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

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ABSTRACT

Depositing eggs in an area with adequate temperature is often crucial for mothers and their offspring, as the eggs are immobile and therefore cannot avoid exposure to sub-optimal temperatures. However, the importance of temperature on oviposition site selection is less clear when mothers can avoid these potential adverse effects by both moving their eggs after oviposition and providing other forms of egg care. In this study, we addressed this question in the European earwig, an insect in which mothers care for the eggs during several months in winter, frequently moving them during this period. We set up 60 females from two random natural populations (as this species often exhibits population-specific life-history traits and behaviours) under controlled thermal gradients, and recorded the temperature at which they built their nests, tested whether they moved their eggs after an experimental temperature change, and measured the effects on egg development and hatching rate. Our results demonstrate that females indeed select oviposition sites according to temperature, and can move their eggs to reach warmer temperatures. We also show that these warmer temperatures are necessary to ensure egg hatching. Although this set of behavioural thermoregulations is present in the two tested populations, we found a population-specific modality of expression. These included the range of temperatures explored before oviposition, temperature selected at oviposition and dynamics of egg transport following a temperature change. Overall, our study sheds light on a new post-oviposition strategy in female insects that overwinter with their eggs for coping with temperature changes. More generally, it also reveals that egg care and/or egg transport do not prevent behavioural thermoregulation via oviposition site selection and highlights the diversity of behaviours that insects can adopt to enhance their tolerance to global climate change.

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

INTRODUCTION

Oviposition site selection shapes the fitness of most oviparous species (Thompson 1988; Refsnider and Janzen 2010; Meunier et al. 2022). This is because choosing the right place to deposit eggs typically provides direct and indirect benefits to egg-laying females, their current eggs, and their future juveniles. This behaviour may first limit the high risk of predation on adult females that is inherent to their lack of mobility during oviposition and favour their direct access to specific food sources necessary for oviposition. For instance, females of the water strider *Aquarius paludum insularis* (Motoschulsky, 1866) avoid ovipositing in sites containing a predator attacking adults only (Hirayama and Kasuya 2013), while females of the orange tip butterfly *Anthocharis cardamines* (Linnaeus, 1758) deposit eggs on plants that have high nutritional value for adults but poor nutritional value for their larvae (Courtney 1981). Oviposition site selection can also provide direct benefits to eggs by limiting the risks of predators finding the eggs or eggs drying out. In the aquatic beetles *Hydroporus incognitus* Sharp, 1869 and *H. nigrita* (Fabricius, 1792), for example, females select waters where no fish can predate on their eggs (Brodin et al. 2006), while in the damselfly *Lestes macrostigmata* (Eversmann, 1836) females prefer to lay their eggs on plants growing in the deeper parts of temporary ponds to minimize the risk of future egg desiccation (Lambret et al. 2018). Finally, oviposition site selection can help future offspring by favouring proximity to suitable habitats and providing direct access to resources necessary for juveniles. This is the case in the sandpaper frog *Lechriodus fletcher* (Boulenger, 1890) and several lady beetle species, where females choose oviposition sites that contain the largest quantities of nutritive resources for their future larvae (Sicsú et al. 2020; Gould et al. 2021).

The effect of temperature on egg development and survival is another potential driver of oviposition site selection by females. Exposure to extreme temperatures can indeed damage living organisms of all ages through alterations in their physiology, immunity and behaviour, which may overall reduce their fitness and/or lead to premature death (Hance et al. 2007; Dillon et al. 2009; Fey et al. 2015; Filazzola et al. 2021)**.** These effects can be particularly strong in eggs because they are immobile and thus unable to escape from environmental temperatures, their shell often provides limited thermal protection, and the development and survival of embryos (contained in eggs) are generally sensitive to subtle changes in surrounding temperatures (Wang et al. 2010; Nicolai et al. 2013; Mortola and Gaonac'h-Lovejoy 2016; Cordero et al. 2018; Yang et al. 2018). As a result, females of many species select oviposition sites according to optimal temperatures for their eggs, such as in the toad-headed agama lizard *Phrynocephalus przewalskii* Strauch, 1876 (Li et al. 2018), the solitary red mason bee *Osmia bicornis* (Linnaeus, 1758) (Ostap-Chec et al. 2021), or the flat-rock spiders *Hemicloea major* (Koch, 1875) (Pike et al. 2012).

By contrast, the importance of temperature for oviposition site selection becomes less clear when mothers can transport their eggs from one location to another, as it may allow them to secondarily adjust the temperature of their eggs throughout development. This transport, included in a broader phenomenon called egg brooding in insects (Machado and Trumbo 2018), is known to allow parents to limit the risk of egg predations or promote egg oxygenation in aquatic species. For instance in the golden egg bug *Phyllomorpha laciniata* (Villers, 1789), females lay their eggs on conspecifics whose mobility improves the avoidance of egg parasitoids (Carrasco and Kaitala 2009). Similarly, in the water bug *Abedus herbeti* Hidalgo, 1935 females lay their eggs on the males' back, which then move (with the eggs) to 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

130 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

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

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

172 We then tested whether mothers moved their eggs depending on experimental
173 changes in environmental temperature and/or egg age during the 15 weeks following
174 oviposition. Three days after each female has laid its eggs, we transferred the mother and all
175 its eggs to a new (shorter) aluminium rail (1.8 x 1.8 x 66 cm), which was deposited into a
176 climate cabinet (Fig 1B) providing three non-linear ranges of temperature: warm (0.9°C to
177 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
178 thermal gradients encompass the above-ground natural range of temperatures of the two
179 populations during the time females were maintained in our laboratory, i.e. during the natural
180 period of egg care (Gingras and Tourneur 2001; Fig 2). To experimentally change the
181 temperature at which females and eggs were maintained at oviposition, we deposited each
182 female and its eggs in the middle of the new rail (Fig 1C), i.e. at either 5.2°C (warm), 1.2°C
183 (intermediate) or 0.1°C (cold). We then measured the distance (in cm) between the centre of
184 the pile of eggs and the coldest edge of the rail once a week during the 15 following weeks.
185 This measurement of egg transport involved the 36 females used in the measurements of
186 temperature range explored before egg production (see above), and the 24 females (12 from
187 HNB and 12 from SJNL) previously maintained in Petri dishes until oviposition (60 females
188 total). We had not been able to use these 24 females in the electrothermal plates due to the
189 lack of space in the units. Overall, we thus tested 10 HNB and 10 SJNL females in the warm,
190 10 HNB and 10 SJNL females in the intermediate and 10 HNB and 10 SJNL females in the cold
191 range. In the climate cabinet, the rails were lined with a layer of wet sand and closed with a
192 plastic cover to ensure complete darkness. They were slightly shorter than those used in the
193 thermoelectric plates for reasons of fit.

194 We finally tested whether the temperatures at which eggs were maintained during the
195 15 weeks following oviposition affect egg development and hatching rate. Fifteen weeks after

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

205 We recorded the thermal gradients present in the different types of aluminium rails to
206 the nearest 0.1°C using 4 channel K type Thermometers (SD. Amazon. CA) connected to four
207 probes located in the sand either at 2.0, 25.5, 49.0 and 72.0 cm (long aluminium rails) or 1.5,
208 22.5, 43.5 and 64.5 cm (short aluminium rails) of the coldest edge of the rails. The recordings
209 occurred every hour during the entire experiment on either four aluminium rails evenly
210 distributed over the thermoelectric plates or six aluminium rails evenly distributed among the
211 trails and thermal constraints in the climate cabinet. There were no edge effects on
212 temperatures. We then used these recordings to compute linear (thermoelectric plates) and
213 non-linear (climate cabinet) equations linking distance to temperature (Fig S1), which we then
214 used to obtain the temperature of the location of the females and their eggs.

215 **Statistical analyses**

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

218 females were observed before oviposition, the warmest and coldest temperatures reached by
219 females before oviposition, the location of females at oviposition, the date of oviposition, the
220 number of eggs produced, the number of weeks until egg hatching and the temperature of
221 the area of egg hatching. Changes in the location of the clutch after oviposition were then
222 analysed using parametric Linear Mixed-effects models (LME) in which the week (1 to 15),
223 population (SJNL and HNB), range of temperature (warm, intermediate and cold) and the
224 interaction between these three factors were entered as fixed explanatory factors, while the
225 ID of each female was used as a random factor to correct for multiple measurements. To
226 interpret the significant interaction between the three fixed explanatory factors, we divided
227 the data set according to temperature range (i.e. in three subsets), in which we ran another
228 series of LMEs in which we used week, population and the interaction as fixed explanatory
229 factors, and the female ID as a random factor. When the interaction between weeks and
230 population were significant, we conducted post hoc pairwise comparisons between the
231 temperature of the location where the eggs were initially transferred (i.e. 5.2, 1.18 and 0.11°C)
232 and the temperature of the location where the eggs were observed each week using a series
233 of one sample Exact Mann-Whitney Rank Sum tests. To correct for multiple testing, the P-
234 values of this series of pairwise comparisons were adjusted using the False Discovery Rate
235 (FDR) method (Benjamini and Hochberg 1995). Finally, the likelihood to produce at least one
236 juvenile and the hatching rate were tested using two Generalized linear models with binomial
237 error distribution and corrected for overdispersion. In these models, the population, the range
238 of temperatures and their interaction were entered as explanatory factors, while we used
239 either the presence of at least one hatched juvenile as a binary response variable (1 or 0) or
240 the hatching rate (the number of eggs that hatched divided by the total number of eggs
241 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

insect with long-overwintering eggs has been able to invade extremely cold climates (Guillet, Josselin, et al. 2000; Quarrell et al. 2018; Hill et al. 2019; Tourneur and Meunier 2020).

Interestingly, St John's females transported their eggs much earlier than Harvey station females. This suggests that the cold tolerance of eggs in the first few weeks after egg laying is less effective at St John's than at Harvey station, either due to population-specific egg quality, as reported in numerous oviparous species (Jing and Kang 2003; Stålhandske et al. 2015), or population-specific egg development time, as egg sensitivity to cold often increases when they are closer to hatching (e.g. Gray, 2009). In line with the last scenario, egg development time greatly varies between natural populations of the European earwig (Tourneur and Gingras 1992; Meunier et al. 2012; Ratz et al. 2016; Tourneur and Meunier 2020), and our data show that eggs produced by St John's females indeed take less time to hatch compared to eggs produced by Harvey station females when reared in similar conditions. At a more general level, it is typically expected that a population-specific cold tolerance of eggs should lead to population-specific timing of oviposition, the less cold-tolerant eggs being laid later in winter than the more cold-tolerant eggs (Tourneur and Meunier 2020). This is again in line with our results: St John's females laid eggs about one month after Harvey station females. Overall, our results thus demonstrate that winter temperatures are an important factor in the pre- and post-oviposition strategies of earwig females.

Somewhat surprisingly, our study finally reveals that the modality of expression of the reported strategies to protect eggs against severe winter cold varies between the two studied populations. Although our experimental design does not allow us to conclude robustly on the reasons for this variation, we propose three potential explanations. First, this could be due to local adaptation to environmental conditions. In line with this explanation, previous studies

354 reported that multiple traits can vary between populations of the European earwig, such as
355 the number of clutches produced by females, clutch size, juvenile quality, the timing of egg
356 production, duration of egg development and female body mass (Ratz et al. 2016; Tourneur
357 2017; Tourneur 2018; Tourneur and Meunier 2020). However, these studies often compared
358 populations with contrasting climatic conditions, which was not the case between St John's
359 and Harvey stations (Fig 2). Second, the reported variation could be due to population-specific
360 differences in the phenology of females at field sampling. However, this is unlikely to explain
361 our results, as the females were sampled late in the breeding season and our setup control
362 for this potential variation by standardising the measurements around the natural day of
363 oviposition for each female. Finally, the behavioural variation reported between the two
364 tested populations could be due to the presence of different genetic clades. In line with this
365 hypothesis, our genetic analyses reveal that females of Harvey station belong to the genetic
366 clade 'A' and females of St John’s to the genetic clade 'B' (this was surprising, as this is the first
367 time that the clade 'B' is found in Canada outside British Columbia). The European earwig is a
368 complex of cryptic species, for which genetic divergence and reproductive isolation are well
369 established (Wirth et al. 1998; Guillet, Josselin, et al. 2000; González-Miguéns et al. 2020), but
370 the specificity of their life-history traits remains largely unexplored. To date, the only known
371 species-specific trait refers to their reproduction, with females 'A' producing one clutch and
372 females 'B' producing two clutches (Wirth et al. 1998; Tourneur 2018). However, other studies
373 demonstrate that the number of clutches produced by a female can vary within *F. auricularia*
374 species (Tourneur and Gingras 1992; Ratz et al. 2016) depending on numerous parameters
375 acting during and after the early life of an earwig female (Meunier et al. 2012; Meunier and
376 Kölliker 2012; Wong and Kölliker 2014; Tourneur 2018). If this third hypothesis is true, our
377 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).

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CONFLICT OF INTEREST

The authors of this preprint declare that they have no financial conflict of interest with the content of this article. J Meunier is one of the PCI Zool recommenders.

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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.

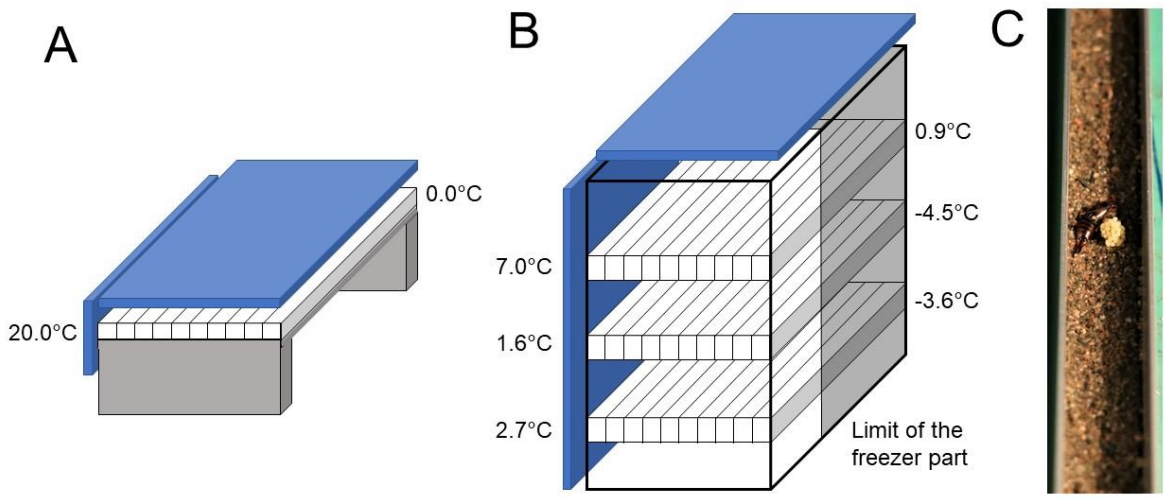
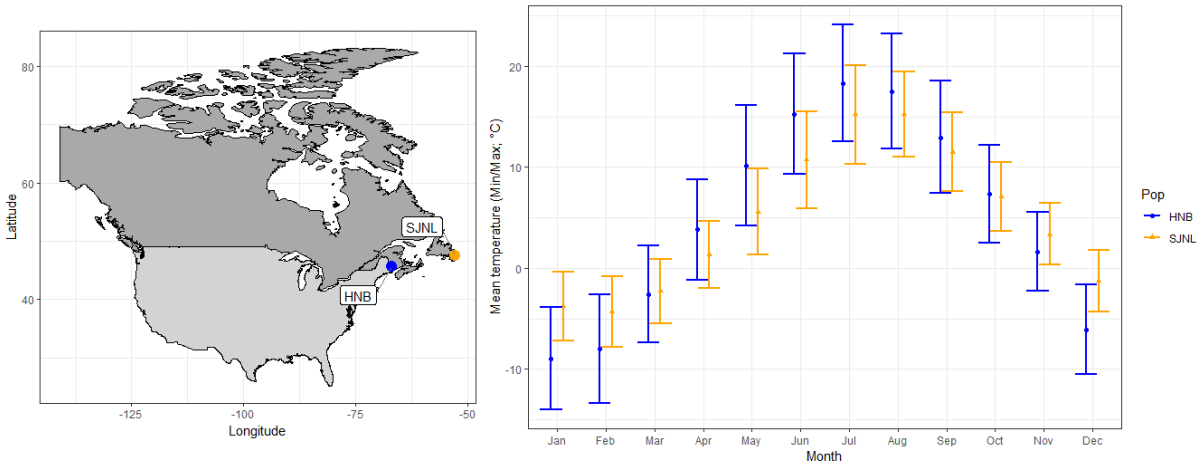
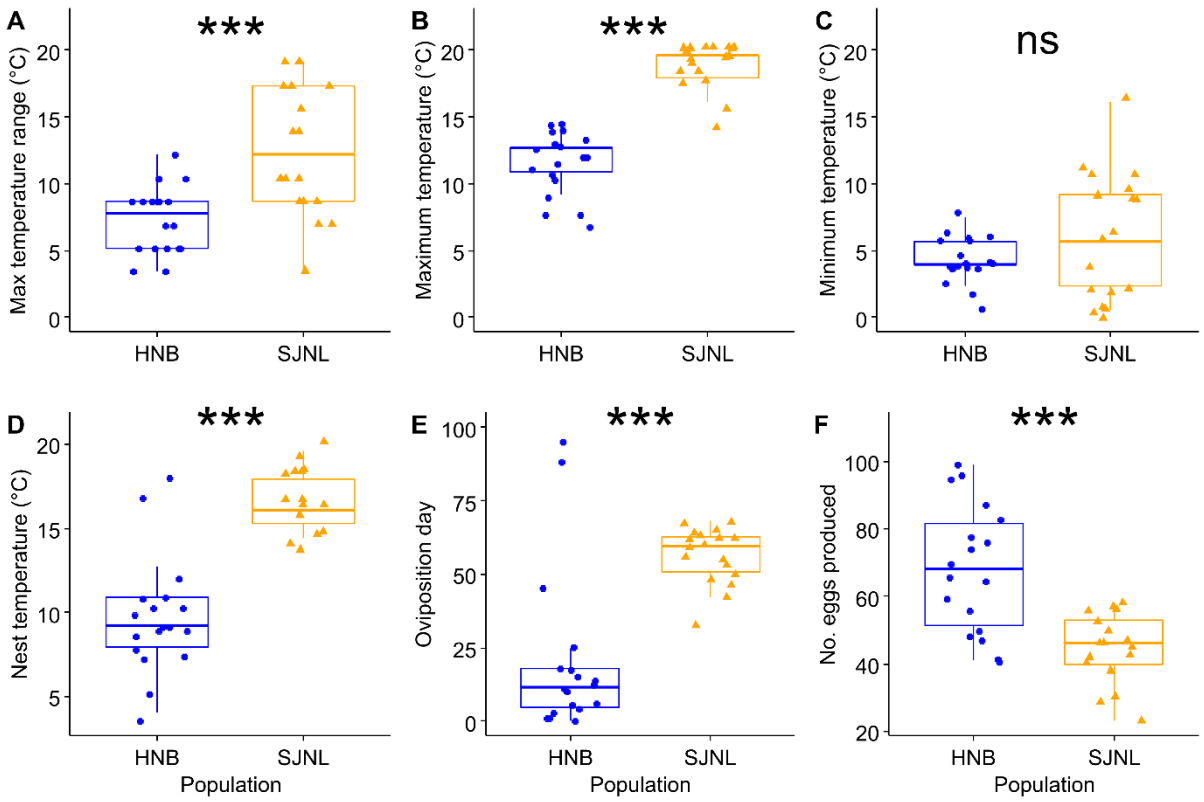


Figure 2 – Locations of Harvey Station (HNB, Canada; Blue) and St Johns (SJNL, Canada; Orange), and their monthly variation of temperatures recorded from 1970 to 2000. Dots depict mean monthly temperatures, with whiskers extending from minimum to maximum mean temperatures. These data were extracted from the WorldClim database.

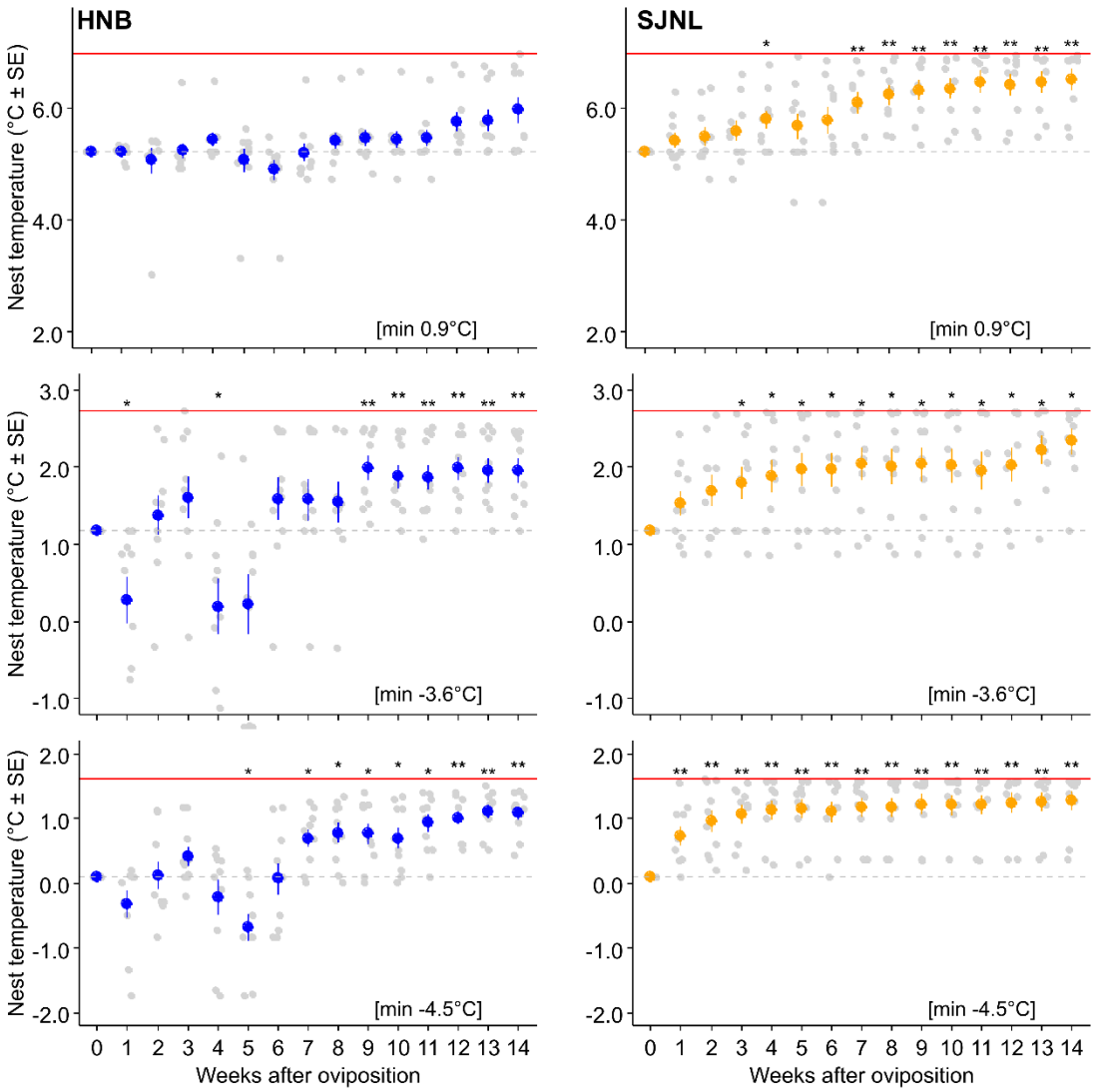


664 **Figure 3** – Effect of population on location and reproduction until oviposition. (A) Maximum
665 temperature range, (B) warmest and (C) coldest location at which females were observed
666 during the 15 days preceding oviposition. (D) Location and (E) day at which females laid eggs,
667 and (F) number of eggs produced. Box plots depict median (middle bar) and interquartile
668 range (light bar), with whiskers extending to 1.5 times the interquartile range and dots
669 representing jittered experimental values. ***P<0.001; ns P> 0.05. HNB: Harvey Station. SJNL:
670 St Johns.



671

672 **Figure 4** – Effect of population and temperature range on egg location during the 15 weeks
673 following oviposition. Brackets indicate thermal ranges. Dashed grey lines indicate the
674 location of mothers and eggs when the experiment was set up. The maximum temperature of
675 each area is indicated with a red line, while its minimum temperature is provided between
676 brackets. Grey dots are jittered experimental values for each clutch of eggs. Coloured dots are
677 mean values ± SE per week. Exact Mann-Whitney tests to compare values of each week to the
678 initial temperature: **P<0.01, *P<0.05. P-values corrected for multiple comparisons. HNB:
679 Harvey Station. SJNL: St Johns.



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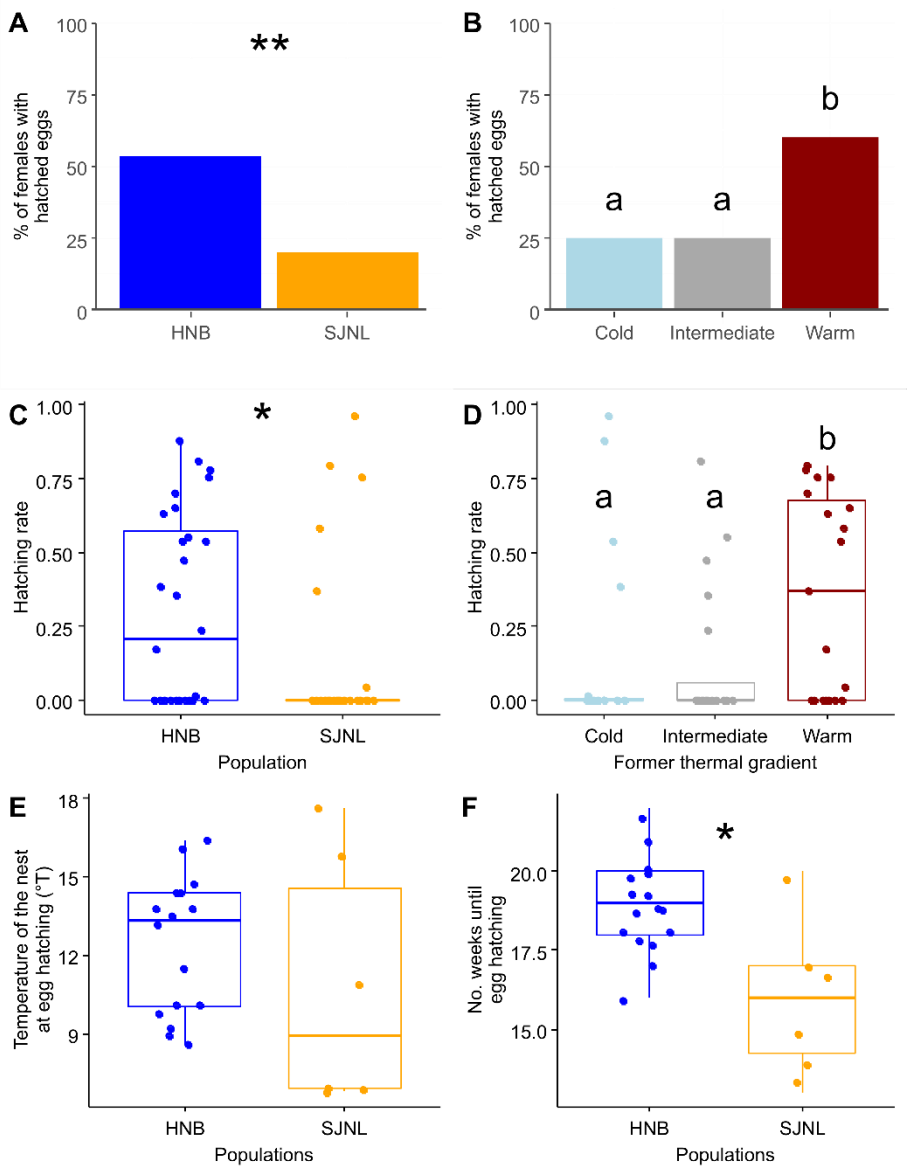
681

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



690

691 # SUPPLEMENTARY MATERIAL

692

693 **Analyses of the genetic clades of *F. auricularia***

694 To determine whether HNB and SJNL females belonged to the same genetic clade (species) of
695 the European earwig (Wirth et al. 1998; González-Miguéns et al. 2020), we analysed the
696 Cytochrome Oxidase I (COI) gene of 6 females per population. This number of females is
697 enough to robustly assess the origin of an entire population, as previous work demonstrated
698 that the two species do not co-exist in the same population (Wirth et al. 1998; Guillet, Guiller,
699 et al. 2000). Genomic DNA was extracted from whole individuals with the NucleoMag® Tissue
700 kit (Macherey Nagel) following manufacturer instructions. The COI gene (658 bp) was
701 amplified from each individual using routine barcoding primers LepF and LepR (Hajibabaei et
702 al. 2006). PCR amplifications was performed with the DreamTaq® PCR Master Mix Kit (Thermo
703 Scientific) using an ESCO Swift Maxi® thermocycler with an initial denaturation step at 95°C (2
704 min) followed by 35 cycles at 95°C (45 sec), 52°C (60 sec) and 72°C (90 sec) and finally an
705 extension step at 72°C (10 min). PCR products were purified, and Sanger sequenced in both
706 direction using an ABI 3730XL sequencing system (Thermo Fisher Scientific) at Eurofins
707 Genomics Company. Sequences obtained were corrected using Geneious® 9.1.8. The species
708 status of each female was identified from NCBI databases using the BLAST tool (Altschul et al.
709 1990). The BLAST results were ranked by percent identity and the reference sequences with
710 at least 100% identity to our sequences were used to assign the species status. All sequences
711 obtained in this study have been submitted to GenBank; their accession numbers are
712 OL512959 to OL512964 for the 6 HNB females and OL512965 to OL512970 for the 6 SJNL
713 females. The COI analyses revealed that all (6/6) HNB females belonged to the species

714 "*Forficula auricularia* A" and all (6/6) SJNL females belonged to the species "*Forficula*

715 *auricularia* B".

716

717 **Figure S1** – Temperatures measured throughout the experiment in the thermoelectric plates

718 (Blue circles) and climate cabinet (Orange squares, Green diamonds, and Grey triangles) as a

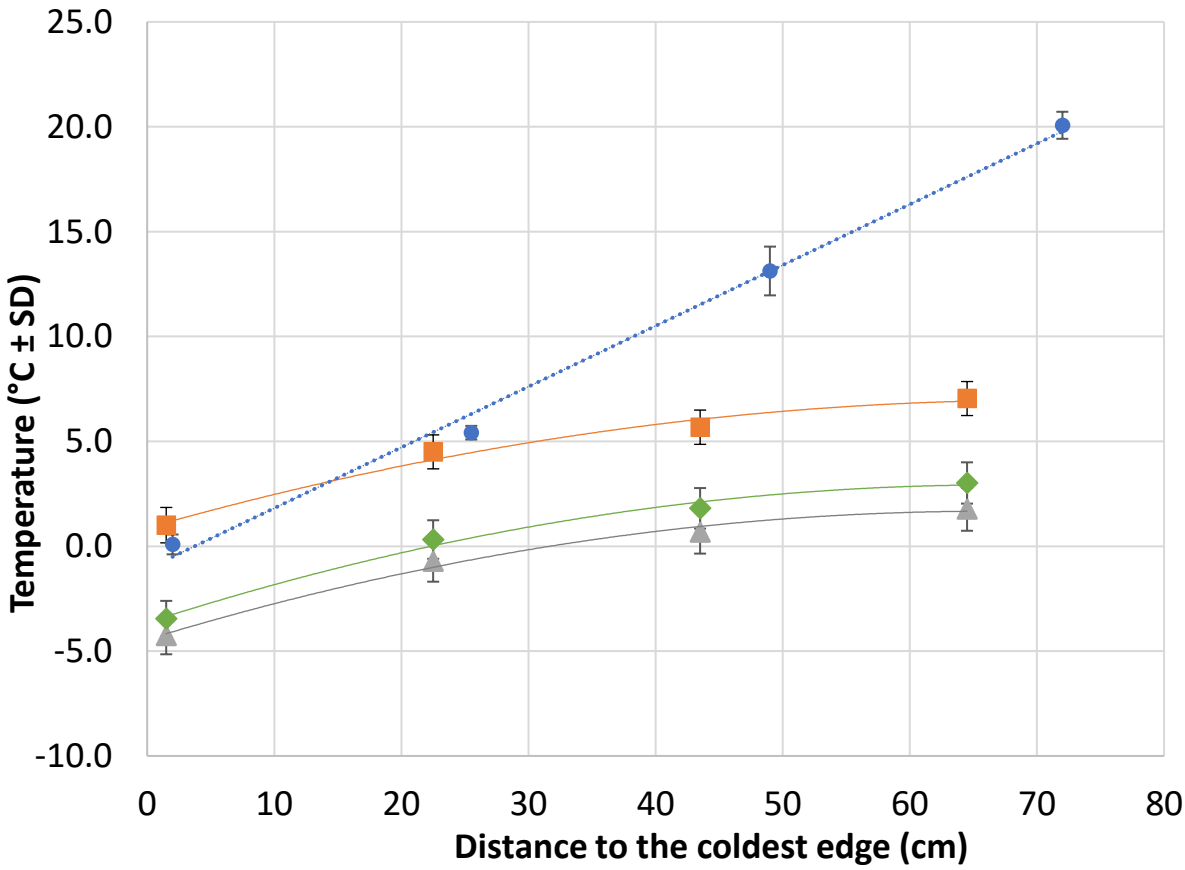
719 function of distance from the coldest edges. In the thermal bridges, the linear regression

720 connecting the measurements is $y = 0.2889x - 0.3452$. In the climate cabinet, the polynomial

721 regressions connecting the measurements differed between the warmest (Orange square; $y =$

722 $-0.0012x^2 + 0.1714x + 0.8747$), intermediate (Blue circle; $y = -0.0015x^2 + 0.1955x - 3.643$) and

723 coldest (Grey triangles; $y = -0.0014x^2 + 0.1842x - 4.445$) temperature ranges.



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