 days and the mean number of larvae per clutch from 11.6 to 44.8. For

190   the 2nd clutches, the mean dates of egg production ranged from 142.0 to 248.2 days after the

191   1st of October, the mean number of eggs from 14.0 to 38.4, the mean egg development time

192   from 10.0 to 63.7 days and the mean number of larvae from 0 to 17.7. Finally, the total

193   number of eggs produced ranged from 28.1 to 83.4, the total number of larvae produced from

194   13.0 to 46.3, the proportion of iteroparous females from 0 to 70.8%, the longevity of males

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195   from 82.0 to 299.8 days after the 1st of October and the longevity of females from 146.0 to

196   322.5 days after the 1st of October.

197   Of the 13 measured traits, 10 varied together with the thermal regimes of the

198   population of origin (Table 3). Five of these 10 traits were exclusively associated with PC2

199   (February-summer temperatures), two traits were exclusively associated with PC3 (autumn-

200   spring temperatures), and three traits were associated with both PC2 and PC3. By contrast, no

201   traits were associated with PC1 (overall mean temperatures). The associations with PC2

202   revealed that populations with cold February and warm summers (high PC2 values) had

203   females that produced their 1st clutch of eggs earlier and these eggs had longer development

204   time compared to populations exhibiting warm February and cold summers (low PC2 values,

205   Figure 2). Similarly, females from the former populations were less likely to produce a

206   second clutch (i.e. to be iteroparous, Figure 3) and when they did so, their 2nd clutches eggs

207   were less numerous (Figure 3) and showed longer development time (Figure 3). Moreover,

208   females and males from populations with cold February and warm summers lived less long

209   compared to adults from warm February and cold summers (Figure 4). On the other hand, the

210   effects of PC3 reveal that populations exhibiting cold autumn and warm spring (high PC3

211   values) had females that produced their 1st clutch of eggs later in the season and these eggs

212   were less numerous compared to females from populations with warm autumn and cold

213   spring (low PC3 values, Figure 2). Females from the former populations also had 2nd clutch

214   eggs that exhibited a shorter developmental time (Figure 3), they produced an overall lower

215   number of eggs (Figure 4) and had males with a longer longevity (Figure 4). By contrast, the

216   number of 1st clutch larvae, as well as their total number and the dates of 2nd clutch egg

217   laying were independent of PC1, PC2 and PC3 (Figures 2, 3 and 4; Table 3).

DISCUSSION

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218   Shedding light on how species successfully adapt to novel environmental constraints is of

219   major importance to improve our general understanding of the mechanisms underlying

220   biological invasions, as well as on the general ecology of animal adaptations. In this study,

221   we demonstrate that the successful invasion of the European earwig across North America

222   came with multiple changes in their life-history traits in response to the thermal regimes (sets

223   of winter-summer and autumn-spring temperatures), but not to the overall mean temperature

224   of the invaded populations. In particular, our 7-years data from 19 populations revealed that

225   females changed their timing of first reproduction, their reproductive strategy and investment

226   into egg production when facing different thermal regimes, while both males and females

227   longevities varied accordingly. By contrast, we found no association between thermal

228   regimes and both the timing of second reproduction and the total number of larvae produced

229   per female.

230   We showed that females produced their first clutch of eggs earlier when they came

231   from populations facing warm summers and/or warm autumns (PC2 and PC3, respectively),

232   and were less likely to produce a second clutch in populations with cold February. The effect

233   of warm temperatures on egg laying date is not surprising: adult earwigs typically develop

234   and mate during summer and autumn, so that warm temperatures during these seasons can

235   accelerate their reproductive physiology (as shown in other insect species, Singh et al., 2018)

236   and thus accelerate egg laying (Tourneur 2018). Similarly, cold Februaries may slow down

237   the development of 1st clutch eggs and thus extend the corresponding period of egg care.

238   This, in turn, may inhibit females physiological transformation to produce a second clutch

239   (Vancassel 1984; Tourneur 2018). This scenario is in line with previous results showing that

240   cold winters increase the duration of egg development time in *F. auricularia* (Gingras and

241   Tourneur 2001; Körner et al. 2018). It is also in line with other results demonstrating that

242   tending eggs inhibits vitellogenic activity and the production of juvenile hormone in the

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243   earwig *Labidura riparia* Pallas, two parameters required to activate ovary development and

244   allow egg production (Vancassel et al. 1984). Overall, these results suggest that changes in

245   the timing of first reproduction and females' reproductive strategy did not evolve to better

246   cope with novel thermal constraints, but instead that they are simple by-product of these

247   constraints. This reveals that *F. auricularia* has the capability to deal with a broad range of

248   thermal constraints (at least the range found across North America), and emphasizes that such

249   constraints are unlikely to preclude its spread to novel populations.

250   Interestingly, our data show that thermal regimes are associated with lifetime egg

251   production, but not with lifetime larvae production. In particular, the total number of eggs

252   produced per female decreased together with autumn temperatures, whereas this association

253   vanished with larvae number. This apparent discrepancy suggests that females from

254   populations with the warmest autumns lost a larger number of eggs during egg development.

255   A first explanation could be that these females were less efficient in egg care, a process that is

256   essential to ensure egg development until hatching in earwigs (Boos et al. 2014; Van Meyel

257   et al. 2019). Whereas this should be tested in future studies, previous results suggest that it

258   could be unlikely, as maternal investment in post-hatching care is not population-specific

259   (Ratz et al. 2016). Another explanation is that females consumed a larger part of their clutch

260   in populations with the warmest compared to the coldest autumns. Filial egg consumption is a

261   common phenomenon in insects (Elgar and Crespi 1992) and it has been recently reported in

262   several Dermapteran species, such as the European earwig *F. auricularia* (Koch and Meunier

263   2014) and the maritime earwig *Anisolabis maritima* Bonelli (Miller and Zink 2012). In the

264   European earwig, this phenomenon has been proposed to reflect an adaptive strategy of

265   females to limit weight loss during the period of egg care (i.e. when they stop all other

266   foraging activities) and by doing so, to reallocate their resources into post-hatching care

267   and/or into a 2nd oogenesis cycle (Koch and Meunier 2014; Tourneur 2018). Given that

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268   females lay eggs earlier in populations with the warmest autumns, this increased egg

269   consumption could be an adaptive strategy to limit the cost of tending newly hatched

270   offspring earlier in the season (middle of winter) when food sources are scarce or absent. If

271   this hypothesis holds true, it would suggest that filial egg cannibalism could be a strategy that

272   *F. auricularia* females have evolved to better cope with thermal constraints and therefore to

273   successfully establish in populations exhibiting warm autumns and/or requiring very long

274   period of parental egg care.

275   We found that the longevity of both males and females were associated with the

276   thermal regime of the population of origin. In particular, female and male longevity

277   decreased together with warm summers (and cold Februaries), while male longevity also

278   decreased with warm autumns (and cold springs). The first results may be a by-product of the

279   effect of temperature on the date of egg laying and/or egg hatching. In particular, we showed

280   that females from populations facing warm summers are the first to lay their eggs. Individuals

281   from these populations might thus have been the oldest at the date of our field sampling,

282   therefore leading to the shortest longevity in our subsequent experiment. Surprisingly, there

283   was a sex-specific effect of spring (and autumn) temperatures on adult longevity: males lived

284   up to two times longer in populations with warm compared to cold springs (as well as cold

285   compared to warm autumns), whereas this effect was absent in females. This finding may

286   reflect sex-specific sensitivity to high temperatures in terms of, for instance, physiology or

287   expression of costly behaviors. Whereas some physiological traits are known to be sex-

288   specific in this species (Kohlmeier et al. 2016; Vogelweith et al. 2017), further studies should

289   explore the effects of temperature on the observed differences. Notwithstanding its

290   underlying mechanisms, the high longevity of males in warm spring populations opens scope

291   for these males to mate with females of the subsequent generation, as well as for an

292   involvement of fathers into larva care. These two processes remain unknown in this species,

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293   but they could be of central importance in their successful adaptation to novel environments.

294   Follow-up studies will thus investigate the (re)mating strategies of earwig males, as well as

295   the expression of paternal care across these populations.

296   To conclude, our results demonstrate that the spread of the European earwigs across

297   North America came with important changes in their life-history traits and life cycle, and that

298   these changes emerged in a bit less than a century and thus less than a hundred generations.

299   Whereas we show that some of these changes are by-products of novel thermal constraints

300   (timing of first reproduction and female iteroparity), we reveal that others are likely to reflect

301   adaptive strategies to cope with different autumn temperatures (egg production and egg

302   cannibalism). Overall, these findings demonstrate that even if temperature can be an

303   important constraint in the life-cycle of the European earwig (Lamb and Wellington 1974;

304   Moerkens et al. 2012; Körner et al. 2018; Hill et al. 2019), it cannot be considered as a long-

305   term constraint for its successful invasion in novel environments. Our findings also

306   emphasize that adaptation does not necessarily operate in response to overall mean

307   temperatures of the invaded populations, but to their thermal regimes – i.e. to seasonality

308   and/or mean temperature at specific time of their life-cycle. Whether the reported thermal

309   adaptations are the product of population-differences in the early-life experience of the tested

310   adults (Wong and Kölliker 2014; English et al. 2016), and/or the product of an inherited

311   genetic basis that varies with thermal regimes (possibly due to an ancestral phenotypic

312   plasticity to thermal regimes; Levis and Pfennig 2016; Corl et al. 2018; Fox et al. 2019), as

313   well as whether these adaptations are similar across the multiple zones of invasions

314   worldwide (Frank 1918; Guillet et al. 2000; Quarrell et al. 2018; Hill et al. 2019) will be

315   investigated in future studies. On a more general level, our results emphasize that predicting

316   the spread of a biological invasion cannot only rely on presence/absence data at a given time,

317   but needs considering the adaptive capability of this species to novel environmental

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318   constraints. This would require collecting data sets exploring such a capability across many

319   species and taxa, a difficult task for which contributes the present study.

AUTHOR CONTRIBUTION STATEMENT

ACKNOWLEDGMENTS

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467

468 **Table 1 – Details of the 19 sampled populations.** The table shows the name and location of

469 each population, their GPS coordinates (Latitude, Longitude), samplings years, total number

470 of mating pair setup across years (N. pairs), and thermal regimes (defined as PC1, PC2 and

471 PC3).

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

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

473

474   **Table 2 – Loadings of the four first principal components (PCs) reflecting combinations**

475   **of the 12 mean monthly temperatures across populations.** The traits having significant

476   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
Variance explained (%)	**67.9**	26.9	3.8	1.1
Cumulative variance explained (%)	67.9	94.8	98.6	99.7

477

Table 3 –Results of the statistical models on the 13 measured life-history traits. PC1 positively reflects the overall mean temperature of a population. High values of PC2 reflect populations with cold February (winter) and warm summer, and vice-versa. High values of PC3 reflect populations with warm spring and cold autumn, and vice-versa. P-values significant after FDR correction (adj-P) are in bold. Model estimates (estim).
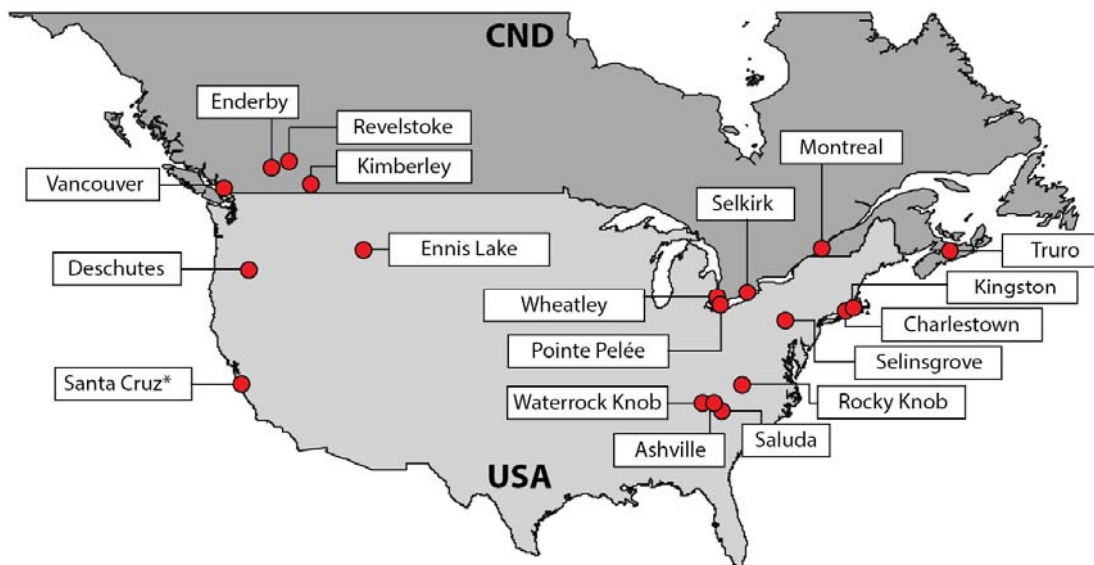
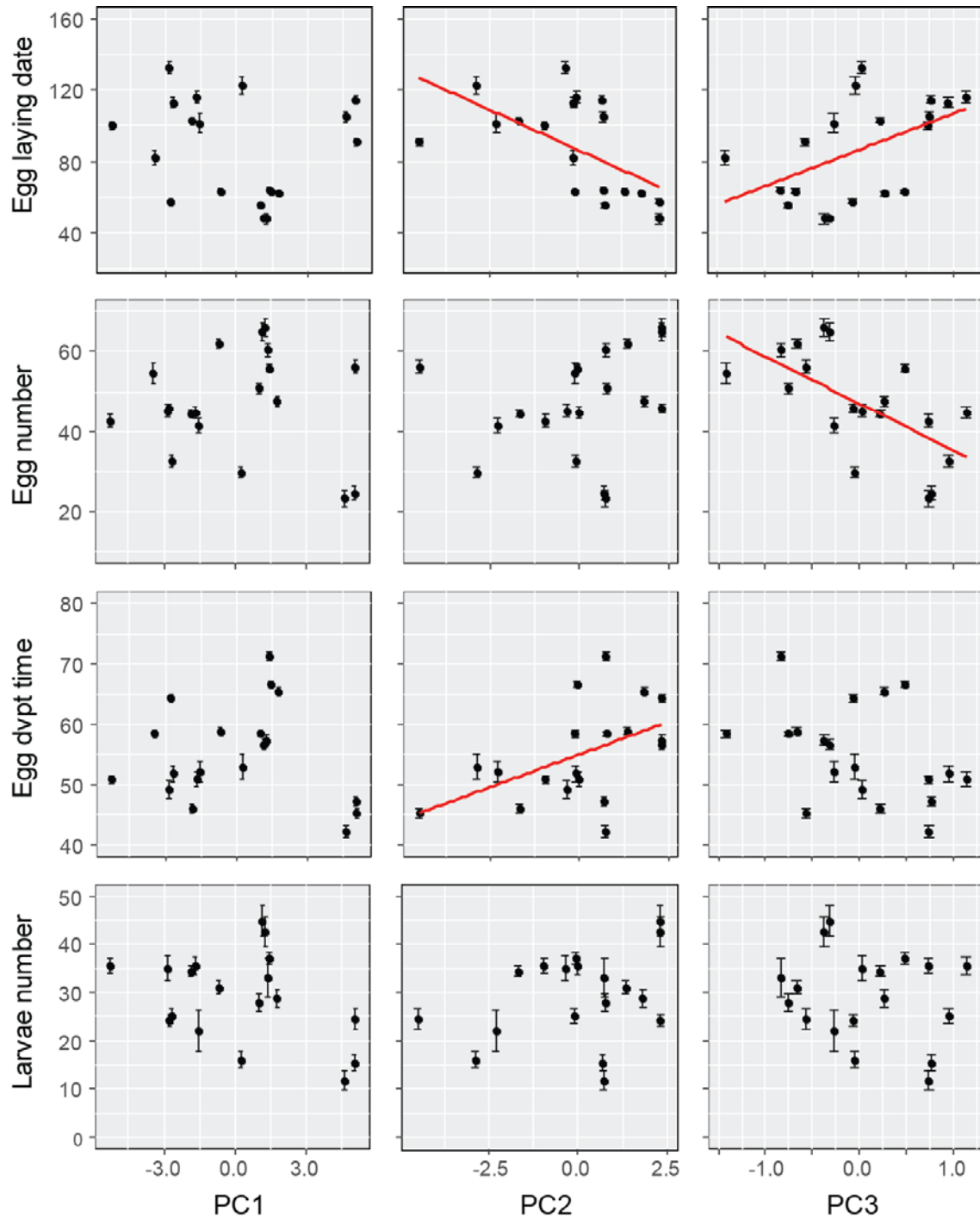|	PC1				PC2				PC3			
	estim.	SE	P	adj-P	estim.	SE	P	adj-P	estim.	SE	P	adj-P
First clutch												
Egg laying date	-1.55	1.47	0.307	0.665	-8.92	2.34	0.002	**0.011**	20.37	6.23	0.005	**0.014**
Egg number	-0.32	0.82	0.705	0.896	1.87	1.30	0.171	0.234	-11.77	3.47	0.004	**0.014**
Egg development time	-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

482

483 **Figure 1 – Map showing the 19 sampled populations across Canada (CND) and United**

484 **States of America (USA)**. * This population was called San Francisco in Tourneur (2018).

485
486

487   **Figure 2** – Associations between the thermal regimes (PC1, PC2, PC3) of the 19 populations

488   of origin and 1st clutch parameters. The red lines represent correlations that are significant

489   after FDR correction. Mean values ± SE. Egg laying date was calculated using October [1st] as
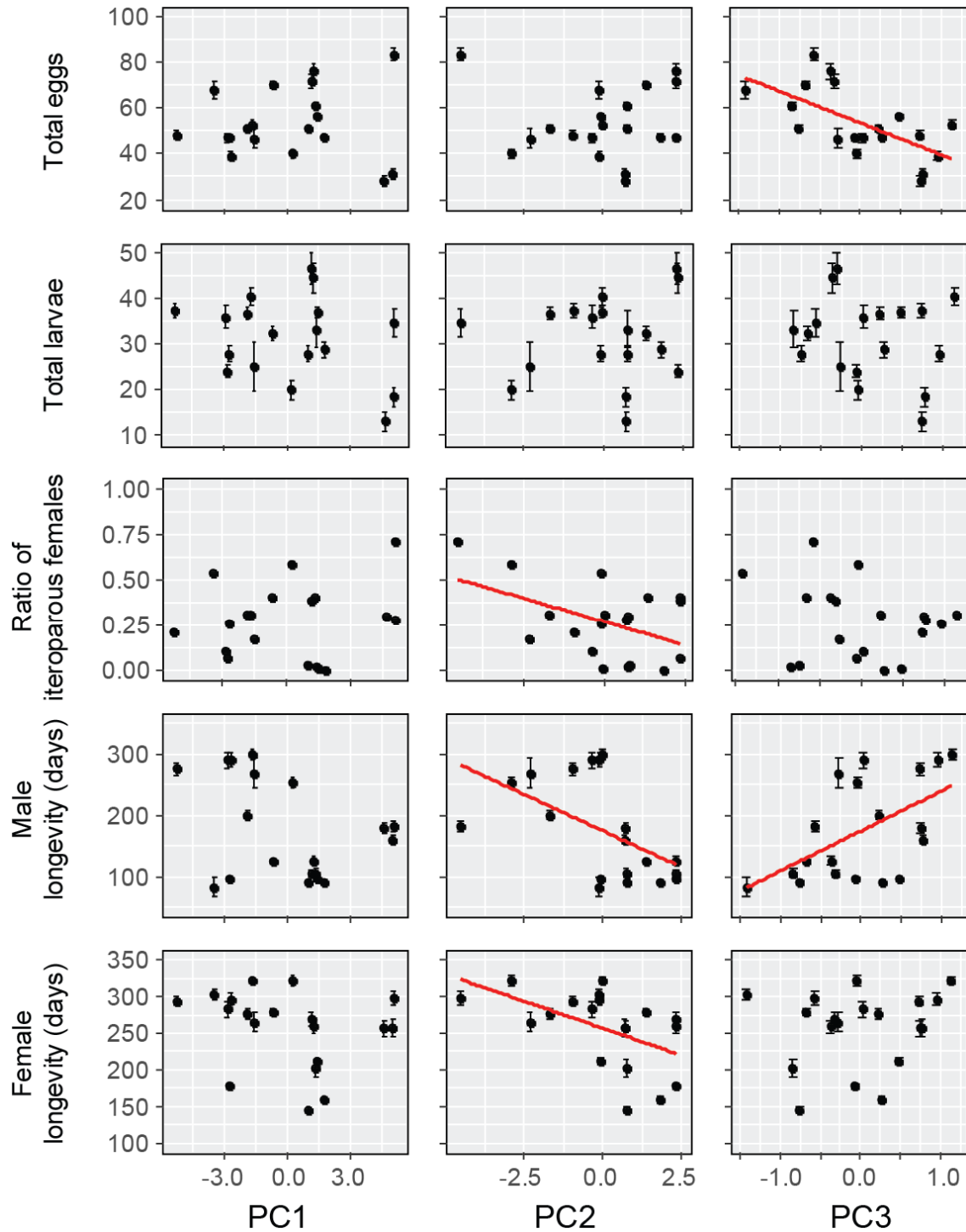
490   a reference (i.e. as day 0).

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493   **Figure 3** – Associations between the thermal regimes (PC1, PC2, PC3) of the 19 populations

494   of origin and 2nd clutch parameters (when produced). The red lines represent correlations that

495   are significant after FDR correction. Mean values $\pm$ SE. Egg laying date was calculated using

496   October 1st as a reference (i.e. as day 0).

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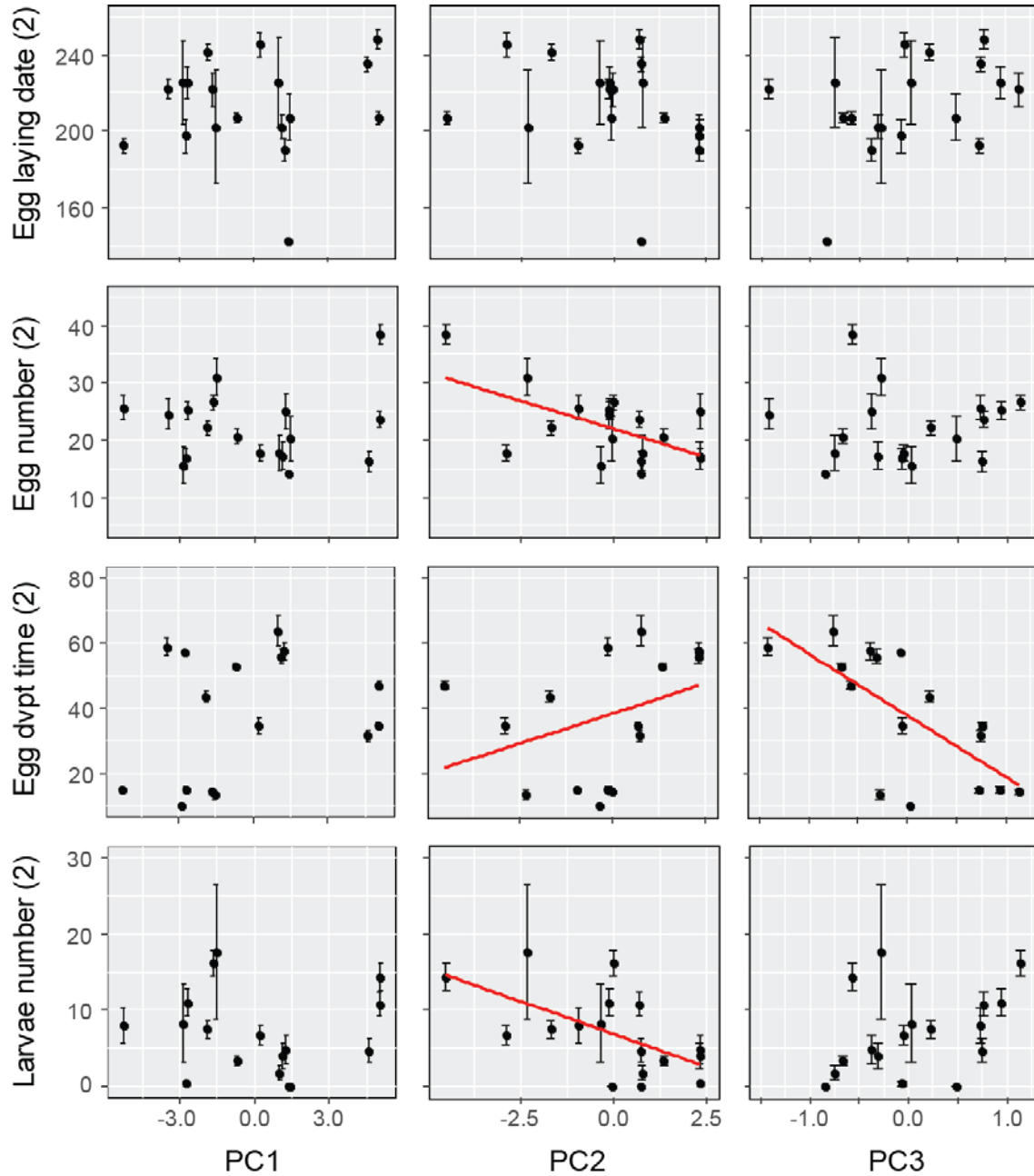
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499   **Figure 4** – Associations between the thermal regimes (PC1, PC2, PC3) of the 19 populations

500   of origin and females' reproductive strategies and outcomes, as well as adult's longevity. The

501   red lines represent correlations that are significant after FDR correction. Mean values ± SE.

502