Pre- and post-oviposition behavioural strategies to protect eggs against extreme winter cold in an insect with maternal care

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ABSTRACT

12 Depositing eggs in an area with adequate temperature is often crucial for mothers and their

13 offspring, as the eggs are immobile and therefore cannot avoid exposure to sub-optimal

14 temperatures. However, the importance of temperature on oviposition site selection is less

15 clear when mothers can avoid these potential adverse effects by both moving their eggs after

16 oviposition and providing other forms of egg care. In this study, we addressed this question in

17 the European earwig, an insect in which mothers care for the eggs during several months in

18 winter, often moving them during this period. We set up 60 females from two random natural

19 populations (as this species often exhibits population-specific life-history traits and

20 behaviours) under controlled thermal gradients, and recorded the temperature at which they

21 built their nests, tested whether they moved their eggs after an experimental temperature

22 change, and measured the effects on egg development and hatching rate. Our results

23 demonstrate that females indeed select oviposition sites according to temperature, and can

24 move their eggs to reach warmer temperatures. We also show that these warmer

25 temperatures are necessary to ensure egg hatching. Although this set of behavioural

26 thermoregulations is present in the two tested populations, we found a population-specific

27 modality of expression. These included the range of temperatures explored before

28 oviposition, temperature selected at oviposition and dynamics of egg transport following a

29 temperature change. Overall, our study sheds light on a new post-oviposition strategy in

30 female insects that overwinter with their eggs for coping with temperature changes. More

31 generally, it also reveals that egg care and/or egg transport do not prevent behavioural

32 thermoregulation via oviposition site selection and highlights the diversity of behaviours that

33 insects can adopt to enhance their tolerance to global climate change.

34 **Keywords:** Dermaptera, Egg brooding, Overwinter, Parental care, Thermal preferences

INTRODUCTION

35   Oviposition site selection shapes the fitness of most oviparous species (Thompson 1988;

36   Refsnider and Janzen 2010; Meunier et al. 2022). This is because choosing the right place to

37   deposit eggs typically provides direct and indirect benefits to egg-laying females, their current

38   eggs, and their future juveniles. This behaviour may first limit the high risk of predation on

39   adult females that is inherent to their lack of mobility during oviposition and favour their direct

40   access to specific food sources necessary for oviposition. For instance, females of the water

41   strider *Aquarius paludum insularis* (Motoschulsky, 1866) avoid ovipositing in sites containing

42   a predator attacking adults only (Hirayama and Kasuya 2013), while females of the orange tip

43   butterfly *Anthocharis cardamines* (Linnaeus, 1758) deposit eggs on plants that have high

44   nutritional value for adults but poor nutritional value for their larvae (Courtney 1981).

45   Oviposition site selection can also provide direct benefits to eggs by limiting the risks of

46   predators finding the eggs or eggs drying out. In the aquatic beetles *Hydroporus incognitus*

47   Sharp, 1869 and *H. nigrita* (Fabricius, 1792), for example, females select waters where no fish

48   can predate on their eggs (Brodin et al. 2006), while in the damselfly *Lestes macrostigmata*

49   (Eversmann, 1836) females prefer to lay their eggs on plants growing in the deeper parts of

50   temporary ponds to minimize the risk of future egg desiccation (Lambret et al. 2018). Finally,

51   oviposition site selection can help future offspring by favouring proximity to suitable habitats

52   and providing direct access to resources necessary for juveniles. This is the case in the

53   sandpaper frog *Lechriodus fletcheri* (Boulenger, 1890) and several lady beetle species, where

54   females choose oviposition sites that contain the largest quantities of nutritive resources for

55   their future larvae (Sicsú et al. 2020; Gould et al. 2021).

56   The effect of temperature on egg development and survival is another potential driver

57   of oviposition site selection by females. Exposure to extreme temperatures can indeed

58   damage living organisms of all ages through alterations in their physiology, immunity and

59   behaviour, which may overall reduce their fitness and/or lead to premature death (Hance et

60   al. 2007; Dillon et al. 2009; Fey et al. 2015; Filazzola et al. 2021). These effects can be

61   particularly strong in eggs because they are immobile and thus unable to escape from

62   environmental temperatures, their shell often provides limited thermal protection, and the

63   development and survival of embryos (contained in eggs) are generally sensitive to subtle

64   changes in surrounding temperatures (Wang et al. 2010; Nicolai et al. 2013; Mortola and

65   Gaonac'h-Lovejoy 2016; Cordero et al. 2018; Yang et al. 2018). As a result, females of many

66   species select oviposition sites according to optimal temperatures for their eggs, such as in

67   the toad-headed agama lizard *Phrynocephalus przewalskii* Strauch, 1876 (Li et al. 2018), the

68   solitary red mason bee *Osmia bicornis* (Linnaeus, 1758) (Ostap-Chec et al. 2021), or the flat-

69   rock spiders *Hemicloea major* (Koch, 1875) (Pike et al. 2012).

70   By contrast, the importance of temperature for oviposition site selection becomes less

71   clear when mothers can transport their eggs from one location to another, as it may allow

72   them to secondarily adjust the temperature of their eggs throughout development. This

73   transport, included in a broader phenomenon called egg brooding in insects (Machado and

74   Trumbo 2018), is known to allow parents to limit the risk of egg predations or promote egg

75   oxygenation in aquatic species. For instance in the golden egg bug *Phyllomorpha laciniata*

76   (Villers, 1789), females lay their eggs on conspecifics whose mobility improves the avoidance

77   of egg parasitoids (Carrasco and Kaitala 2009). Similarly, in the water bug *Abedus herbeti*

78   Hidalgo, 1935 females lay their eggs on the males' back, which then move (with the eggs) to

79   ensure that they receive a proper level of oxygenation (Smith 1997). However, whether active

80　　egg transport (e.g. parents actively moving their eggs from one location to another) could be

81　　an adaptive behaviour by which mothers adjust the thermal needs of the embryo during

82　　development remains unexplored. Yet, this process could operate in the European earwig

83　　*Forficula auricularia* Linnaeus, 1758. In this complex of cryptic species (Wirth et al. 1998;

84　　González-Miguéns et al. 2020) that can be found on almost all continents (Lamb and

85　　Wellington 1975; Guillet, Josselin, et al. 2000; Quarrell et al. 2018; Hill et al. 2019), females

86　　usually lay their eggs just before or during winter, and then remain with their eggs several

87　　weeks or months until they hatch (Lamb 1976; Gingras and Tourneur 2001). During this period,

88　　females provide extensive forms of egg care including, for instance, grooming behaviours to

89　　remove pathogens, the application of chemical compounds on eggshells to improve resistance

90　　against desiccation (Liu et al. 1997; Boos et al. 2014), and fierce protection against predators

91　　(Thesing et al. 2015; Van Meyel et al. 2019). Moreover, females are frequently observed

92　　transporting their eggs from one location to another by holding them individually between

93　　their mouthparts (Diehl and Meunier 2018; Meunier et al. 2020).

94　　　　Recent results and observations suggest that earwig eggs could benefit from

95　　temperature-dependent oviposition site selection and temperature-dependent maternal

96　　transport during development. First, the duration of egg development in winter varies from

97　　three weeks (e.g. in Southern Europe) to several months (e.g. in North America) (Ratz et al.

98　　2016; Tourneur 2018). This suggests that eggs could be exposed to extremely low (and

99　　damaging) temperatures for a very long time if females do not select the oviposition site

100　　accordingly and/or do not transport the eggs during development. Second, a recent study

101　　shows that prolonging egg exposure to cold (5°C) for 15-day during winter delays the hatching

102　　date and development of juveniles to adulthood (which typically takes two months in *F.*

103　　*auricularia*), leads to the production of lighter adult females, and shapes the basal immunity

104 of these females: it increases their overall phenoloxidase activity and reduces the number of

105 haemocytes in females facing a changing social environment (Körner et al. 2018). Because

106 these traits are likely to affect negatively and/or positively the fitness of the resulting adults

107 (Koch and Meunier 2014), temperature-dependent oviposition site selection and egg

108 transport during development could be adaptive strategies in *F. auricularia* mothers. Finally,

109 several laboratory breeding trials indicate that eggs of some populations need to be exposed

110 to near-zero temperatures to trigger embryo development and that subsequently the

111 temperature needs to be increased to continue this development, while others do not (e.g.

112 Wirth et al. 1998; Meunier et al. 2012; Ratz et al. 2016; Tourneur and Meunier 2020).

113   In this study, we investigated whether European earwig females select an oviposition

114 site based on environmental temperature, and then move their eggs depending on egg age

115 and experimental changes in environmental temperature. Because previous studies point out

116 that the European earwig may show population-specific life-history traits and behaviours (Ratz

117 et al. 2016; Tourneur 2017; Tourneur 2018; Tourneur and Meunier 2020), we also tested

118 whether temperature-dependent oviposition site selection and egg transport vary between

119 two (randomly selected) populations naturally and experimentally sharing comparable

120 climatic conditions. We set up 60 females from two Canadian populations in two experimental

121 devices (Fig 1) allowing different thermal gradients and then recorded 1) the range of

122 temperatures explored by each female during the 15 days preceding oviposition, 2) the

123 temperature at which females laid their eggs, 3) whether and how mothers transported their

124 clutch along three thermal gradients throughout egg development and finally, 4) how the

125 temperature of these gradients affected juvenile production. Overall, our results reveal that

126 environmental temperature shapes female exploration before oviposition, oviposition site

127 selection, egg transport during development and the production of juveniles. They also show

128   that both oviposition site selection and the dynamic of egg transport during development

129   varies between the tested populations.

MATERIAL AND METHODS

Earwig sampling and experimental process

131   The experiment involved a total of 60 *F. auricularia* females field sampled in Harvey station

132   (67°00'52.2"W, 45°38'23.6"N; New Brunswick, Canada; HNB) and St John's (47°34'42.6"N,

133   52°44'37.0"W; Newfoundland and Labrador, Canada; SJNL) in September 2020 and then

134   maintained in plastic containers until October 2020. These two populations were selected as

135   independent random units on the basis that they were 2500 km apart by land (1000 km by

136   sea) and had comparable climatic conditions (Fig 2). Subsequent genetic analyses revealed

137   that HNB individuals belonged to the *F. auricularia* genetic clade 'A' and SJNL females to the

138   *F. auricularia* genetic clade 'B' (see details in the supplementary material and discussion; Wirth

139   et al. 1998, González-Miguéns et al. 2020). The field sampled females were maintained in

140   groups with males from the same population (sampled at the same time as the females) to

141   allow the completion of the gregarious phase of the life-cycle, which lasts several months

142   during which females mate with multiple partners (Sandrin et al. 2015) and express simple

143   social behaviours (Costa 2006; Weiß et al. 2014). The plastic containers were lined with wet

144   sand, contained two small shelters, and were maintained at room temperature under natural

145   day : light. In October 2020, we isolated each female as this is the period when they usually

146   leave their group to search for a future nesting site (Lamb 1976). To this end, we transferred

147   36 of 60 females (18 from HNB and 18 from SJNL) to the middle of 36 aluminium rails (Fig 1C;

148   1.8 x 1. 8 x 72 cm = height x width x length) covered with a layer of wet sand and closed with

a plastic cover for subsequent measurement of the temperature range explored before and at oviposition. We isolated the remaining 24 females (12 from HNB and 12 from SJNL) in Petri dishes (diameter 10 cm) covered with moist sand and kept in complete darkness until their use in the measurement of egg transport after oviposition.

To determine the temperature range explored by each female before egg production and the temperature chosen to deposit eggs, we transferred the 36 aluminium rails containing one female each on thermoelectric plates (AHP-1200CPV- Thermoelectric Cooling America Corporation. 4049W Schubert Avenue. Chicago IL. USA) with temperatures linearly ranging from 0°C to 20°C (Fig 1A and S1). We then measured the distance between each female and the coldest edge of its rail every day from the time they were placed in the rails until they produced eggs (including the day of oviposition). Because the date of oviposition greatly varies within populations (up to several months between the first and last oviposition; e.g. Tourneur and Meunier 2020), we standardised our measurement to the temperature range explored by each female 15 days before its own oviposition. To facilitate distance measurement, we divided each rail into 12 zones of 6 cm length and defined the distance between a female and the coldest edge as the centre of the zone she was in. In the very few cases where females were observed between two zones, we assigned females' location to the colder of the two zones. From field sampling to oviposition, we fed the 36 females twice a week with fresh carrots placed on a soaked cotton pad, plus an artificial diet composed of 1/3 dry power of egg yolk, 1/3 bee collected pollen (Community Apiaries. 576 Plymouth road, Richmond Corner, New-Brunswick. Canada) and 1/3 cricket powder (Entomo Farms. 31 industrial drive Norwood, Ontario. Canada). We then did not feed females from the day of oviposition to egg hatching, as earwig mothers typically stop foraging during this period (Kölliker 2007).

We then tested whether mothers moved their eggs depending on experimental changes in environmental temperature and/or egg age during the 15 weeks following oviposition. Three days after each female has laid its eggs, we transferred the mother and all its eggs to a new (shorter) aluminium rail (1.8 x 1.8 x 66 cm), which was deposited into a climate cabinet (Fig 1B) providing three non-linear ranges of temperature: warm (0.9°C to 7.0°C), intermediate (-3.6°C to 2.7°C) or cold (-4.5°C to 1.6°C) (Fig 1B and S1). These three thermal gradients encompass the above-ground natural range of temperatures of the two populations during the time females were maintained in our laboratory, i.e. during the natural period of egg care (Gingras and Tourneur 2001; Fig 2). To experimentally change the temperature at which females and eggs were maintained at oviposition, we deposited each female and its eggs in the middle of the new rail (Fig 1C), i.e. at either 5.2°C (warm), 1.2°C (intermediate) or 0.1°C (cold). We then measured the distance (in cm) between the centre of the pile of eggs and the coldest edge of the rail once a week during the 15 following weeks. This measurement of egg transport involved the 36 females used in the measurements of temperature range explored before egg production (see above), and the 24 females (12 from HNB and 12 from SJNL) previously maintained in Petri dishes until oviposition (60 females total). We had not been able to use these 24 females in the electrothermal plates due to the lack of space in the units. Overall, we thus tested 10 HNB and 10 SJNL females in the warm, 10 HNB and 10 SJNL females in the intermediate and 10 HNB and 10 SJNL females in the cold range. In the climate cabinet, the rails were lined with a layer of wet sand and closed with a plastic cover to ensure complete darkness. They were slightly shorter than those used in the thermoelectric plates for reasons of fit.

We finally tested whether the temperatures at which eggs were maintained during the 15 weeks following oviposition affect egg development and hatching rate. Fifteen weeks after

oviposition, we transferred the 60 (short) rails containing the mothers and their eggs (i.e. 5 rails per thermal range and population) to thermoelectric plates with temperatures linearly ranging from 0°C to 19°C (and not 20°C due to the shorter rails). This transfer allowed females to have access to a wider thermal range, as expected in Spring – the moment at which eggs typically hatch in *F. auricularia*. We then checked each female daily to record the date of the first egg hatching, the location of the clutch at hatching (based on the distance between the centre of the clutch and the coldest edge of the rail) and the number of newly hatched juveniles. All distance recordings were made very gently so that the females were not disturbed during the observation.

We recorded the thermal gradients present in the different types of aluminium rails to the nearest 0.1°C using 4 channel K type Thermometers (SD. Amazon. CA) connected to four probes located in the sand either at 2.0, 25.5, 49.0 and 72.0 cm (long aluminium rails) or 1.5, 22.5, 43.5 and 64.5 cm (short aluminium rails) of the coldest edge of the rails. The recordings occurred every hour during the entire experiment on either four aluminium rails evenly distributed over the thermoelectric plates or six aluminium rails evenly distributed among the trails and thermal constraints in the climate cabinet. There were no edge effects on temperatures. We then used these recordings to compute linear (thermoelectric plates) and non-linear (climate cabinet) equations linking distance to temperature (Fig S1), which we then used to obtain the temperature of the location of the females and their eggs.

Statistical analyses

We used a series of eight non-parametric Exact Mann-Whitney Rank Sum tests correcting for tied observations to test the effect of population on the amplitude of temperatures at which

females were observed before oviposition, the warmest and coldest temperatures reached by females before oviposition, the location of females at oviposition, the date of oviposition, the number of eggs produced, the number of weeks until egg hatching and the temperature of the area of egg hatching. Changes in the location of the clutch after oviposition were then analysed using parametric Linear Mixed-effects models (LME) in which the week (1 to 15), population (SJNL and HNB), range of temperature (warm, intermediate and cold) and the interaction between these three factors were entered as fixed explanatory factors, while the ID of each female was used as a random factor to correct for multiple measurements. To interpret the significant interaction between the three fixed explanatory factors, we divided the data set according to temperature range (i.e. in three subsets), in which we ran another series of LMEs in which we used week, population and the interaction as fixed explanatory factors, and the female ID as a random factor. When the interaction between weeks and population were significant, we conducted post hoc pairwise comparisons between the temperature of the location where the eggs were initially transferred (i.e. 5.2, 1.18 and 0.11°C) and the temperature of the location where the eggs were observed each week using a series of one sample Exact Mann-Whitney Rank Sum tests. To correct for multiple testing, the P-values of this series of pairwise comparisons were adjusted using the False Discovery Rate (FDR) method (Benjamini and Hochberg 1995). Finally, the likelihood to produce at least one juvenile and the hatching rate were tested using two Generalized linear models with binomial error distribution and corrected for overdispersion. In these models, the population, the range of temperatures and their interaction were entered as explanatory factors, while we used either the presence of at least one hatched juvenile as a binary response variable (1 or 0) or the hatching rate (the number of eggs that hatched divided by the total number of eggs produced) as a continuous response variable. We checked that the assumptions of the LMEs

242 were met using the DHARMa package (Hartig 2020). The analyses were conducted with the

243 software R v4.1.1 (R Core Team, 2017) loaded with the packages *car* (Fox and Weisberg 2019),

244 *exactRankTests* (Hothorn and Hornik 2021), *emmeans* (Lenth 2021) and *DHARMa* (Hartig

245 2020). The R-script and data are available in an open data repository (see below).

RESULTS

246 Earwig females explored non-random ranges of temperature during the 15 days preceding

247 oviposition (Fig 3). The maximum temperature range was greater for the more artic SJNL than

248 the HNB females (median = 12.2 and 7.8°C, respectively; Fig 3A; W = 53, P < 0.001). The

249 warmest temperature at which females were observed was higher in SJNL than HNB females

250 (median = 19.6 and 12.7°C, respectively; Fig 3B; W = 2, P < 0.001), whereas the coldest location

251 was the same for SJNL and HNB females (median = 5.7 and 4.0°C, respectively; Fig 3C; W =

252 135.5, P = 0.404).

253 Earwig females chose their oviposition site according to the environmental

254 temperature (Fig 3). The temperature of the oviposition site was higher in SJNL compared to

255 HNB females (median = 16.1 and 9.2°C, respectively; Fig 3D; W = 17.5, P < 0.001). Moreover,

256 HNB females produced their eggs earlier in the season (median = 12 and 60 days after first egg

257 production in all females tested, respectively; Fig 3E; W = 38, P < 0.001) and laid overall more

258 eggs (median = 68 and 46, respectively; Fig 3F; W = 261, P < 0.001) than SJNL females.

259 During the 15 weeks following oviposition, earwig mothers moved their eggs

260 depending on experimental changes in environmental temperature, egg age and population

261 (Fig 4; Triple interaction between weeks, population and range of temperature: Likelihood

262 ratio χ^2_5= 33.13, P < 0.001). Egg location depended on an interaction between week and

263   population in the warmest range of temperatures (LR χ^2= 12.43, P < 0.001), which reveals that

264   SJNL females moved their eggs towards warmer locations about 7 weeks after oviposition,

265   whereas HNB females did not specifically target warmer locations (Fig 4). Egg location also

266   depended on an interaction between week and population in both the intermediate and the

267   coldest range of temperatures (LR χ^2= 16.53, P < 0.001 and χ^2= 6.27, P = 0.012, respectively),

268   which shows that both SJNL and HNB females moved their eggs towards warmer locations but

269   that this move started six weeks earlier in SJNL compared to HNB populations (Fig 4).

270   Interestingly, the mothers did not only move their eggs on the sand but built new nests each

271   time they moved their eggs.

272   Finally, the temperatures at which eggs were maintained during the 15 weeks

273   following oviposition affected both egg development and hatching rate. The likelihood to

274   produce juveniles (i.e. that at least one egg hatched) and the egg hatching rate were overall

275   higher for HNB compared to SJNL females (Fig 5A; 53% versus 20%; LR χ^2= 8.52, P = 0.004 and

276   Fig 5C; 30% versus 12%, LR χ^2= 6.20, P = 0.013, respectively), overall higher in females

277   previously maintained under the warmest range of temperatures (Fig 5B; 60% versus 25% and

278   25%; LR χ^2= 8.09, P = 0.018 and Fig 5D; 36% versus 12% and 15%, LR χ^2=7.99, P = 0.018,

279   respectively), and not affected by the interaction between these two factors (LR χ^2= 3.49, P =

280   0.175 and LR χ^2=0.61, P = 0.737, respectively). When they hatched, the temperature of the

281   place at which the first juveniles were observed was the same for both populations (Fig 5C; W

282   = 60, P = 0.396), while the eggs took overall more time to develop in HNB compared to SJNL

283   females (Fig 5D; W = 80.5, P = 0.012).

DISCUSSION

284   While temperature often drives oviposition site selection to ensure that the lack of egg

285   mobility does not result in exposure to sub-optimal or extreme temperatures (Pike et al. 2012;

286   Li et al. 2018; Ostap-Chec et al. 2021), the role of temperature on oviposition site selection is

287   less clear when mothers can transport the eggs after oviposition. Here, we show in the

288   European earwig that this capability does not prevent females from selecting oviposition sites

289   according to temperature and that egg transport can indeed help mothers to adjust egg

290   temperature after oviposition. Although this set of behavioural thermoregulations is present

291   in the two tested populations, we found that their modality of expression varied between the

292   two tested populations: St John's (Newfoundland and Labrador, Canada) females explore a

293   greater range of temperatures before oviposition, lay their eggs in warmer areas, move their

294   eggs quicker toward warm locations when suddenly exposed to cold, but were overall less

295   likely to produce juveniles under our experimental conditions than mothers from Harvey

296   station (New Brunswick, Canada).

297   Earwig females of both populations chose oviposition sites with temperatures above

298   10°C, which is in stark contrast to the sub-zero temperatures measured above ground in these

299   two locations during the natural oviposition period (Fig 2). This finding highlights the fact that

300   some ectotherms, such as earwigs, cannot only develop physiological mechanisms to

301   withstand their own freezing during wintering (Toxopeus and Sinclair 2018), but may also

302   prefer to find places exhibiting a large thermal difference from the ground temperature to

303   establish nests and deposit their eggs (Leather et al. 1993). Multiple strategies have been

304   reported in insects to achieve this goal, among which digging nests or burrows to obtain

305   efficient isolation from above-ground temperatures (Davis et al. 2015; Huang et al. 2020),

306   hiding under rocks and nesting into trunks to use the thermal inertia of the substrate as a

307   shelter (Brower et al. 2009; Trájer et al. 2014), and nesting close to human constructions (e.g.

308   underground pipeline, houses, building walls, etc) to benefit from their constant source of

309   heat during winter (Labrie et al. 2008; Trájer et al. 2014). These three strategies are also likely

310   to be adopted by the European earwig, as earwig adults are frequently found in human

311   habitations, underground burrows and under rock and trunks during winter (Goodacre 1997;

312   Gingras and Tourneur 2001; Kölliker and Vancassel 2007; Binns et al. 2021). Moreover,

313   another study suggests that the nest proximity to human constructions could be an effective

314   overwintering strategy for Canadian populations of earwigs (Goodacre 1997).

315   When experimentally exposed to temperatures below 5.5°C after oviposition, earwig

316   mothers of both populations transported their eggs to warmer locations. Interestingly, these

317   eggs were less likely to hatch when mothers were experimentally prevented from reaching

318   warmer locations, i.e. when mother and eggs were maintained in the cold and intermediate

319   temperature ranges. These results overall support the hypothesis that egg transport is an

320   adaptive post-oviposition behaviour by which earwig mothers protect eggs against extreme

321   cold and/or adjust the thermal needs of their embryos. This discovery sheds light on a new

322   strategy in female insects that overwinter with their eggs for coping with temperature changes

323   (Lee and Dellinger 1991; Sinclair et al. 2003), and emphasizes that the potential costs

324   associated with building a nest and finding a burrow in another location during winter do not

325   prevent such egg transport (Danks 2002). It now calls for future studies on the physiological

326   costs of egg transport for females at a time when they typically stop their foraging activity

327   (Kölliker 2007)(but see Van Meyel and Meunier 2020), and on the impact of temperature

328   variation during egg development (see Figure 4) on hatching success and offspring quality.

329   More generally, the egg transport capability of earwig females combined with their

330   oviposition site selection based on temperature could explain, at least in part, how such an

331   insect with long-overwintering eggs has been able to invade extremely cold climates (Guillet,

332   Josselin, et al. 2000; Quarrell et al. 2018; Hill et al. 2019; Tourneur and Meunier 2020).

333   Interestingly, St John's females transported their eggs much earlier than Harvey station

334   females. This suggests that the cold tolerance of eggs in the first few weeks after egg laying is

335   less effective at St John's than at Harvey station, either due to population-specific egg quality,

336   as reported in numerous oviparous species (Jing and Kang 2003; Stålhandske et al. 2015), or

337   population-specific egg development time, as egg sensitivity to cold often increases when they

338   are closer to hatching (e.g. Gray, 2009). In line with the last scenario, egg development time

339   greatly varies between natural populations of the European earwig (Tourneur and Gingras

340   1992; Meunier et al. 2012; Ratz et al. 2016; Tourneur and Meunier 2020), and our data show

341   that eggs produced by St John's females indeed take less time to hatch compared to eggs

342   produced by Harvey station females when reared in similar conditions. At a more general

343   level, it is typically expected that a population-specific cold tolerance of eggs should lead to

344   population-specific timing of oviposition, the less cold-tolerant eggs being laid later in winter

345   than the more cold-tolerant eggs (Tourneur and Meunier 2020). This is again in line with our

346   results: St John's females laid eggs about one month after Harvey station females. Overall, our

347   results thus demonstrate that winter temperatures are an important factor in the pre- and

348   post-oviposition strategies of earwig females.

349   Somewhat surprisingly, our study finally reveals that the modality of expression of the

350   reported strategies to protect eggs against severe winter cold varies between the two studied

351   populations. Although our experimental design does not allow us to conclude robustly on the

352   reasons for this variation, we propose three potential explanations. First, this could be due to

353   local adaptation to environmental conditions. In line with this explanation, previous studies

reported that multiple traits can vary between populations of the European earwig, such as the number of clutches produced by females, clutch size, juvenile quality, the timing of egg production, duration of egg development and female body mass (Ratz et al. 2016; Tourneur 2017; Tourneur 2018; Tourneur and Meunier 2020). However, these studies often compared populations with contrasting climatic conditions, which was not the case between St John's and Harvey stations (Fig 2). Second, the reported variation could be due to population-specific differences in the phenology of females at field sampling. However, this is unlikely to explain our results, as the females were sampled late in the breeding season and our setup control for this potential variation by standardising the measurements around the natural day of oviposition for each female. Finally, the behavioural variation reported between the two tested populations could be due to the presence of different genetic clades. In line with this hypothesis, our genetic analyses reveal that females of Harvey station belong to the genetic clade 'A' and females of St John's to the genetic clade 'B' (this was surprising, as this is the first time that the clade 'B' is found in Canada outside British Columbia). The European earwig is a complex of cryptic species, for which genetic divergence and reproductive isolation are well established (Wirth et al. 1998; Guillet, Josselin, et al. 2000; González-Miguéns et al. 2020), but the specificity of their life-history traits remains largely unexplored. To date, the only known species-specific trait refers to their reproduction, with females 'A' producing one clutch and females 'B' producing two clutches (Wirth et al. 1998; Tourneur 2018). However, other studies demonstrate that the number of clutches produced by a female can vary within *F. auricularia* species (Tourneur and Gingras 1992; Ratz et al. 2016) depending on numerous parameters acting during and after the early life of an earwig female (Meunier et al. 2012; Meunier and Kölliker 2012; Wong and Kölliker 2014; Tourneur 2018). If this third hypothesis is true, our results may thus have shed light on the first behavioural difference between 'A' and 'B'

378 females. Nevertheless, better understanding what drives population-specific dynamics of

379 maternal strategies to protect eggs against cold needs additional studies involving, for

380 instance, several populations of 'A' and 'B' females and/or population transplants.

381   Whereas ectotherms typically have very limited to no physiological capacities to limit

382 the costs of exposure to extreme temperatures via internal regulation (Stevenson 1985), some

383 have evolved forms of behavioural thermoregulation to avoid locations with extreme

384 temperatures (Lee Jr. 1991; Terrien 2011). Our study demonstrates that ectotherm females of

385 the European earwig adopt a broad set of behavioural thermoregulations when tending their

386 eggs overwinter. In particular, they select oviposition sites exhibiting specific temperatures

387 and transport their eggs to warmer locations when experimentally exposed to cold. While this

388 set of behavioural thermoregulations is present in the two studied populations, its modality

389 of expression varied between Harvey station and St John's – either as a result of local

390 adaptation or as species-specific traits among the complex of species composing the European

391 earwig (Wirth et al. 1998; Guillet, Josselin, et al. 2000; González-Miguéns et al. 2020). Overall,

392 our findings emphasize that earwig females have evolved behavioural strategies to mitigate

393 the risks inherent to tending eggs during several months and extreme winter cold. More

394 generally, they highlight the diversity of behaviours that insects can adopt to cope with

395 extreme temperatures, and could favour their tolerance to the effects of moderate climate

396 change.

DATA ACCESSIBILITY

397 The complete data set and R script are archived and freely available in the open data

398 repository Zenodo (https://doi.org/10.5281/zenodo.6338078).

399

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403

CONFLICT OF INTEREST

404   The authors of this preprint declare that they have no financial conflict of interest with the

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REFERENCES

406   Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ. 1990. Basic local alignment search tool.
407   J Mol Biol. 215(3):403–410. doi:10.1016/S0022-2836(05)80360-2.

408   Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful
409   approach to multiple testing. J R Stat Soc Ser B. 57(1):289–300. doi:10.2307/2346101.

410   Binns M, Hoffmann AA, Helden M, Heddle T, Hill MP, Macfadyen S, Nash MA, Umina PA.
411   2021. Lifecycle of the invasive omnivore, *Forficula auricularia*, in Australian grain growing
412   environments. Pest Manag Sci. 77(4):1818–1828. doi:10.1002/ps.6206.
413   https://onlinelibrary.wiley.com/doi/10.1002/ps.6206.

414   Boos S, Meunier J, Pichon S, Kölliker M. 2014. Maternal care provides antifungal protection
415   to eggs in the European earwig. Behav Ecol. 25(4):754–761. doi:10.1093/beheco/aru046.
416   http://www.beheco.oxfordjournals.org/cgi/doi/10.1093/beheco/aru046.

417   Brodin T, Johansson F, Bergsten J. 2006. Predator related oviposition site selection of aquatic
418   beetles (*Hydroporus* spp.) and effects on offspring life-history. Freshw Biol. 51(7):1277–1285.
419   doi:10.1111/j.1365-2427.2006.01563.x.

420   Brower LP, Williams EH, Slayback DA, Fink LS, Ramirez IM, Zubieta RR, Limon Garcia MI, Gier
421   P, Lear JA, Van hook T. 2009. Oyamel fir forest trunks provide thermal advantages for
422   overwintering monarch butterflies in Mexico. Insect Conserv Divers. 2(3):163–175.
423   doi:10.1111/j.1752-4598.2009.00052.x. https://onlinelibrary.wiley.com/doi/10.1111/j.1752-
424   4598.2009.00052.x.

425   Carrasco D, Kaitala A. 2009. Egg-laying tactic in *Phyllomorpha laciniata* in the presence of

426   parasitoids. Entomol Exp Appl. 131(3):300–307. doi:10.1111/j.1570-7458.2009.00857.x.

427   Cordero GA, Telemeco RS, Gangloff EJ. 2018. Reptile embryos are not capable of behavioral
428   thermoregulation in the egg. Evol Dev. 20(1):40–47. doi:10.1111/ede.12244.

429   Costa JT. 2006. Dermaptera. Earwig mothers. In: The other insect societies. Cambridge,
430   Massachusetts & London, England: The Belknap Press of Harvard University Press. p. 49–80.

431   Courtney SP. 1981. Coevolution of pierid butterflies and their cruciferous foodplants - III.
432   *Anthocharis cardamines* (L.) survival, development and oviposition on different hostplants.
433   Oecologia. 51(1):91–96. doi:10.1007/BF00344658.

434   Danks H V. 2002. Modification of adverse conditions by insects. Oikos. 99(1):10–24.
435   doi:10.1034/j.1600-0706.2002.990102.x. [accessed 2019 Sep 3].
436   https://onlinelibrary.wiley.com/doi/pdf/10.1034/j.1600-0706.2002.990102.x.

437   Davis JM, Coogan LE, Papaj DR. 2015. Big maggots dig deeper: size-dependent larval
438   dispersal in flies. Oecologia. 179(1):55–62. doi:10.1007/s00442-015-3314-6.
439   http://dx.doi.org/10.1007/s00442-015-3314-6.

440   Diehl JM, Meunier J. 2018. Surrounding pathogens shape maternal egg care but not egg
441   production in the European earwig. Behav Ecol. 29(1):128–136. doi:10.1093/beheco/arx140.
442   http://academic.oup.com/beheco/article/doi/10.1093/beheco/arx140/4560300.

443   Dillon ME, Wang G, Garrity PA, Huey RB. 2009. Thermal preference in Drosophila. J Therm
444   Biol. 34(3):109–119. doi:10.1016/j.jtherbio.2008.11.007.

445   Fey SB, Siepielski AM, Nusslé S, Cervantes-Yoshida K, Hwan JL, Huber ER, Fey MJ, Catenazzi
446   A, Carlson SM. 2015. Recent shifts in the occurrence, cause, and magnitude of animal mass
447   mortality events. Proc Natl Acad Sci U S A. 112(4):1083–1088.
448   doi:10.1073/pnas.1414894112.

449   Filazzola A, Matter SF, MacIvor JS. 2021. The direct and indirect effects of extreme climate
450   events on insects. Sci Total Environ. 769:145161. doi:10.1016/j.scitotenv.2021.145161.
451   https://doi.org/10.1016/j.scitotenv.2021.145161.

452   Fox J, Weisberg S. 2019. An R Companion to Applied Regression. Sage, Thousand Oaks CA,
453   3rd edition. URL http://z.umn.edu/carbook. http://z.umn.edu/carbook.

454   Gingras J, Tourneur J-C. 2001. Timing of adult mortality, oviposition, and hatching during the
455   underground phase of *Forficula auricularia* (Dermaptera: Forficulidae). Can Entomol.
456   133:269–278.

457   González-Miguéns R, Muñoz-Nozal E, Jiménez-Ruiz Y, Mas-Peinado P, Ghanavi HR, García-
458   París M. 2020. Speciation patterns in the *Forficula auricularia* species complex: cryptic and
459   not so cryptic taxa across the western Palaearctic region. Zool J Linn Soc. 190(3):788–823.
460   doi:10.1093/zoolinnean/zlaa070. https://academic.oup.com/zoolinnean/advance-
461   article/doi/10.1093/zoolinnean/zlaa070/5894910.

462   Goodacre S. 1997. The overwintering biology of the European earwig *Forficula auricularia*
463   Linneaus (Insecta: Dermaptera: Forficulinae). [Ottawa]: Carleton University.

464   Gould J, Clulow J, Rippon P, Doody JS, Clulow S. 2021. Complex trade-offs in oviposition site
465   selection in a cannibalistic frog. Anim Behav. 175:75–86.
466   doi:10.1016/j.anbehav.2021.02.021. https://doi.org/10.1016/j.anbehav.2021.02.021.

467 Gray DR. 2009. Age-dependent postdiapause development in the gypsy moth (Lepidoptera:
468 Lymantriidae) life stage model. Environ Entomol. 38(1):18–25. doi:10.1603/022.038.0104.

469 Guillet S, Guiller A, Deunff J, Vancassel M. 2000. Analysis of a contact zone in the *Forficula*
470 *auricularia* L. (Dermaptera: Forficulidae) species complex in the Pyrenean Mountains.
471 Heredity (Edinb). 85(5):444–449. doi:10.1046/j.1365-2540.2000.00775.x.
472 http://www.nature.com/doifinder/10.1046/j.1365-2540.2000.00775.x.

473 Guillet S, Josselin N, Vancassel M. 2000. Multiple introductions of the *Forficula auricularia*
474 species complex (Dermaptera: Forficulidae) in eastern North America. Can Entomol.
475 132(1):49–57. doi:10.4039/Ent13249-1.

476 Hajibabaei M, Janzen DH, Burns JM, Hallwachs W, Hebert PDN. 2006. DNA barcodes
477 distinguish species of tropical Lepidoptera. Proc Natl Acad Sci U S A. 103(4):968–971.
478 doi:10.1073/pnas.0510466103.

479 Hance T, Van Baaren J, Vernon P, Boivin G. 2007. Impact of extreme temperatures on
480 parasitoids in a climate change perspective. Annu Rev Entomol. 52:107–126.
481 doi:10.1146/annurev.ento.52.110405.091333.

482 Hartig F. 2020. DHARMa: Residual diagnostic for hierarchical (Multi-level / mixed) regression
483 models. http://florianhartig.github.io/DHARMa/.

484 Hill MP, Binns M, Umina PA, Hoffmann AA, Macfadyen S. 2019. Climate, human influence
485 and the distribution limits of the invasive European earwig, *Forficula auricularia*, in Australia.
486 Pest Manag Sci. 75(1):134–143. doi:10.1002/ps.5192.
487 http://doi.wiley.com/10.1002/ps.5192.

488 Hirayama H, Kasuya E. 2013. Effect of adult females' predation risk on oviposition site
489 selection in a water strider. Entomol Exp Appl. 149(3):250–255. doi:10.1111/eea.12124.

490 Hothorn T, Hornik K. 2021. Exact distributions for rank and permutation tests. R package
491 version v0.8-34.

492 Huang J, Li G, Lei H, Fan C, Tian C, Chen Q, Huang B, Li H, Lu Z, Feng H. 2020. Low-
493 temperature derived temporal change in the vertical distribution of *Sesamia inferens* larvae
494 in winter, with links to its latitudinal distribution. PLoS One. 15(7 July):1–15.
495 doi:10.1371/journal.pone.0236174. http://dx.doi.org/10.1371/journal.pone.0236174.

496 Jing XH, Kang L. 2003. Geographical variation in egg cold hardiness: A study on the
497 adaptation strategies of the migratory locust *Locusta migratoria* L. Ecol Entomol. 28(2-):151–
498 158. doi:10.1046/j.1365-2311.2003.00497.x.

499 Koch LK, Meunier J. 2014. Mother and offspring fitness in an insect with maternal care:
500 phenotypic trade-offs between egg number, egg mass and egg care. BMC Evol Biol.
501 14(1):125. doi:10.1186/1471-2148-14-125.
502 http://www.ncbi.nlm.nih.gov/pubmed/24913927.

503 Kölliker M. 2007. Benefits and costs of earwig (*Forficula auricularia*) family life. Behav Ecol
504 Sociobiol. 61(9):1489–1497. doi:10.1007/s00265-007-0381-7.
505 http://link.springer.com/10.1007/s00265-007-0381-7.

506 Kölliker M, Vancassel M. 2007. Maternal attendance and the maintenance of family groups
507 in common earwigs (*Forficula auricularia*): a field experiment. Ecol Entomol. 32(1):24–27.
508 doi:10.1111/j.1365-2311.2006.00831.x.

509 Körner M, Foitzik S, Meunier J. 2018. Extended winters entail long-term costs for insect
510 offspring reared in an overwinter burrow. J Therm Biol. 74:116–122.
511 doi:10.1016/j.jtherbio.2018.03.021.
512 http://linkinghub.elsevier.com/retrieve/pii/S0306456517304321.

513 Labrie G, Coderre D, Lucas É. 2008. Overwintering strategy of multicolored Asian lady beetle
514 (Coleoptera: Coccinellidae): Cold-free space as a factor of invasive success. Ann Entomol Soc
515 Am. 101(5):860–866. doi:10.1603/0013-8746(2008)101[860:OSOMAL]2.0.CO;2.

516 Lamb RJ. 1976. Parental behavior in the dermaptera with special reference to *Forficula*
517 *auricularia* (Dermaptera: Forficulidae). Can Entomol. 108(6):609–619.
518 doi:10.4039/ent108609-6.

519 Lamb RJ, Wellington WG. 1975. Life history and population characteristics of the european
520 earwig, *Forficula auricularia* (Dermaptera: forficulidae), at Vancouver, British columbia. Can J
521 Entomol. 107:819–824.

522 Lambret P, Rutter I, Grillas P, Stoks R. 2018. Oviposition plant choice maximizes offspring
523 fitness in an aquatic predatory insect. Hydrobiologia. 823(1):1–12. doi:10.1007/s10750-018-
524 3663-3. https://doi.org/10.1007/s10750-018-3663-3.

525 Leather SR, Walters KFA, Bale JS. 1993. The ecology of insect overwintering. Cambridge
526 University Press.
527 https://www.cambridge.org/core/product/identifier/9780511525834/type/book.

528 Lee Jr. R E. 1991. Principles of insect low temperature tolerance. In: Lee Jr. Richard E.,
529 Denlinger DL, editors. Insects at Low Temperature. Boston, MA: Springer US. p. 17–43.

530 Lee RE, Dellinger DL. 1991. Insects at low temperatures. New York, USA: Chapman and Hall.

531 Lenth R V. 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package
532 version 1.5.5-1. https://cran.r-project.org/package=emmeans.

533 Li S, Hao X, Wang Y, Sun B, Bi J, Zhang Y, Janzen FJ, Du W. 2018. Female lizards choose warm,
534 moist nests that improve embryonic survivorship and offspring fitness. Wilson R, editor.
535 Funct Ecol. 32(2):416–423. doi:10.1111/1365-2435.12995.
536 https://onlinelibrary.wiley.com/doi/10.1111/1365-2435.12995.

537 Liu Z, Vancassel M, Quris R. 1997. Female feeding aid in common earwig *Forficula auricularia*
538 L. Entomol Sin. 4(1):67–73. doi:10.1111/j.1744-7917.1997.tb00074.x.

539 Machado G, Trumbo ST. 2018. Parental care. In: Cordoba-aguilar A, Gonzalez-Tokman D,
540 Gonzalez-santoyo I, editors. Insect behavior: from mechanisms to ecological and
541 evolutionary consequences. Oxford: Oxford University Press. p. 203–218.

542 Meunier J, Dufour J, Van Meyel S, Rault M, Lécureuil C. 2020. Sublethal exposure to
543 deltamethrin impairs maternal egg care in the European earwig *Forficula auricularia*.
544 Chemosphere. 258:127383. doi:10.1016/j.chemosphere.2020.127383.
545 https://linkinghub.elsevier.com/retrieve/pii/S0045653520315769.

546 Meunier J, Kölliker M. 2012. Parental antagonism and parent-offspring co-adaptation
547 interact to shape family life. Proc R Soc London B Biol Sci. 279(1744):3981–8.
548 doi:10.1098/rspb.2012.1416.
549 http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2012.1416.

550 Meunier J, Körner M, Kramer J. 2022. Parental care. In: Omkar, Mishra G, editors.

551   Reproductive Strategies in Insects. Boca Raton: CRC Press. p. 337–348.
552   https://www.taylorfrancis.com/books/9781003043195.

553   Meunier J, Wong JWY, Gómez Y, Kuttler S, Röllin L, Stucki D, Kölliker M. 2012. One clutch or
554   two clutches? Fitness correlates of coexisting alternative female life-histories in the
555   European earwig. Evol Ecol. 26:669–682. doi:10.1007/s10682-011-9510-x.
556   http://www.springerlink.com/index/10.1007/s10682-011-9510-x.

557   Van Meyel S, Devers S, Meunier J. 2019. Love them all: mothers provide care to foreign eggs
558   in the European earwig *Forficula auricularia*. Behav Ecol. 30(3):756–762.
559   doi:10.1093/beheco/arz012. https://academic.oup.com/beheco/article/30/3/756/5311762.

560   Van Meyel S, Meunier J. 2020. Filial egg cannibalism in the European earwig: its
561   determinants and implications in the evolution of maternal egg care. Anim Behav. 164:155–
562   162. doi:10.1016/j.anbehav.2020.04.001.
563   https://linkinghub.elsevier.com/retrieve/pii/S0003347220300920.

564   Mortola JP, Gaonac'h-Lovejoy V. 2016. The cooling time of fertile chicken eggs at different
565   stages of incubation. J Therm Biol. 55:7–13. doi:10.1016/j.jtherbio.2015.10.009.
566   http://dx.doi.org/10.1016/j.jtherbio.2015.10.009.

567   Nicolai A, Vernon P, Lenz R, Le Lannic J, Briand V, Charrier M. 2013. Well wrapped eggs:
568   Effects of egg shell structure on heat resistance and hatchling mass in the invasive land snail
569   *Cornu aspersum*. J Exp Zool Part A Ecol Genet Physiol. 319(2):63–73. doi:10.1002/jez.1767.

570   Ostap-Chec M, Kierat J, Kuszewska K, Woyciechowski M. 2021. Red mason bee (*Osmia
571   bicornis*) thermal preferences for nest sites and their effects on offspring survival.
572   Apidologie. 52(3):707–719. doi:10.1111/j.1365- 2435.2011.01946.x.

573   Pike DA, Webb JK, Shine R, Ť DAP, Webb JK, Shine R. 2012. Hot mothers, cool eggs : nest-site
574   selection by thermal optima egg-guarding spiders accommodates conflicting. Funct Ecol.
575   26(2):469–475. doi:65-2435.201 1.01946.x Hot.

576   Quarrell SR, Arabi J, Suwalski A, Veuille M, Wirth T, Allen GR. 2018. The invasion biology of
577   the invasive earwig, *Forficula auricularia* in Australasian ecosystems. Biol Invasions.
578   20(6):1553–1565. doi:10.1007/s10530-017-1646-3.
579   http://link.springer.com/10.1007/s10530-017-1646-3.

580   Ratz T, Kramer J, Veuille M, Meunier J. 2016. The population determines whether and how
581   life-history traits vary between reproductive events in an insect with maternal care.
582   Oecologia. 182(2):443–452. doi:10.1007/s00442-016-3685-3.
583   http://link.springer.com/10.1007/s00442-016-3685-3.

584   Refsnider JM, Janzen FJ. 2010. Putting eggs in one basket: Ecological and evolutionary
585   hypotheses for variation in oviposition-site choice. Annu Rev Ecol Evol Syst. 41(1):39–57.
586   doi:10.1146/annurev-ecolsys-102209-144712.
587   http://www.annualreviews.org/doi/10.1146/annurev-ecolsys-102209-144712.

588   Sandrin L, Meunier J, Raveh S, Walser J-C, Kölliker M. 2015. Multiple paternity and mating
589   group size in the European earwig, *Forficula auricularia*. Ecol Entomol. 40(2):159–166.
590   doi:10.1111/een.12171. http://doi.wiley.com/10.1111/een.12171.

591   Sicsú PR, Macedo RH, Sujii ER. 2020. Lady beetle oviposition site choices: Maternal effects on
592   offspring performance. Florida Entomol. 103(2):228–235. doi:10.1653/024.103.0212.

593   Sinclair BJ, Vernon P, Klok CJ, Chown SL. 2003. Insects at low temperatures: An ecological
594   perspective. Trends Ecol Evol. 18(5):257–262. doi:10.1016/S0169-5347(03)00014-4.

595   Smith RL. 1997. Evolution of paternal care in the giant water bugs (Heteroptera:
596   Belostomatidae). In: Choe JC, Crespi BJ, editors. The evolution of social behavior in insects
597   and arachnids. Cambridge: Cambridge University Press. p. 116–149.

598   Stålhandske S, Lehmann P, Pruisscher P, Leimar O. 2015. Effect of winter cold duration on
599   spring phenology of the orange tip butterfly, *Anthocharis cardamines*. Ecol Evol. 5(23):5509–
600   5520. doi:10.1002/ece3.1773.

601   Stevenson RD. 1985. The relative importance of behavioral and physiological adjustments
602   controlling body temperature in terrestrial ectotherms. Am Nat. 126(3):362–386.

603   Terrien J. 2011. Behavioral thermoregulation in mammals: a review. Front Biosci. 16(1):1428.
604   doi:10.2741/3797. https://fbscience.com/Landmark/articles/10.2741/3797.

605   Thesing J, Kramer J, Koch LK, Meunier J. 2015. Short-term benefits, but transgenerational
606   costs of maternal loss in an insect with facultative maternal care. Proc R Soc London B Biol
607   Sci. 282(1817):20151617. doi:10.1098/rspb.2015.1617.
608   http://rspb.royalsocietypublishing.org/lookup/doi/10.1098/rspb.2015.1617.

609   Thompson JN. 1988. Evolutionary ecology of the relationship between oviposition
610   preference and performance of offspring in phytophagous insects. Entomol Exp Appl.
611   47(1):3–14. doi:10.1111/j.1570-7458.1988.tb02275.x.

612   Tourneur J-C. 2017. Epigeal phase of the biological cycle of *Forficula auricularia* Linnaeus
613   (Dermaptera: Forficulidae) in eastern Canada. Can Entomol. 149(5):600–606.
614   doi:10.4039/tce.2017.33.

615   Tourneur J-C. 2018. Factors affecting the egg-laying pattern of *Forficula auricularia*
616   (Dermaptera: Forficulidae) in three climatologically different zones of North America. Can
617   Entomol. 150(4):511–519. doi:10.4039/tce.2018.24.

618   Tourneur J-C, Gingras J. 1992. Egg laying in a northeastern North American (Montréal,
619   Québec) population of *Forficula auricularia* L. (Dermaptera: Forficulidae). Can Entomol.
620   124:1055–1061.

621   Tourneur J-C, Meunier J. 2020. Variations in seasonal (not mean) temperatures drive rapid
622   adaptations to novel environments at a continent scale. Ecology. 101(4):e02973.
623   doi:10.1002/ecy.2973. https://onlinelibrary.wiley.com/doi/abs/10.1002/ecy.2973.

624   Toxopeus J, Sinclair BJ. 2018. Mechanisms underlying insect freeze tolerance. Biol Rev.
625   93(4):1891–1914. doi:10.1111/brv.12425.

626   Trájer A, Mlinárik L, Juhász P, Bede-Fazekas Á. 2014. The combined impact of urban heat
627   island, thermal bridge effect of buildings and future climate change on the potential
628   overwintering of *Phlebotomus* species in a central European metropolis. Appl Ecol Environ
629   Res. 12(4):887–908. doi:10.15666/aeer/1204_887908.

630   Wang SF, Sun SC, Okazaki RK. 2010. Comparative study on thermotolerance of Artemia
631   resting eggs from Qinghai-Xizang Plateau, China. Aquaculture. 307(1–2):141–149.
632   doi:10.1016/j.aquaculture.2010.07.009.
633   http://dx.doi.org/10.1016/j.aquaculture.2010.07.009.

634   Weiß C, Kramer J, Holländer K, Meunier J. 2014. Influences of relatedness, food deprivation,

635   and sex on adult behaviors in the group-living insect *Forficula auricularia*. Ethology. 120:923–
636   932. doi:10.1111/eth.12261. http://doi.wiley.com/10.1111/eth.12261.

637   Wirth T, Guellec R Le, Vancassel M, Veuille M. 1998. Molecular and reproductive
638   characterization of sibling species in the european earwig (*Forficula auricularia*). Evolution.
639   52(1):260.

640   Wong JWY, Kölliker M. 2014. Effects of food restriction across stages of juvenile and early
641   adult development on body weight, survival and adult life history. J Evol Biol. 27(11):2420–
642   30. doi:10.1111/jeb.12484.

643   Yang C, Huang Q, Wang L, Du W-G, Liang W, Møller AP. 2018. Keeping eggs warm: thermal
644   and developmental advantages for parasitic cuckoos of laying unusually thick-shelled eggs.
645   Sci Nat. 105(1–2):10. doi:10.1007/s00114-017-1532-y.
646   http://link.springer.com/10.1007/s00114-017-1532-y.

647

Figure 1 – Schema of the thermal setups used in the experiment. (A) Schema of one of the two thermoelectric plates with temperatures linearly ranging from 0°C to 20°C and insulated on every side with thick foam (blue) to ensure complete darkness and thermal isolation. Each plate received 16 rails, each containing one female until they laid eggs and then from the 15th week after oviposition until egg hatching. (B) Schema of the homemade climate cabinet build from a small vertical freezer whose door had been removed and the apparatus covered with plywood enclosure (blue=foam) to ensure complete darkness and thermal isolation, and a vertically sliding front door to allow removal. The cabinet was subdivided into three parts to obtain warm (0.9°C to 7.0°C), cold (-4.5°C to 1.6°C) and intermediate (-3.6°C to 2.7°C) temperature ranges. This cabinet hosted 60 females (20 per temperature range) and their eggs for 15 weeks after oviposition. (C) Picture of a female with its eggs in an experimental rail.
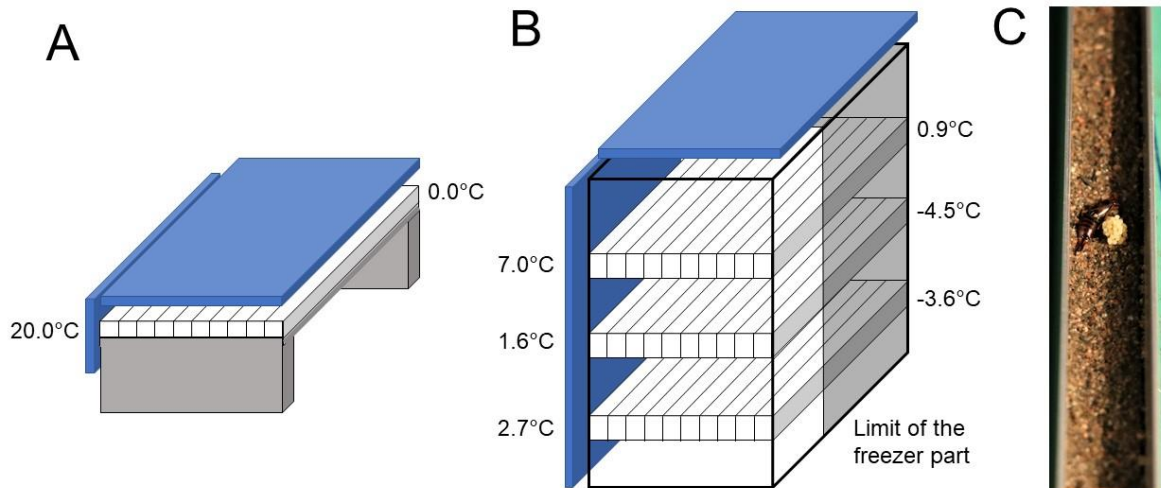
661 **Figure 2** – Locations of Harvey Station (HNB, Canada; Blue) and St Johns (SJNL, Canada;

662 Orange), and their monthly variation of temperatures recorded from 1970 to 2000. Dots

663 depict mean monthly temperatures, with whiskers extending from minimum to maximum

664 mean temperatures. These data were extracted from the WorldClim database.
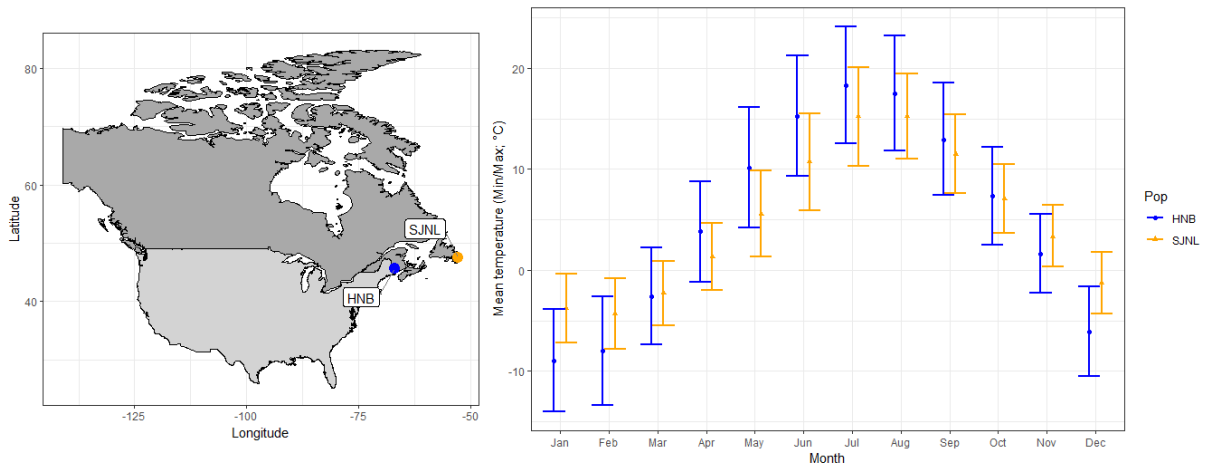
665

666 **Figure 3** – Effect of population on location and reproduction until oviposition. (A) Maximum

667 temperature range, (B) warmest and (C) coldest location at which females were observed

668 during the 15 days preceding oviposition. (D) Location and (E) day at which females laid eggs,

669 and (F) number of eggs produced. Box plots depict median (middle bar) and interquartile

670 range (light bar), with whiskers extending to 1.5 times the interquartile range and dots

671 representing jittered experimental values. ***P<0.001; ns P> 0.05. HNB: Harvey Station. SJNL:

672 St Johns.
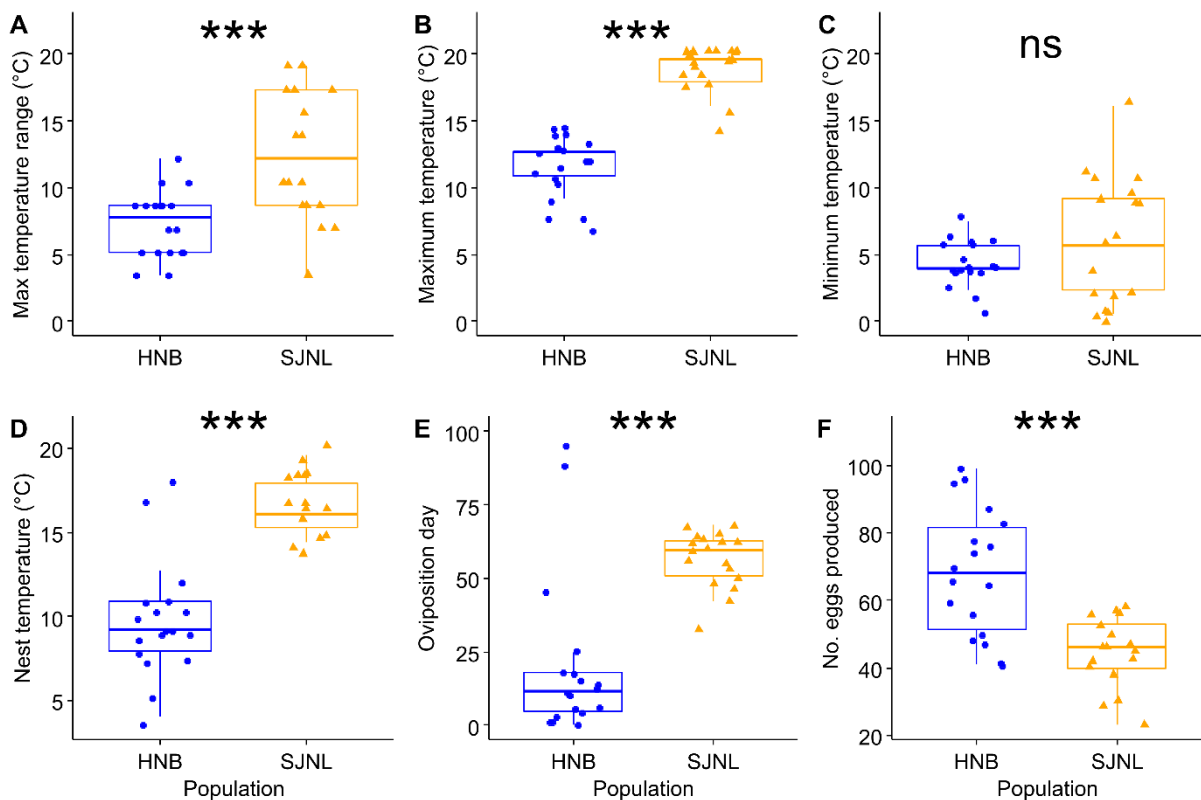
673

674 **Figure 4** – Effect of population and <mark>temperature range</mark> on egg location during the 15 weeks

675 following oviposition. Brackets indicate thermal ranges. Dashed grey lines indicate the

676 location of mothers and eggs when the experiment was set up. <mark>The maximum temperature of</mark>

677 <mark>each area is indicated with a red line, while its minimum temperature is provided between</mark>

678 <mark>brackets.</mark> Grey dots are jittered experimental values for each clutch of eggs. Coloured dots are

679 mean values ± SE per week. Exact Mann-Whitney tests to compare values of each week to the

680 initial temperature: **P<0.01, *P<0.05. P-values corrected for multiple comparisons. HNB:

681 Harvey Station. SJNL: St Johns.
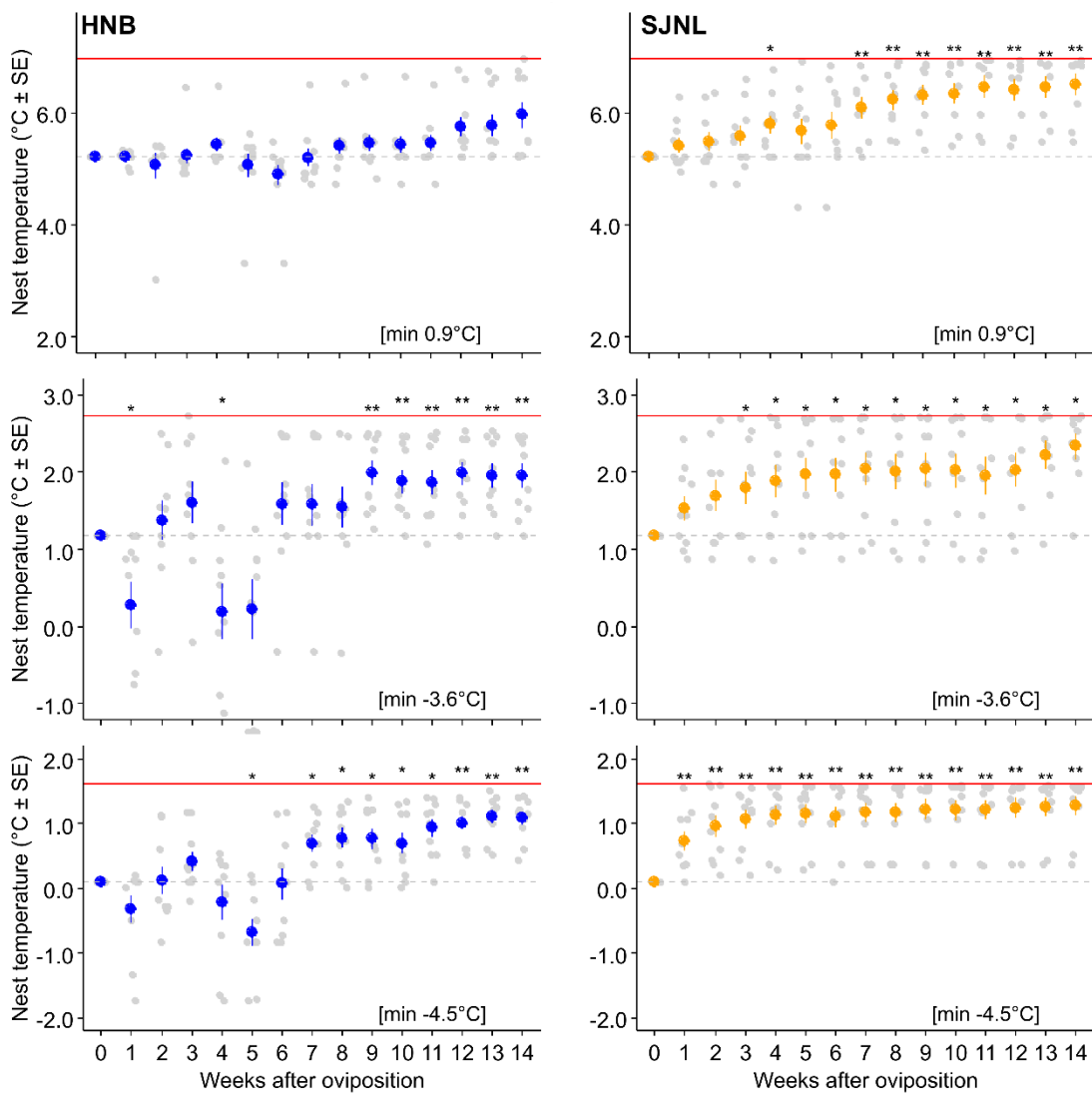
684 **Figure 5** – Effect of population and temperature range on (A,B) the percentage of females with
685 at least one hatched egg and (C,D) the egg hatching rate. Effect of population on the location
686 of the eggs at the time of hatching (E) and the number of weeks between oviposition and egg
687 hatching (F). Figures E and F involved females from the warmest range of temperature only,
688 as their numbers were too limited in the other range of temperatures. Box plots depict median
689 (middle bar) and interquartile range (light bar), with whiskers extending to 1.5 times the
690 interquartile range and dots representing jittered experimental values. ns: P>0.05; *P<0.05;
691 **P<0.01; . p = 0.07. Different letters indicate P<0.05. HNB: Harvey Station. SJNL: St Johns.
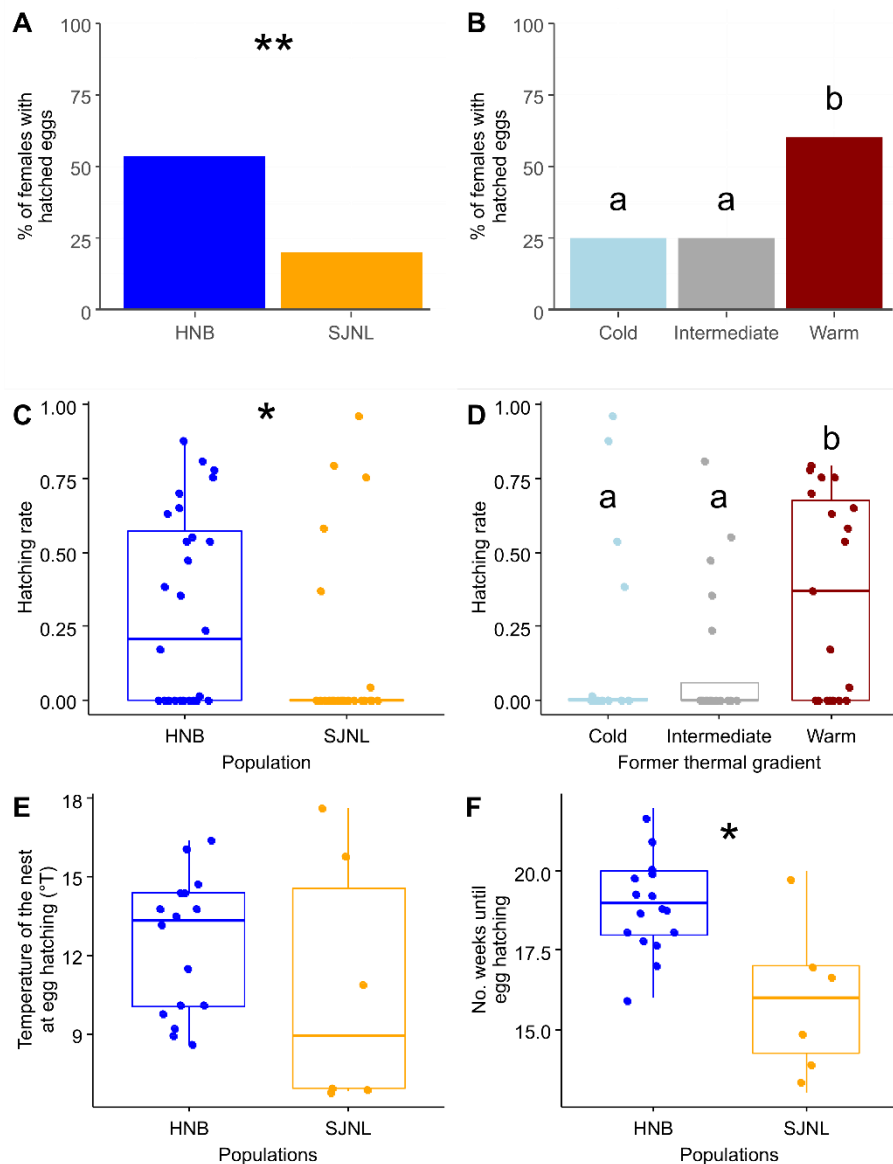
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SUPPLEMENTARY MATERIAL

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Analyses of the genetic clades of *F. auricularia*

To determine whether HNB and SJNL females belonged to the same genetic clade (species) of the European earwig (Wirth et al. 1998; González-Miguéns et al. 2020), we analysed the Cytochrome Oxidase I (COI) gene of 6 females per population. This number of females is enough to robustly assess the origin of an entire population, as previous work demonstrated that the two species do not co-exist in the same population (Wirth et al. 1998; Guillet, Guiller, et al. 2000). Genomic DNA was extracted from whole individuals with the NucleoMag® Tissue kit (Macherey Nagel) following manufacturer instructions. The COI gene (658 bp) was amplified from each individual using routine barcoding primers LepF and LepR (Hajibabaei et al. 2006). PCR amplifications was performed with the DreamTaq® PCR Master Mix Kit (Thermo Scientific) using an ESCO Swift Maxi® thermocycler with an initial denaturation step at 95°C (2 min) followed by 35 cycles at 95°C (45 sec), 52°C (60 sec) and 72°C (90 sec) and finally an extension step at 72°C (10 min). PCR products were purified, and Sanger sequenced in both direction using an ABI 3730XL sequencing system (Thermo Fisher Scientific) at Eurofins Genomics Company. Sequences obtained were corrected using Geneious® 9.1.8. The species status of each female was identified from NCBI databases using the BLAST tool (Altschul et al. 1990). The BLAST results were ranked by percent identity and the reference sequences with at least 100% identity to our sequences were used to assign the species status. All sequences obtained in this study have been submitted to GenBank; their accession numbers are OL512959 to OL512964 for the 6 HNB females and OL512965 to OL512970 for the 6 SJNL females. The COI analyses revealed that all (6/6) HNB females belonged to the species

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