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Microclimate and resource quality determine resource use in a range-expanding herbivore.

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17

18 **<u>Abstract</u>**

19 The consequences of climate change for biogeographic range dynamics depend on the

20 spatial scales at which climate influences focal species directly, and indirectly via biotic

21 interactions. An overlooked question concerns the extent to which microclimates modify

22 specialist biotic interactions, with emergent properties for communities and range dynamics.

23 Here, we use an in-field experiment to assess egg-laying behaviour of a range-expanding

24 herbivore across a range of natural microclimatic conditions. We show that variation in

25 microclimate, resource condition, and individual fecundity can generate differences in egg-

26 laying rates of almost two orders of magnitude in an exemplar species, the brown argus

27 butterfly (*Aricia agestis*). This within-site variation in fecundity dwarfs variation resulting from

28 differences in average ambient temperatures among populations. Although higher

29 temperatures did not reduce female selection for host plants in good condition, the thermal

30 sensitivities of egg-laying behaviours have the potential to accelerate climate-driven range

31 expansion by increasing egg-laying encounters with novel hosts in increasingly suitable

32 microclimates. Understanding the sensitivity of specialist biotic interactions to microclimatic

33 variation is therefore critical to predict the outcomes of climate change across species'

34 geographic ranges, and the resilience of ecological communities.

35 Keywords: *Aricia agestis*, ectotherm, host shift, Lepidoptera, local adaptation, thermal

36 biology

37   **Background**

38   Responses to climate change occur through a combination of geographic range shifts [1,2]

39   and *in situ* plastic and genetic changes that modify the phenology, behaviour or resource

40   use of phenotypes [1,3,4]. These changes determine the abundance, distribution and

41   persistence of species and their biotic interactions [1,5–8]. Where biotic interactions are

42   specialised (e.g. feeding by many phytophagous insects), they create locally suitable habitat

43   patches with steep 'suitability gradients' at patch edges [9], embedded within a matrix of

44   unsuitable habitats which limit dispersal and colonization. Specialist interspecific interactions

45   can therefore constrain range expansion [10,11].

46   The effects of climate change on how individuals encounter, select and exploit resources, or

47   on resource quality itself, could alter range dynamics by smoothing or steepening existing

48   suitability gradients, for example by promoting or precluding certain biotic interactions [12–

49   17]. Research on Lepidoptera host use suggests that range expansion itself promotes

50   incorporation of novel hosts in herbivore diets [18,19], while egg shortfall related to the

51   availability of suitable (micro)habitats and climatic conditions is an important limiting factor at

52   species' range margins [20,21]. Therefore, understanding how individuals' behaviours are

53   mediated by local conditions during species' interactions such as host selection represents a

54   critical step in predicting ecological and evolutionary outcomes of climate change, but is

55   often overlooked [22–25]. Assessments of responses to environmental change also rarely

56   account for the sub-daily and sub-metre temporal and spatial resolutions over which

57   interaction partners and climate vary [26,27]. Such fine-scale variation influences individual

58   behaviour, resource acquisition and fitness, understanding of which may be critical to predict

59   broader ecological responses to climate change [28–35].

60   In this paper, we consider how the steepness of habitat suitability gradients may be modified

61   by individual responses to variation in microclimate and resource condition. We use as a

62   case study a specialist butterfly that has undergone a rapid range expansion associated with

63   the evolution of its biotic interactions to exploit more widespread novel host plants [5,11].

64   Until the 1990s, the UK distribution of the brown argus butterfly (*Aricia agestis*, Lycaenidae)

65   was largely restricted to calcareous grasslands, where it used the perennial common

66   rockrose (*Helianthemum nummularium*, Cistaceae) as its main larval host [36]. Since then,

67   populations have colonised formerly unsuitable regions by increasingly (and apparently

68   exclusively) exploiting Geraniaceae, including the annuals *Erodium cicutarium*, *Geranium*

69   *dissectum* and *G. molle* [5,11,14,37,38]. Studies suggest that warming has enabled

70   increasing use of Geraniaceae and persistence of populations in areas that were previously

71   too cool, coupled with evolutionary changes to increase the frequency of females using only

72   Geraniaceae as hosts [5,11,14,37,39]. These analyses have focused on changes in coarse

73   climate metrics (i.e. Central England Temperature). However, temperature variation at finer

74   scales can dwarf that observed more broadly [26,40]. For example, ground-level

3

75   temperatures of south-facing grasslands in England can be >15 °C warmer than adjacent

76   north-facing slopes [41]. Understanding how microclimate determines egg-laying behaviour

77   in this species can therefore act as a model for the effects of warming on a biotic interaction

78   that determines ecological and evolutionary range dynamics.

79   We test the extent to which within-site microclimatic temperature variation affects egg-laying

80   behaviour of individual butterflies on the novel host *G. dissectum*. We show that individual

81   responses to variation in microclimate and the condition of host plants can generate 75-fold

82   differences in egg-laying rates. These exogenous drivers of expressed fecundity could

83   therefore have important impacts on broader-scale host use and range dynamics, by

84   smoothing or steepening habitat suitability gradients at range margins.

85   **Methods**

86   *Experimental approach*

87   We carried out experiments on wild-caught female brown argus between 5th August and 7th

88   September 2017 to test how natural microclimatic variation mediates *in situ* egg-laying

89   behaviours on *G. dissectum*, a Geraniaceae species widely used as a larval host in recently

90   established populations [14]. We established 25 experimental cages (Figure 1a) in the dune

91   system of Holkham National Nature Reserve (Norfolk, UK), in locations chosen to represent

92   the local range of slopes and aspects (Appendix 1). At 30 minute intervals, we measured in-

93   cage ground-level temperatures (two dataloggers per cage), ambient temperatures (single

94   datalogger with Stevenson screen 1.5 m above ground) and ground-level air temperatures

95   (29 individual dataloggers at randomly-selected locations across the site) (Appendix 1).

96   Cages contained ≥95% bare ground, no natural host plants, and two greenhouse-grown

97   *G. dissectum* ('experimental hosts') per cage (Figure 1a; Appendix 1). Ground albedo and

98   degree of thermal coupling between ground and air temperature will therefore have been

99   similar between cages, and representative of microclimates in open dune areas [42], where

100   *A. agestis* lay eggs on wild Geraniaceae at this site. Differences between cages in slope,

101   aspect and topographic shading likely caused large variation in net radiation absorbed by the

102   ground, thereby generating large variation in cage temperatures (microclimates) for a given

103   ambient temperature. In-cage microclimates were representative of the range and averages

104   of ambient and ground-level temperatures experienced at the site (Figure 1b; Appendix 1).

105   All experimental hosts were watered daily and, though our experimental focus was on

106   microclimatic temperature variation, we monitored host condition and phenophase every two

107   days, to quantify temporal variation in plant traits that may influence acceptability for egg-

108   laying. Host plant condition was visually assessed on a scale of 0–3 (poor–high quality for

109   egg-laying, following [36]; see Appendix 1 for details and justification), and phenophase was

110   recorded on a four-point scale describing whether the plant was in leaf, bud, flower or had

111   set seed. Average plant condition within cages was maintained at ≥2.0 by replacing plants

112   that deteriorated to category 2, and plants were typically replaced before flowers were visible

113   (<5% of cage exposures included one flowering plant). This was achieved by growing 240

114   plants in four cohorts over a six-week period, so all plants used were similar in age, condition

115   and phenophase. Adult female butterflies were captured and housed individually in mesh

116   pots overnight prior to individual release into experimental cages (see Appendix 1 for

117   husbandry).

118   Females were individually assigned to cage exposures each morning, in a pseudo-

119   randomised manner to control for order effects (Appendix 1). A total of 109 females were

120   exposed to host plant and thermal environments during 433 cage exposures. To avoid

121   including data from unmated females, we use data from those 43 females which laid during

122   at least one exposure. These females experienced 251 exposures (5.8 ± 2.8 (SD) exposures

123   each) lasting on average 7 h 49 m (± 47 m (SD)) per exposure. After each exposure, all

124   experimental hosts were systematically searched for eggs; because there were only two

125   plants per cage it was possible to find all eggs, which were removed to avoid double

126   counting. Plant phenophase and the condition of the focal leaf and plant were recorded for

127   each egg-laying location. Post-exposure, butterflies were housed overnight in mesh pots

128   before release into a new cage on the following days. We consider data from all exposures

129   occurring between the hours of 07:30–18:30 which included at least six hours of favourable

130   weather (Appendix 1).

131   *Analysis*

132   We modelled egg-laying probability per exposure using logistic regression with 'lme4' [43].

133   For exposures in which eggs were laid, hourly egg-laying rate was modelled using a gamma

134   GLMM (log link) with 'glmmTMB' [44].

135   For both analyses we considered female ID as a random intercept term (to account for

136   individual variability due to factors such as age) and mean cage temperature (during the

137   appropriate exposure for each cage) as a candidate random slope term representing among-

138   individual variation in thermal sensitivity. As candidate fixed effects, we considered cage

139   temperature (mean temperature of the relevant cage during the exposure) and its quadratic

140   term, exposure number (whether it was the individual's 1st, 2nd, etc. exposure), study day

141   and cumulative eggs laid in prior exposures as scaled continuous predictors, and mean host

142   plant condition and phenophase as ordered factors (with three and five factor levels

143   respectively; Appendix 1). We also tested for a host condition-cage temperature interaction.

144   We constructed candidate model sets by considering all plausible parameter combinations,

145   estimated parameters using maximum likelihood, and used AIC-based model selection to

146   determine model parsimony (see Appendix 1 for details and diagnostic checks). Random

147   effects significance was tested with likelihood ratio tests, and power to detect random slopes

5

148   was tested with simulation-based power analyses (Appendix 1). We used R version 3.5.1

149   [45–47].

150   **Results**

151   Egg-laying probability increased as a function of in-cage temperature (Table 1; Figure 1c),

152   such that the odds of laying increased by 27% per 1 °C temperature increase. There was

153   also a negative effect of study day (Table 1; Figure S4); candidate models showed limited

154   support for positive effects of exposure number and host condition. There was no support for

155   effects of prior laying experience or host phenology in models of egg-laying probability or

156   rate (Table 1).

157   Egg-laying rate increased as a function of in-cage temperature and host condition (Figure

158   1d): by ~12% per 1 °C (Figure 1e), and by a factor of ~7.9 on good vs poor condition hosts

159   (Figure 1f). This equates to an egg-laying rate that is ~75 times higher on the best condition

160   hosts in the warmest microclimate than on the poorest condition hosts in the coolest

161   microclimate. Candidate models showed limited support for a positive effect of exposure

162   number and a negative effect of study day (Table 1).

163   The random effect variance (Table 1) demonstrates between-individual variation in egg-

164   laying probability (LRT = 9.016, p = 0.003) and rate (LRT = 10.903, p < 0.001). There was no

165   support for inclusion of random slopes regarding temperature for laying probability (LRT =

166   0.065, p = 0.968) or rate (LRT = 0.974, p = 0.615): females differed in their fecundity overall

167   but not in their sensitivity to temperature. Power analyses demonstrated low power to detect

168   random slopes (5.6% in a model of laying probability; Appendix 1).

169   **Discussion**

170   We assessed egg-laying on a novel host across a temperature range that is representative

171   of natural microclimates, but wider than the mean ambient temperature range typically

172   experienced by the range-expanding brown argus butterfly across England [11]. Our data

173   show that individual responses to variation in microclimates and host plant condition can

174   combine to generate differences in egg-laying rates that are almost two orders of magnitude

175   greater than population-average differences in egg-laying rates observed between host

176   species [14].

177   Egg-laying females were remarkably sensitive to small variations in host condition, a factor

178   we sought to minimise in our experiment. This is the first time such discrimination has been

179   shown in the Geraniaceae hosts used in the brown argus' range expansion, and

180   complements a previous [36] demonstration that females select lush green leaves (with thick

181   mesophylls and high nitrogen content) when laying on the traditional perennial host,

182   *H. nummularium*. Compared to *H. nummularium*, the condition of wild Geraniaceae hosts

183   appears more temporally variable [48]. As annuals, Geraniaceae may be less reliable

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184 resources in terms of quality and availability at a fine spatial scale, even though they are

185 more widely distributed at larger scales [37,49]. In this context, the bottom-up influences of

186 plant phenotypic variation can provide a strong mechanistic basis for understanding

187 population dynamic responses to global change in herbivores and plants [3,50,51].

188 A methodological concern is that cage experiments may eliminate use of long-distance, pre-

189 alighting cues for egg-laying site choice such as habitat structure or odour plumes of plant

190 volatile compounds (e.g. [52]). Such cues could have altered the acceptability of the host

191 plants with which the butterflies were confined (for example, relative to other host species).

192 However, observations of eggs laid on natural hosts by free-flying brown argus suggest

193 similar preferences regarding host condition [48]. These observations suggest either that the

194 cage experiments do not introduce cue bias, or that long-distance and short-distance cues

195 are well-correlated, as observed in some other species [53]. Furthermore, *G. dissectum* is

196 often preferred in direct choices between host species, though population-level host species

197 preference varies between sites [14].

198 The odds and rate of egg-laying increased dramatically with microclimatic temperature (by

199 27% and 12% per 1 °C, respectively). Warming may therefore increase population growth

200 through increased fecundity, provided suitable hosts are available. At ecological margins,

201 warming also increases the distribution and connectivity of microhabitats that are suitable for

202 egg laying [21]. Microclimatic variation could thereby drive range expansion at a faster rate

203 than ambient temperatures would predict, and may account for recent range expansions by

204 temperature-sensitive species across previously unsuitable landscapes [11,54,55].

205 Behavioural thermoregulation in ectotherms (e.g. basking), allows some thermal

206 independence from the environment. However, many species (including the brown argus)

207 are more dependent on microhabitat selection and their immediate thermal environment for

208 thermoregulation [30]. Fine-scale temperature variation in the immediate proximity of

209 resources may therefore have important effects on population responses to climate change

210 [28–30,56,57].

211 In our experiment, the relationship between egg-laying rate and host condition did not vary

212 with temperature. Though this experiment did not address inter-species host preferences,

213 these results suggest that warming alone may not explain the concurrent host and range

214 shifts observed in this species. Given the odds and rate of egg-laying increase dramatically

215 with microclimatic temperature, warmer summers may increase the likelihood of females

216 encountering and sampling alternative hosts in newly favourable microclimates, increasing

217 the probability of host shifts during range expansion [18]. Larvae grow 10% larger and faster

218 on Geraniaceae than on *H. nummularium* [5,58], provided temperatures are high and

219 relatively stable. This may combine with increased fecundity to promote establishment and

220 growth of populations using the novel host plants, once threshold temperatures are reached.

221 Beyond the potentially beneficial effects of warming on herbivore population growth, further
222 warming may generate maladaptive behaviours. For example, if host condition is correlated
223 with local temperature or moisture regimes then high egg-laying rates under warm, dry
224 conditions may increase herbivore mortality through exposure to poor condition, desiccated
225 hosts. Inflexible preferences for plants growing in drought-stressed habitats were
226 maladaptive for *Melitaea cinxia* butterflies in an extremely dry year, reducing population
227 persistence [59]. Given the capacity for behavioural responses to the environment to
228 become maladaptive as climates change, there is a need for better understanding of genetic
229 variation among individuals and the potential for the evolution of novel behaviours [35]. With
230 this in mind, although we found significant among-individual variation in fecundity (random
231 intercepts), our experiment had insufficient power to detect significant among-individual
232 variation in behaviour [60,61].

233 Here, we show how biotic interactions can be determined by individual responses to
234 variation in microclimate and resource condition. Spatial variation in microclimate may
235 therefore be crucial in determining the steepness of habitat suitability gradients, which
236 regulate rates of range expansion in fragmented landscapes [62]. Advances in modelling
237 fine-scale spatial and temporal variation in microclimate can increasingly reveal when
238 climatic conditions acting on individuals or biotic interactions regulate such range expansions
239 [40,63,64]. Such approaches may permit a mechanistic understanding of range shifts, and
240 higher resolution models of species distributions [48,65,66]. Incorporating robust evidence of
241 the effects of microclimate and biotic interactions on range dynamics may thus improve
242 understanding and prediction of ecological responses to climate change.

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References

251 1. Parmesan C. 2006 Ecological and evolutionary responses to recent climate change.
252   Annual Review of Ecology, Evolution, and Systematics **37**, 637–669.
253   (doi:10.1146/annurev.ecolsys.37.091305.110100)

254 2. Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011 Rapid range shifts of
255   species associated with high levels of climate warming. Science **333**, 1024–1026.
256   (doi:10.1126/science.1206432)

257 3. Visser ME, Both C. 2005 Shifts in phenology due to global climate change: the need for
258   a yardstick. Proceedings of the Royal Society B: Biological Sciences **272**, 2561–2569.
259   (doi:10.1098/rspb.2005.3356)

8

260   4.   Johnson SN, Jones TH. 2017 Global Climate Change and Terrestrial Invertebrates.
261   Oxford, United Kingdom: John Wiley & Sons.

262   5.   Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, Conradt L.
263   2001 Ecological and evolutionary processes at expanding range margins. Nature **411**,
264   577–581. (doi:10.1038/35079066)

265   6.   Miller-Rushing AJ, Høye TT, Inouye DW, Post E. 2010 The effects of phenological
266   mismatches on demography. Philosophical Transactions of the Royal Society B:
267   Biological Sciences **365**, 3177–3186.

268   7.   Macgregor CJ et al. 2019 Climate-induced phenology shifts linked to range expansions
269   in species with multiple reproductive cycles per year. Nature Communications **10**, 1–10.
270   (doi:10.1038/s41467-019-12479-w)

271   8.   Stewart JE, Illán JG, Richards SA, Gutiérrez D, Wilson RJ. 2019 Linking inter-annual
272   variation in environment, phenology, and abundance for a montane butterfly community.
273   Ecology **101**, e02906. (doi:10.1002/ecy.2906)

274   9.   Bridle JR, Kawata M, Butlin RK. 2019 Local adaptation stops where ecological gradients
275   steepen or are interrupted. Evolutionary Applications **12**, 1449–1462.
276   (doi:10.1111/eva.12789)

277   10. Merrill RM, Gutiérrez D, Lewis OT, Gutiérrez J, Díez SB, Wilson RJ. 2008 Combined
278   effects of climate and biotic interactions on the elevational range of a phytophagous
279   insect. Journal of Animal Ecology **77**, 145–155. (doi:10.1111/j.1365-2656.2007.01303.x)

280   11. Pateman RM, Hill JK, Roy DB, Fox R, Thomas CD. 2012 Temperature-dependent
281   alterations in host use drive rapid range expansion in a butterfly. Science **336**, 1028–
282   1030. (doi:10.1126/science.1216980)

283   12. Cudmore TJ, Björklund N, Carroll AL, Lindgren BS. 2010 Climate change and range
284   expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naïve
285   host tree populations. Journal of Applied Ecology **47**, 1036–1043. (doi:10.1111/j.1365-
286   2664.2010.01848.x)

287   13. Rockwell RF, Gormezano LJ, Koons DN. 2011 Trophic matches and mismatches: can
288   polar bears reduce the abundance of nesting snow geese in western Hudson Bay?
289   Oikos **120**, 696–709. (doi:10.1111/j.1600-0706.2010.18837.x)

290   14. Bridle JR, Buckley J, Bodsworth EJ, Thomas CD. 2014 Evolution on the move:
291   specialization on widespread resources associated with rapid range expansion in
292   response to climate change. Proceedings of the Royal Society B: Biological Sciences
293   **281**, 20131800. (doi:10.1098/rspb.2013.1800)

294   15. Singer MC, McBride CS. 2012 Geographic mosaics of species' association: a definition
295   and an example driven by plant–insect phenological synchrony. Ecology **93**, 2658–2673.
296   (doi:10.1890/11-2078.1)

297   16. Moir ML, Hughes L, Vesk PA, Leng MC. 2014 Which host-dependent insects are most
298   prone to coextinction under changed climates? Ecology and Evolution **4**, 1295–1312.
299   (doi:10.1002/ece3.1021)

300   17. Forister ML et al. 2020 Predicting patch occupancy reveals the complexity of host range
301   expansion. Science Advances **6**, eabc6852. (doi:10.1126/sciadv.abc6852)

302   18. Lancaster LT. 2020 Host use diversification during range shifts shapes global variation in
303   Lepidopteran dietary breadth. Nature Ecology & Evolution **4**, 963–969.
304   (doi:10.1038/s41559-020-1199-1)

9

305 19. Singer MC, Parmesan C. 2020 Colonizations drive host shifts, diversification of
306   preferences and expansion of herbivore diet breadth. bioRxiv , 2020.03.31.017830.
307   (doi:10.1101/2020.03.31.017830)

308 20. Courtney SP, Duggan AE. 1983 The population biology of the Orange Tip butterfly
309   *Anthocharis cardamines* in Britain. Ecological Entomology **8**, 271–281.
310   (doi:https://doi.org/10.1111/j.1365-2311.1983.tb00508.x)

311 21. Davies ZG, Wilson RJ, Coles S, Thomas CD. 2006 Changing habitat associations of a
312   thermally constrained species, the silver-spotted skipper butterfly, in response to climate
313   warming. Journal of Animal Ecology **75**, 247–256. (doi:10.1111/j.1365-
314   2656.2006.01044.x)

315 22. Araújo MB, Rozenfeld A. 2014 The geographic scaling of biotic interactions. Ecography
316   **37**, 406–415. (doi:10.1111/j.1600-0587.2013.00643.x)

317 23. Jenkins DA, Lecomte N, Andrews G, Yannic G, Schaefer JA. 2020 Biotic interactions
318   govern the distribution of coexisting ungulates in the Arctic Archipelago – A case for
319   conservation planning. Global Ecology and Conservation **24**, e01239.
320   (doi:10.1016/j.gecco.2020.e01239)

321 24. Staniczenko PPA, Sivasubramaniam P, Suttle KB, Pearson RG. 2017 Linking
322   macroecology and community ecology: refining predictions of species distributions using
323   biotic interaction networks. Ecology Letters **20**, 693–707. (doi:10.1111/ele.12770)

324 25. Flores-Tolentino M, García-Valdés R, Saénz-Romero C, Ávila-Díaz I, Paz H, Lopez-
325   Toledo L. 2020 Distribution and conservation of species is misestimated if biotic
326   interactions are ignored: the case of the orchid *Laelia speciosa*. Scientific Reports **10**,
327   9542. (doi:10.1038/s41598-020-63638-9)

328 26. Suggitt AJ, Gillingham PK, Hill JK, Huntley B, Kunin WE, Roy DB, Thomas CD. 2011
329   Habitat microclimates drive fine-scale variation in extreme temperatures. Oikos **120**, 1–
330   8. (doi:10.1111/j.1600-0706.2010.18270.x)

331 27. Maclean IMD, Suggitt AJ, Wilson RJ, Duffy JP, Bennie JJ. 2017 Fine-scale climate
332   change: modelling spatial variation in biologically meaningful rates of warming. Global
333   Change Biology **23**, 256–268. (doi:10.1111/gcb.13343)

334 28. Suggitt AJ et al. 2018 Extinction risk from climate change is reduced by microclimatic
335   buffering. Nature Climate Change **8**, 713–717. (doi:10.1038/s41558-018-0231-9)

336 29. Suggitt AJ, Wilson RJ, August TA, Fox R, Isaac NJB, Macgregor NA, Morecroft MD,
337   Maclean IMD. 2015 Microclimate affects landscape level persistence in the British
338   Lepidoptera. Journal of Insect Conservation **19**, 237–253. (doi:10.1007/s10841-014-
339   9749-y)

340 30. Bladon AJ et al. 2020 How butterflies keep their cool: Physical and ecological traits
341   influence thermoregulatory ability and population trends. Journal of Animal Ecology **89**,
342   2440–2450. (doi:10.1111/1365-2656.13319)

343 31. Bladon AJ, Donald PF, Jones SEI, Collar NJ, Deng J, Dadacha G, Abebe YD, Green
344   RE. 2019 Behavioural thermoregulation and climatic range restriction in the globally
345   threatened Ethiopian Bush-crow *Zavattariornis stresemanni*. Ibis **161**, 546–558.
346   (doi:10.1111/ibi.12660)

347 32. Weiss SB, Murphy DD, White RR. 1988 Sun, slope, and butterflies: topographic
348   determinants of habitat quality for *Euphydryas editha*. Ecology **69**, 1486–1496.
349   (doi:10.2307/1941646)

10

350 33. Michielsen RJ, Ausems ANMA, Jakubas D, Pętlicki M, Plenzler J, Shamoun-Baranes J,
351   Wojczulanis-Jakubas K. 2019 Nest characteristics determine nest microclimate and
352   affect breeding output in an Antarctic seabird, the Wilson's storm-petrel. PLOS ONE **14**,
353   e0217708. (doi:10.1371/journal.pone.0217708)

354 34. Nadeau CP, Urban MC, Bridle JR. 2017 Climates past, present, and yet-to-come shape
355   climate change vulnerabilities. Trends in Ecology & Evolution **32**, 786–800.
356   (doi:10.1016/j.tree.2017.07.012)

357 35. Bridle J, van Rensburg A. 2020 Discovering the limits of ecological resilience. Science
358   **367**, 626–627. (doi:10.1126/science.aba6432)

359 36. Bourn NAD, Thomas JA. 1993 The ecology and conservation of the brown argus
360   butterfly *Aricia agestis* in Britain. Biological Conservation **63**, 67–74. (doi:10.1016/0006-
361   3207(93)90075-C)

362 37. Buckley J, Bridle JR. 2014 Loss of adaptive variation during evolutionary responses to
363   climate change. Ecology Letters **17**, 1316–1325. (doi:10.1111/ele.12340)

364 38. Buckley J, Butlin RK, Bridle JR. 2012 Evidence for evolutionary change associated with
365   the recent range expansion of the British butterfly, *Aricia agestis*, in response to climate
366   change. Mol. Ecol. **21**, 267–280. (doi:10.1111/j.1365-294X.2011.05388.x)

367 39. Bodsworth EJ. 2002 Dispersal and behaviour of butterflies in response to their habitat.
368   PhD thesis, University of Leeds, Leeds, United Kingdom.

369 40. Bramer I et al. 2018 Advances in monitoring and modelling climate at ecologically
370   relevant scales. Next Generation Biomonitoring, part 1 **58**, 101–161.
371   (doi:http://dx.doi.org/10.1016/bs.aecr.2017.12.005)

372 41. Maclean IMD, Mosedale JR, Bennie JJ. 2019 Microclima: An R package for modelling
373   meso- and microclimate. Methods in Ecology and Evolution **10**, 280–290.
374   (doi:10.1111/2041-210X.13093)

375 42. Liddle MJ, Moore KG. 1974 The microclimate of sand dune tracks: the relative
376   contribution of vegetation removal and soil compression. Journal of Applied Ecology **11**,
377   1057–1068. (doi:10.2307/2401765)

378 43. Bates D, Maechler M, Bolker B, Walker S. 2018 lme4: Linear Mixed-Effects Models
379   using 'Eigen' and S4. R package version 1.1-19. See https://cran.r-
380   project.org/web/packages/lme4/index.html.

381 44. Brooks M E, Kristensen K, Benthem K J ,van, Magnusson A, Berg C W, Nielsen A,
382   Skaug H J, Mächler M, Bolker B M. 2017 glmmTMB balances speed and flexibility
383   among packages for zero-inflated generalized linear mixed modeling. The R Journal **9**,
384   378–400. (doi:10.32614/RJ-2017-066)

385 45. R Core Team. 2018 R: A language and environment for statistical computing. Vienna,
386   Austria: R Foundation for Statistical Computing. See https://www.R-project.org/.

387 46. Stewart JE, Maclean IMD, Edney AJ, Bridle J, Wilson RJ. 2021 Data from: Microclimate
388   and resource quality determine resource use in a range-expanding herbivore. Dryad
389   Digital Repository.

390 47. Stewart JE, Maclean IMD, Edney AJ, Bridle J, Wilson RJ. 2021 R Code from:
391   Microclimate and resource quality determine resource use in a range-expanding
392   herbivore. Zenodo.

11

393 48. Stewart JE. 2020 Linking Phenology to Population Dynamics and Distribution Change in
394   a Changing Climate. Unpublished PhD Thesis, University of Exeter.

395 49. Kemp RJ, Hardy PB, Roy DB, Dennis RLH. 2008 The relative exploitation of annuals as
396   larval host plants by European butterflies. Journal of Natural History **42**, 1079–1093.
397   (doi:10.1080/00222930801937608)

398 50. Hunter MD, Varley GC, Gradwell GR. 1997 Estimating the relative roles of top-down and
399   bottom-up forces on insect herbivore populations: A classic study revisited. PNAS **94**,
400   9176–9181. (doi:10.1073/pnas.94.17.9176)

401 51. Price PW, Hunter MD. 2015 Population dynamics of an insect herbivore over 32 years
402   are driven by precipitation and host-plant effects: testing model predictions.
403   Environmental Entomology **44**, 463–473. (doi:10.1093/ee/nvv039)

404 52. Conchou L, Lucas P, Meslin C, Proffit M, Staudt M, Renou M. 2019 Insect odorscapes:
405   from plant volatiles to natural olfactory scenes. Frontiers in Physioogy. **10**, 972.
406   (doi:10.3389/fphys.2019.00972)

407 53. Schöps K, Hanski I. 2001 Population level correlation between pre-alighting and post-
408   alighting host plant preference in the Glanville fritillary butterfly. Ecological Entomology
409   **26**, 517–524. (doi:10.1046/j.1365-2311.2001.00357.x)

410 54. Cannizzo ZJ, Griffen BD. 2019 An artificial habitat facilitates a climate-mediated range
411   expansion into a suboptimal novel ecosystem. PLOS ONE **14**, e0211638.
412   (doi:10.1371/journal.pone.0211638)

413 55. Bennie J, Hodgson JA, Lawson CR, Holloway CTR, Roy DB, Brereton T, Thomas CD,
414   Wilson RJ. 2013 Range expansion through fragmented landscapes under a variable
415   climate. Ecology Letters **16**, 921–929. (doi:10.1111/ele.12129)

416 56. Curtis RJ, Isaac NJB. 2015 The effect of temperature and habitat quality on abundance
417   of the Glanville fritillary on the Isle of Wight: implications for conservation management in
418   a warming climate. Journal of Insect Conservation **19**, 217–225. (doi:10.1007/s10841-
419   014-9738-1)

420 57. Greenwood O, Mossman HL, Suggitt AJ, Curtis RJ, Maclean IMD. 2016 Using in situ
421   management to conserve biodiversity under climate change. Journal of Applied Ecology
422   **53**, 885–894. (doi:10.1111/1365-2664.12602)

423 58. Pateman RM. 2012 Climate change and habitat associations at species' range
424   boundaries. PhD thesis, University of York.
425   (http://etheses.whiterose.ac.uk/2910/1/Thesis_RM_Pateman_2012.pdf)

426 59. Salgado AL, DiLeo MF, Saastamoinen M. 2020 Narrow oviposition preference of an
427   insect herbivore risks survival under conditions of severe drought. Functional Ecology
428   **34**, 1358–1369. (doi:10.1111/1365-2435.13587)

429 60. Schäpers A, Petrén H, Wheat CW, Wiklund C, Friberg M. 2017 Female fecundity
430   variation affects reproducibility of experiments on host plant preference and acceptance
431   in a phytophagous insect. Proceedings of the Royal Society B: Biological Sciences **284**,
432   20162643. (doi:10.1098/rspb.2016.2643)

433 61. de Villemereuil P, Gaggiotti OE, Mouterde M, Till-Bottraud I. 2016 Common garden
434   experiments in the genomic era: new perspectives and opportunities. Heredity **116**, 249–
435   254. (doi:10.1038/hdy.2015.93)

436 62. Platts PJ, Mason SC, Palmer G, Hill JK, Oliver TH, Powney GD, Fox R, Thomas C. 2019
437   Habitat availability explains variation in climate-driven range shifts across multiple
438   taxonomic groups. Scientific Reports **9**, 15039.

439 63. Bennie J, Wilson RJ, Maclean IMD, Suggitt AJ. 2014 Seeing the woods for the trees –
440   when is microclimate important in species distribution models? Global Change Biology
441   **20**, 2699–2700. (doi:10.1111/gcb.12525)

442 64. Nadeau CP, Urban MC, Bridle JR. 2017 Coarse climate change projections for species
443   living in a fine-scaled world. Global Change Biology **23**, 12–24. (doi:10.1111/gcb.13475)

444 65. Rebaudo F, Faye E, Dangles O. 2016 Microclimate data improve predictions of insect
445   abundance models based on calibrated spatiotemporal temperatures. Front. Physiol. **7**.
446   (doi:10.3389/fphys.2016.00139)

447 66. Schouten R, Vesk PA, Kearney MR. 2020 Integrating dynamic plant growth models and
448   microclimates for species distribution modelling. Ecological Modelling **435**, 109262.
449   (doi:10.1016/j.ecolmodel.2020.109262)

450

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451 Table 1. Summary of AIC analyses for GLMMs of egg-laying probability (*LP*) and rate (*LR*).

452 Showing models with ΔAIC ≤ 6, including the best AIC model (M_{AIC}), selected model (M_{final})

453 and null model (M_{null}). Parameter estimates (with standard errors) are shown for the intercept

454 ($β_0$), study day (*D*), exposure number (*E*), mean cage temperature (*T*) and mean host

455 condition (*Q*). *Q* is an ordered factor with orthogonal polynomial contrasts: estimates are

456 presented for the linear (Q_L) and quadratic terms (Q_Q). Variance of the female ID random

457 intercept term is denoted V_{RE}. *LL* is the log-likelihood.

Model	Model parameters							LL	ΔAIC
	$β_0$	D	E	T	Q_L	Q_Q	V_{RE}		
LP_{AIC}	0.194 (0.351)	-0.877 (0.253)	0.334 (0.212)	1.090 (0.197)	0.866 (0.647)	0.035 (0.462)	0.716	-133.71	0.00
LP_a	0.616 (0.215)	-0.855 (0.247)	0.306 (0.209)	1.023 (0.190)	–	–	0.712	-135.74	0.06
LP_{final}	0.587 (0.213)	-0.648 (0.203)	–	1.006 (0.188)	–	–	0.736	-136.83	0.25
LP_{null}	0.542 (0.195)	–	–	–	–	–	0.664	-162.12	46.83
LR_{AIC}	-0.231 (0.189)	-0.241 (0.118)	0.205 (0.103)	0.428 (0.084)	1.593 (0.351)	-0.331 (0.243)	0.223	-248.84	0.00
LR_{final}	-0.207 (0.196)	–	–	0.441 (0.085)	1.458 (0.345)	-0.276 (0.241)	0.279	-251.12	0.57
LR_{null}	0.649 (0.126)	–	–	–	–	–	0.266	-269.38	31.08

458

459 **Figure legends**

460 Figure 1. (a) Experimental cage with two greenhouse-grown *Geranium dissectum* and

461 iButton dataloggers. (b) Daily minimum, mean and maximum temperature across all cages

462 (In-cage), compared with daily average across 29 iButtons distributed randomly at ground

463 level around the site outside of cages (Ground), and ambient temperature measured at 1.5

464 m above ground (Ambient) (c) Probability of egg-laying increases with mean cage

465 temperature (model LP_{final}). Point clouds indicate exposures during which eggs were (1) and

466 were not (0) laid, lines represent among-female variation. (d) Mean egg-laying rate grouped

467 by host condition and mean cage temperature (range = 13.7 – 34.3 °C; grouping for display

468 only) during the relevant exposure; bar labels show sample size. (e) Marginal effects of

469 mean cage temperature on egg-laying rate; lines show among-female variation (model

470 LR_{final}), points show raw data. (f) Egg-laying rate grouped by host condition, showing

471 marginal effects (model LR_{final}), 95% confidence intervals, and raw data (coloured points).
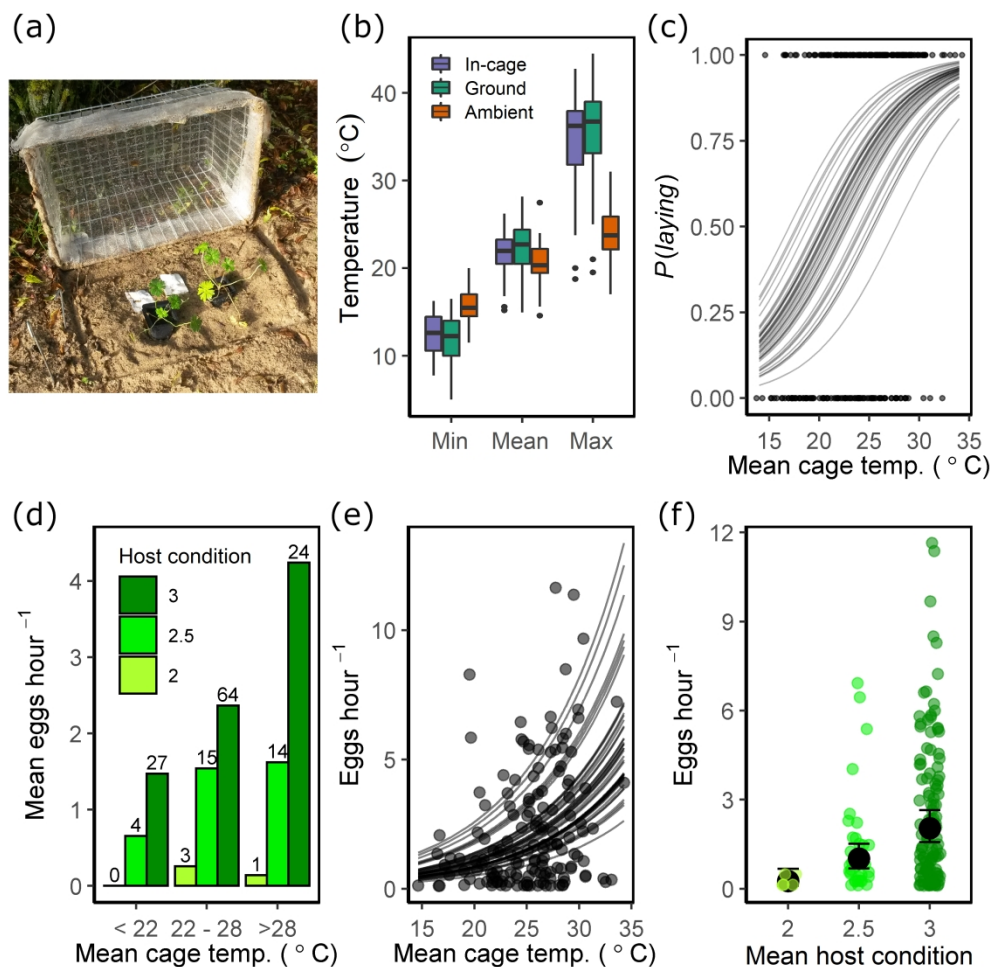
Figure 1. (a) Experimental cage with two greenhouse-grown *Geranium dissectum* and iButton dataloggers. (b) Daily minimum, mean and maximum temperature across all cages (In-cage), compared with the daily average across 29 iButtons distributed randomly at ground level around the site outside of cages (Ground), and ambient temperature measured at 1.5 m above ground (Ambient) (c) Probability of egg-laying increases with mean cage temperature (model LP_{final}). Point clouds indicate exposures during which eggs were (1) and were not (0) laid, lines represent variation among females. (d) Mean egg-laying rate grouped by host condition and mean cage temperature (range = 13.7 – 34.3 °C; grouping for display only) during the relevant exposure; bar labels show sample size. (e) Marginal effects of mean cage temperature on egg-laying rate; lines show variation among females (model LR_{final}), points show raw data. (f) Egg-laying rate grouped by host condition, showing marginal effects and 95% confidence intervals (model LR_{final}), and raw data (coloured points).

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