

1 Title: Microclimate and resource quality determine resource use in a range-expanding
2 herbivore.

3 Running Head: Insect egg-laying and microclimate

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17

18 **Abstract**

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

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

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

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.

243 **Acknowledgments**

244 C. Milne, S. Speak, S. Henderson and Holkham estate staff assisted with fieldwork.
245 Research was funded by the Natural Environment Research Council (grant NE/L002434/1 to
246 JES). Holkham Estate and Natural England kindly granted research permits. Thanks to Rosa
247 Menéndez and Jon Bennie for helpful comments on the research, and to Susanne Foitzik,
248 Ed Turner, and three anonymous reviewers for their contributions through the review
249 process.

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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 $\Delta AIC \leq 6$, 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						V_{RE}	LL	ΔAIC
	β_0	D	E	T	Q_L	Q_Q			
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).

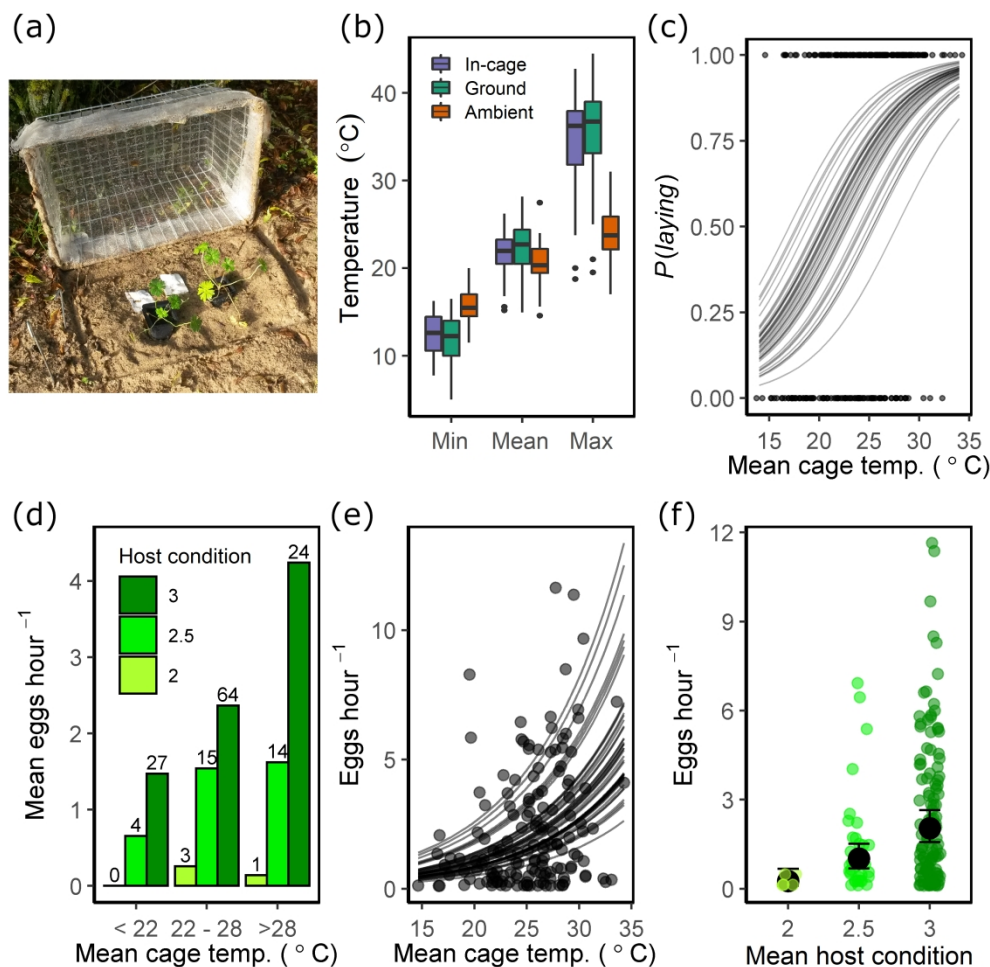


Figure 1. (a) Experimental cage with two greenhouse-grown *Geranium dissectum* and iButton dataloggers. (b) Daily minimum, mean and maximum temperature across all cages (In-cage), compared with the daily average across 29 iButtons distributed randomly at ground level around the site outside of cages (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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