

1 **Individual plasticity drives boldness senescence in a territorial butterfly**

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3 Running title: Boldness senescence in a butterfly

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28

29 **Abstract**

30 Most behavioural traits show plastic responses to changes in internal or external conditions.
31 Similarly, animal personality is not necessarily fixed during an individual's lifetime, leading to
32 age-related changes. Both individual plasticity (i.e. within-individual effect) and non-random
33 selective (dis)appearance of behavioural types (i.e. between-individual effect) may contribute
34 to age-related changes observed at the population level. Here, we investigated how boldness
35 changes with age in a woodland population of the Speckled wood butterfly (*Pararge aegeria*
36 L.) using a capture-mark-recapture approach. We used wing wear as an index for age and we
37 show that fresh individuals are bolder than worn individuals. Using the subsample of recaptured
38 butterflies, we found that this pattern is most likely driven by individual plasticity. Our design
39 also allowed us to explore some aspects of the species' spatial ecology and how it relates to
40 personality. We found no relationship between boldness and net displacement between
41 successive captures, a finding which we discuss within a movement ecology framework.

42 **Keywords**

43 Animal personality – Behavioural syndrome – Lepidoptera – Movement ecology – *Pararge*
44 *aegeria* – Routine movements – Thermal ecology

45 **Introduction**

46 Phenotypic plasticity is an important trait that enables organisms to cope with changing
47 environmental conditions. Virtually all phenotypic traits can show plastic responses at some
48 point, either triggered by external or internal cues. In this context, ageing can be a major driver
49 of within-individual changes. For example, reproductive senescence, the age-related decline in
50 reproductive output, is widely documented in wild animals (Lemaître and Gaillard 2017) and
51 is thought to occur mainly as a consequence of within-individual changes (Nussey et al. 2008).
52 Yet, between-individual changes such as selective (dis-)appearance of certain phenotypes may
53 also explain trait differences between age classes. At the population level, reduced reproductive
54 performance in older individuals may well be due to good reproducers trading off reproductive
55 output with lifespan, and hence dying earlier than poor reproducers (i.e. selective
56 disappearance). Alternatively, poor reproducers may be excluded from reproducing at a young
57 age by more competitive individuals and they may gain access to reproduction only late in life
58 (i.e. selective appearance) (van de Pol and Verhulst 2006). Obviously, a wide array of
59 morphological, physiological and behavioural traits may differ between age classes.
60 Consequently, a proper evaluation of within- versus between-individual changes is needed to
61 fully understand such dynamics.

62 The study of personalities has gained ground within behavioural ecology (David and Dall
63 2016). While in humans there is a long tradition of quantifying personality traits, only during
64 the last twenty years or so a lot of evidence has been accumulating on conceptually similar
65 variation in non-human animals (Gosling 2008). Personality refers to inter-individual,
66 intraspecific behavioural variation that is stable over time and in different contexts (Stamps and
67 Groothuis 2010). Nonetheless, the concept of personality does not imply that personality traits
68 are necessarily fixed within an individual's lifetime. Just as with other behaviours, individuals
69 may display plastic adjustments to personality traits. Recent studies have shown that personality

70 changes with age (e.g. Humphries et al. 2015; Favati et al. 2016; Polverino et al. 2016; Stanley
71 et al. 2017). Although only few studies have tried to tease apart within- and between-individual
72 changes, age-related changes in personality traits appear so far to be mainly caused by within-
73 individual changes (i.e. individual plasticity) (e.g. Class and Brommer 2016; Fisher et al. 2018).

74 The Speckled wood butterfly (*Pararge aegeria*) is a long-established study system in
75 behavioural ecology. Particularly the mate location behaviour in males has attracted much
76 attention since the game theory-inspired pioneer field study by Nick Davies (Davies 1978).
77 Males try to monopolize a sunlit patch on the forest floor as a rendezvous site for receptive
78 females, which they aggressively defend against other males (reviewed in Van Dyck 2003).
79 More recently, consistent inter-individual variation in behavioural traits has been documented
80 in *P. aegeria*, providing evidence for personality traits in this butterfly (Ducatez et al. 2014;
81 Kaiser et al. 2018). Here, within the same species, we tested the repeatability of a boldness
82 measure under variable field conditions and we investigated age-related changes in this
83 personality trait in a wild woodland population. In a recent study, we reported on boldness
84 senescence in laboratory-reared Speckled woods (Kaiser et al. 2019a). While between-
85 individual changes were an unlikely cause of age-related decline in boldness in this F1 captive-
86 reared population, different mechanisms may be at work in natural populations. Indeed,
87 maintaining animals in laboratories often involves providing *ad-libitum* food and ensuring the
88 absence of predators and pathogens, but such conditions may disrupt the relationship between
89 behaviour and survival (Moiron et al. 2020). In this context, typically harsher natural conditions
90 provide useful set-ups to investigate the role of between-individual patterns. Because bold
91 individuals are supposed to take more risks when exposed to threats (Réale et al. 2007), one
92 may expect bold phenotypes to be removed first from a population (i.e. selective disappearance
93 of bold types). However, since the boldness test we developed mimics a butterfly being stuck
94 in, for example, a spider web or a bird's beak (see below), we can actually expect the opposite

95 pattern as bold individuals may be able to escape their predators more easily by moving more
96 under stressful conditions. Whatever their direction, such between-individual changes may be
97 reinforced (or instead, counteracted) by within-individual changes, as both mechanisms may
98 play a role in shaping age-related changes in boldness in natural populations (van de Pol and
99 Verhulst 2006). As such, a proper evaluation of the underlying processes is required.

100 Our capture-mark-recapture study also enabled us to test hypotheses on species-specific thermal
101 ecology and to evaluate whether boldness relates to space use in male Speckled woods.
102 Recently, Spiegel et al. (2017) proposed a framework that links personality traits with some
103 aspects of spatial dynamics in animal populations. While several studies have shown that
104 dispersal is often non-random and biased towards some behavioural types (i.e. personality-
105 dependent dispersal – Cote et al. 2010), few studies have investigated the co-variation between
106 personality traits and aspects of daily space use such as home range size (Spiegel et al. 2017).
107 As an attempt to investigate this in an invertebrate species, we used the net displacement
108 between successive captures as a proxy for space use. While some personality traits, such as
109 activity and exploration, are inherently linked to movements, the relationship between boldness
110 and daily movements is less straightforward. Yet, we expect such a co-variation to arise because
111 shy individuals are expected to take less risks and to more strongly avoid risky environments.
112 We thus expect shy butterflies to settle with high fidelity on territories that they perceive as
113 safe, while we expect bolder individuals to move longer distances between successive captures,
114 indicating larger home ranges.

115

116 **Material and methods**

117 *Study species*

118 The Speckled wood (*P. aegeria* L.) is a satyrine butterfly occurring principally in woodland
119 and along woodland edges across its European range (Settele et al. 2008). In Belgium and The
120 Netherlands, it is a very common and widespread species (Van Dyck et al. 2009). The species
121 has a monandrous mating system (Svärd 1985) and males typically emerge before females (i.e.
122 protandry – Gotthard et al. 1994). Under woodland habitat conditions males locate females by
123 either territorial perching or by patrolling (Van Dyck et al. 1997).

124 *Study site*

125 Our study was conducted in a 231 ha woodland, called ‘Bois de Lauzelle’. This mixed
126 woodland is locally dominated by oak trees (*Quercus robur*). It is owned by the UCLouvain
127 university and situated near the university campus. Data were collected in the summer of 2018,
128 from July to September, within the period corresponding to the cohort of directly developed
129 summer generation adults (i.e. development without a larval or pupal diapause – Wiklund et al.
130 1983). A map of the study area showing the location of all capture events is shown in Figure
131 S1.

132 *Personality trait, temperature, body size and net displacement*

133 We collected data on Speckled wood males adopting a territorial perching mate location
134 strategy. If a male was spotted during the walking route across the study area, its behaviour was
135 observed to confirm the status of being a territorial male on a sunlit patch at the forest floor (see
136 Van Dyck et al. 1997). Next, the male was captured with a butterfly net and relative adult age
137 was estimated based on the level of wing wear. We used a four-level scale (1 = freshly emerged
138 adult, to 4 = heavily damaged wings, i.e. lost wing scales and a significant loss of wing
139 fragments) (cf. Kemp and Alcock 2003; Takeuchi 2006).

140 Then, the butterfly was gently placed with closed wings in a semi-transparent glassine envelope
141 (63 x 97 mm) and we counted the number of movements the butterfly made either with the

142 head, the wings or the legs during one minute under these stressful conditions. For further
143 details about this boldness test and its significance, we refer to our previous work (Kaiser et al.
144 2018, 2019a, b). After the test, the butterfly was marked by writing a unique number on the left
145 ventral hind wing and we measured body temperature by making contact at the level of the
146 thorax with an infrared thermometer (IBP TS 402). We took three measures within a minute
147 and calculated the average value. Simultaneously, ambient temperature was also measured in
148 the shade close to the sunlit patch (HOBO Pendant Temperature/Light 64K data logger). Before
149 we released the butterfly, we measured the right forewing length from the wing base (i.e. close
150 to the thorax) to the wing tip with a digital calliper (precision: ± 0.1 mm). Wing length was
151 measured three times and we calculated the average as a measure of body size for each
152 individual male. We also recorded capture coordinates (World Geodetic System – WGS84)
153 using the free smartphone app “My GPS Coordinates”. Coordinates were written down when
154 the spatial accuracy provided by the app was at least 15 m. A single observer (ME) conducted
155 all behavioural observations and carried out all measurements.

156 For recaptured individuals, we also calculated the net displacement (i.e. Euclidean distance)
157 between the first and the second capture site, based on capture coordinates imported into QGIS
158 (version 3.6). As very few individuals ($N = 4$) were captured more than two times, we calculated
159 the net displacement between the first and second capture only.

160 *Statistical analysis*

161 All statistical analyses were performed with R 3.5.1 (R Core Team 2020) and all continuous
162 variables were scaled prior to analysis. We analysed the relationship between thorax
163 temperature and ambient temperature using a linear mixed model (*lme4* package). Thorax
164 temperature was the response variable and ambient temperature and forewing length (used as a
165 proxy for body size) were the explanatory variables. Because some individuals were measured
166 several times, we included individual ID as a random effect (i.e. random intercept). We also

167 included date as a random effect (random intercept). For the analysis of thorax temperature, we
168 used the complete dataset (N observations = 212; N individuals = 183). Boldness was analysed
169 with a generalized linear model, with a Poisson error structure and log link function. We fitted
170 two models. The first model included wing wear (treated as a factor), thorax temperature and
171 forewing length as explanatory variables. Again, we included individual ID and date as random
172 effects in the model. This first model included all behavioural observations (i.e. complete
173 dataset, see above). Based on this model, we estimated boldness repeatability (using the *rptR*
174 package).

175 Because we found that boldness decreased with wing wear (i.e. a proxy for age) at the
176 population level and we aimed to unravel whether this was due to within- or between-individual
177 effects, we fitted a second model for boldness using a within-individual centring approach (see
178 van de Pol and Wright 2009). The general idea is to decompose age effects into two variables
179 that would reflect within- and between-individual changes. Because the precise age of wild-
180 caught individuals could not be known with precision, we used the number of days since the
181 first capture (to which we applied within-individual centring) as a proxy for within-individual
182 effects. We used individual's maximum wing wear values as a proxy for between-individual
183 effects (treated as a factor) because we aimed at testing the effect of selective disappearance
184 (van de Pol and Verhulst 2006). The model again included thorax temperature and forewing
185 length as explanatory variables and individual ID and date as random effects. The dataset used
186 for this model only contained individuals which were assessed multiple times for boldness (N
187 observations = 54; N individuals = 25).

188 Net displacement (in meters) between the first and second captures was log-transformed prior
189 to analysis to achieve normality of the residuals. Using data collected from recaptured males
190 (N = 25), we fitted a linear model with forewing length and the number of days elapsed between
191 the two captures as explanatory variables.

192 Finally, we assessed the correlation between boldness and net displacement in recaptured males
193 using a bivariate Bayesian model (*MCMCglmm* package). The model contained boldness and
194 net displacement (log-transformed) as response variables. Similar to the univariate models
195 presented above, we included trait-specific fixed effects: wing wear, thorax temperature and
196 forewing length for boldness; forewing length and the number of days elapsed between the two
197 captures for net displacement. Random effects included individual ID and date. Boldness and
198 net displacement were fitted with a Poisson and a Gaussian error structure, respectively. We
199 used a non-informative prior, with 300,000 iterations, from which we discarded the first 30,000
200 (burn-in), while using a thinning interval of 100. These model specifications resulted in low
201 autocorrelation and we performed three runs to confirm the robustness of the outputs. Then, we
202 computed the between-individual correlation between boldness and net displacement. The
203 correlation was considered significant when the 95% credible interval did not overlap with zero.

204

205 **Results**

206 A total of 183 territorial males were captured at least once. Among those, 158 were captured
207 once, 21 twice and four individuals were captured three times (i.e. overall recapture rate of
208 13.7%). Their thorax temperatures varied between 24.5 and 35.1°C, with 74.5% of the values
209 in the 28 to 32°C range. Thorax temperature increased with ambient temperature ($F_{1,165.3} =$
210 187.54 , $P < 0.001$; Fig. 1), being on average $3.6 \pm 1.4^\circ\text{C}$ (mean \pm SD) above ambient
211 temperatures, and was not related to body size ($F_{1,165.7} = 0.0001$, $P = 0.99$).

212 During the one-minute test the boldness score varied considerably among males, from no
213 movement at all in 45.8% (97/212) of the assessments to 32 movements (Fig. S2). Boldness
214 shows a significant repeatability of 0.65 (95% confidence interval: 0.27 – 0.88). Overall,
215 boldness scores increased with increasing thorax temperature ($\chi^2_1 = 5.15$; $P = 0.023$) and older

216 males, as measured by their level of wing wear, had lower boldness scores than young males
217 ($\chi^2_3 = 13.39$; $P = 0.004$; Fig. 2). Pairwise comparisons (Tukey post-hoc test) showed that young
218 individuals had on average higher boldness scores than worn individuals (wing wear 1 versus
219 3: $P = 0.004$; wing wear 1 versus 4: $P = 0.024$; wing wear 2 versus 3: $P = 0.010$; P-values
220 obtained after applying Benjamini & Hochberg adjustment for multiple testing) (Fig. 2).
221 Boldness was independent of body size ($\chi^2_1 = 1.19$; $P = 0.28$).

222 Using the subset of individuals that were assessed multiple times for boldness, we explored
223 whether the observed age-related decline in mean boldness occurred because of individual
224 plasticity *versus* selective disappearance. Maximum wing wear (used as a proxy for between-
225 individual effects) was unrelated to boldness ($\chi^2_3 = 4.53$; $P = 0.21$), while boldness tended to
226 decrease with time since the first capture (after applying within-individual centring – used as a
227 proxy for within-individual effects) ($\chi^2_1 = 2.78$; $P = 0.095$) (Fig. 3).

228 The distance moved between the first and second capture varied between 2 and 445 m.
229 However, more than half of the recaptures (14/25) occurred within 50 m (Fig. S3). Net
230 displacement was neither related to forewing length ($F_{1,22} = 0.29$, $P = 0.59$), nor to the number
231 of days elapsed between both captures ($F_{1,22} = 1.89$, $P = 0.18$). We found no significant
232 correlation between boldness and net displacement in recaptured males (between-individual
233 correlation: -0.09 – credible interval: -0.59; 0.42).

234

235 **Discussion**

236 Using a capture-recapture design, we assessed variation in boldness in a woodland population
237 of the Speckled wood butterfly. Our field study showed that, at the population level, boldness
238 declined with increasing age, and we show that this is probably due to within- rather than
239 between-individual changes. We also investigated whether boldness correlated with net

240 displacement between captures as a simple measure of space use, but we did not find evidence
241 for such a relationship. In the following sections, we will discuss these results in the light of the
242 ecology of the study species and integrate our current findings with the existing knowledge on
243 butterfly personality.

244 *Body temperature*

245 While the age dynamic of boldness and its co-variation with space use were the primary focus
246 of our study, our experimental design also allowed us to study some aspects of the thermal
247 ecology of the Speckled wood in woodland habitat and to compare our results and methods to
248 previously published works on this species. Thoracic temperature scaled with ambient
249 temperature and about 75% of the butterflies had a thoracic temperature in the range of 28 to
250 32°C. While our results are overall similar to those obtained by Van Dyck & Matthysen (1998),
251 some slight discrepancies can be pointed out that probably relate to methodological differences.
252 For instance, the latter study reported slightly higher (i.e. +2°C) thoracic temperatures, which
253 may be due to the use of a thermocouple sensor inserted inside the thorax while we measured
254 surface temperature. In the butterfly *Heteronympha merope*, internal thorax temperature
255 measured with such a probe was indeed 1.3°C higher than surface temperature (Nève and Hall
256 2016). Also, Van Dyck & Matthysen (1998) measured internal temperature shortly after capture
257 (within 5 seconds) while in our study at least 1 minute (i.e. the duration of the boldness
258 assessment and butterfly marking) systematically elapsed before we recorded thoracic
259 temperature. Accounting for those methodological aspects may well explain the difference
260 between both studies.

261 *Age-related change in boldness: within- versus between-individual changes*

262 Here, we tested for personality under field conditions in the Speckled wood. By far most
263 personality studies make use of laboratory settings, often with reared individuals as we did

264 previously too (Kaiser et al. 2019a, b). It is therefore interesting to underscore that despite the
265 increased environmental variation under woodland conditions (e.g. in temperature, humidity
266 level or solar radiation), we were still able to show a significant repeatability for boldness.
267 While our simple test proved to be useful to assess boldness under controlled, laboratory
268 conditions, our current results show that the envelope test can also be used to quantify boldness
269 variation in wild populations.

270 Using wing wear as a proxy for age, we detected an age-related decline in boldness at the
271 population level. Based on the subset of individuals that were captured and assessed for
272 boldness multiple times, we aimed to unravel the underlying mechanisms responsible for the
273 observed decline in boldness with age. Although our ability to discriminate within- and
274 between-individual changes was ultimately limited by the relatively low recapture rate, our
275 results suggest that individual plasticity (i.e. within-individual changes) was the main cause of
276 boldness senescence in the study population. Moiron et al. (2020) found that shy individuals
277 generally have a reduced lifespan under natural conditions (i.e. wild populations as opposed to
278 laboratory conditions). Thus, one could expect selective disappearance to play an important role
279 in shaping age-related changes in personality traits at the population level, but we found no
280 evidence for such an effect in our study. Rather, we found a trend for within-individual changes
281 in boldness. Interestingly, a similar decline of boldness at the population level occurred in
282 laboratory-reared Speckled wood butterflies (Kaiser et al. 2019a) which also appeared to be
283 driven by within-individual changes as mortality was typically very low in the laboratory and
284 selective disappearance of bold types was unlikely to cause the observed pattern. This strongly
285 suggests that individual plasticity is the underlying mechanism explaining the age-related
286 decline in the mean level of boldness, and this in both wild and laboratory populations of the
287 Speckled wood butterfly.

288 Individual plasticity of personality traits as individuals get older has been reported a few times,
289 but the direction of those changes appears to vary among species. For example, handling
290 aggression decreased with age in a wild population of Great tits (*Parus major*) (Class and
291 Brommer 2016), while activity and the tendency to leave a tube both increased as individual
292 Field crickets (*Gryllus campestris*) get older (Fisher et al. 2015, 2018). The direction of the
293 change probably depends on the trait itself, how it relates to fitness components and the
294 proximate mechanism underlying this change. Identifying the proximate cause of the decline in
295 boldness observed here was beyond the scope of this study. We can only speculate about
296 potential proximate mechanisms, which for instance include age-related decline in brain size
297 (Pasquet et al. 2018) and energy depletion, both of which could negatively affect the expression
298 of personality traits. This now warrants further research.

299 *Within-site movements and boldness*

300 In his pioneer work on the Speckled wood butterfly, Davies (1978) noted that males tend to be
301 very sedentary, with as much as 90% of the marked individuals spending their entire life within
302 50 m of the point of first capture. Similarly, Bergerot et al. (2012) found that recapture
303 probability of Speckled woods was highest at 25m from the initial capture location. Males in
304 our study population display a high site fidelity too, with 56% of the recaptures occurring within
305 50 m, and 80% within 100 m.

306 Many personality traits are (in-) directly linked to information gathering and spatial processes,
307 and thus they may be expected to influence daily movements occurring at relatively small
308 spatial scales (Spiegel et al. 2017). Recent empirical studies confirmed that personality indeed
309 plays a role in shaping such movements (e.g. Minderman et al. 2010; Spiegel et al. 2015;
310 Villegas-Ríos et al. 2018; Schirmer et al. 2019). Yet, our current knowledge on animal
311 personality, and how it relates to other biological processes, remains heavily biased towards
312 vertebrates (Kralj-Fišer and Schuett 2014). Here, as a first attempt to explore the relationship

313 between a personality trait and space use in a territorial butterfly species, we investigated under
314 natural conditions whether boldness related to net displacement in the Speckled wood.
315 However, neither boldness nor forewing length affected local movements within a sunlit patch
316 or between sunlit patches. Thus, net displacement appears to be independent of personality and
317 flight morphology in our study. Perhaps this pattern is not surprising as we focused on territorial
318 males whose mate-location strategy mainly involves routine movements biased towards their
319 territories. Here we should stress that there are clear differences between routine movements
320 and large-scale movements such as dispersal. The former include movements associated with
321 daily activities like foraging and mate-location (Van Dyck and Baguette 2005), while the latter
322 involve between-population movements underpinned by a decision to leave a habitat patch for
323 another (Stevens et al. 2010, 2014). Large-scale movements associated with dispersal likely
324 require a special set of behavioural, physiological and morphological traits, integrated within
325 dispersal syndromes (Stevens et al. 2014). In butterflies, dispersal syndromes typically include
326 long wings (Stevens et al. 2012) and strong flight performance (as measured under stressful
327 conditions; Legrand et al. 2015). Routine movements, however, may not require such a special
328 design (Van Dyck and Baguette 2005), while we can expect the spatial distribution and
329 dynamics of resources to play an important role in shaping daily movements. This has been
330 shown, for example, in two related satyrine butterfly species, where local flight activity at both
331 the individual and species level was not linked to forewing length – and hence dispersal capacity
332 – but where local occurrence was closely linked to the presence of habitat resources (Merckx
333 and Van Dyck 2002).

334 Yet, we acknowledge that our study does not provide final, clear-cut evidence for the absence
335 of a personality/space use relationship in the Speckled wood. Here, we considered only one
336 aspect of local space use that relates to territoriality. It would now be interesting to monitor a
337 set of males more closely and more frequently than we did in our current study to obtain precise

338 estimates of their realized home range. It could well be that bold perchers are able to hold larger
339 territories and to cover larger home ranges than perchers that are less bold. Additionally, we
340 only considered territorial males, but the mate-locating behaviour system in the Speckled wood
341 butterfly involves both territorial and patrolling males within the same population (Van Dyck
342 2003 and references therein). Both patrollers and females (i.e. the dispersive sex in *P. aegeria*
343 – Hill et al. 1999) are by nature less territorial and even their routine movements are likely to
344 occur at wider spatial scales compared to territorial males. Consequently, for females and
345 patrolling males we do expect a relationship between personality and space use. As such, we
346 hope our work will inspire and stimulate further research on the interplay between personality
347 traits and spatial ecology in the Speckled wood, and more generally in other invertebrate taxa.
348 Invertebrates play important roles in ecosystems and understanding how personality shapes
349 their daily movements relative to other factors is therefore important. In this regard, the further
350 miniaturization of (GPS) tracking devices (see for example Woodgate et al. 2016) will benefit
351 this field of research. Indeed, obtaining long-term data on individual animal movements is
352 currently challenging, but of prime importance to accurately explore personality and space use
353 relationships (Spiegel et al. 2017).

354

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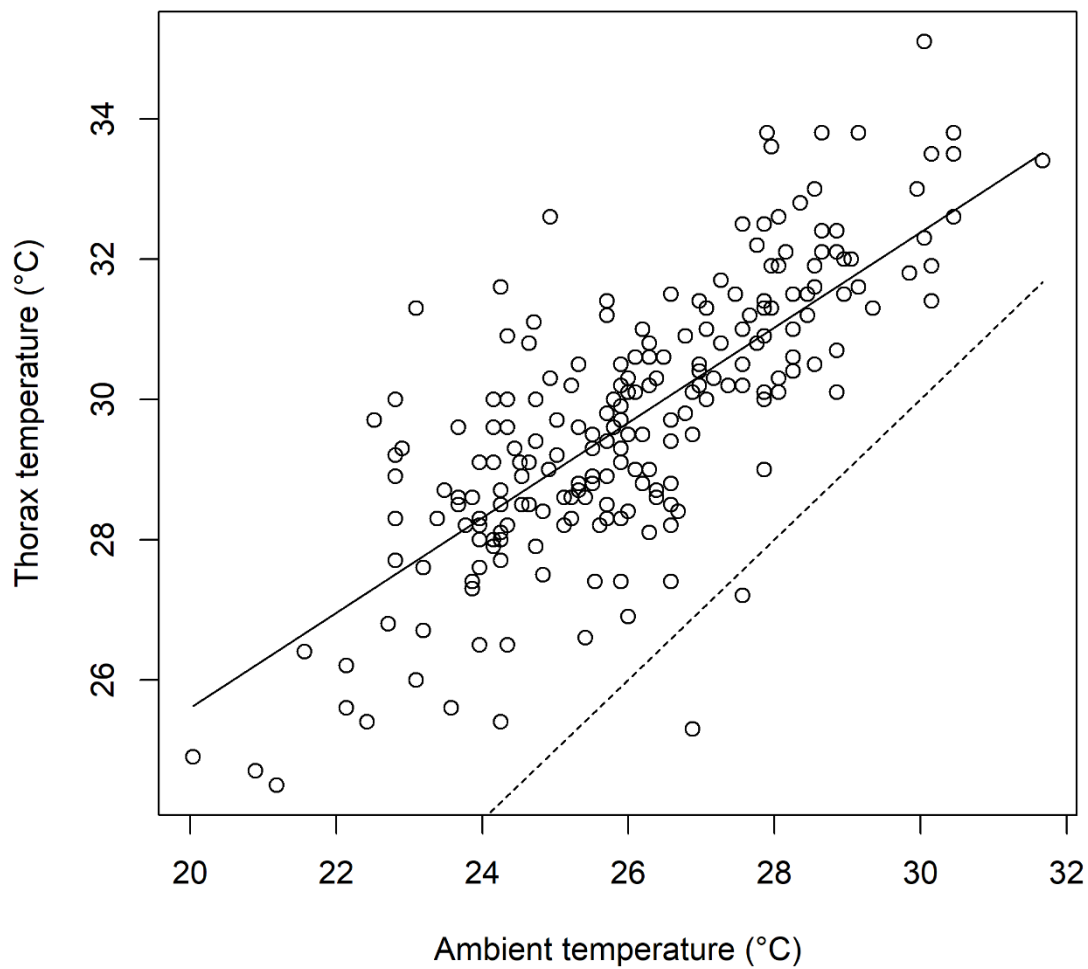
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484

485 **Figure legends**

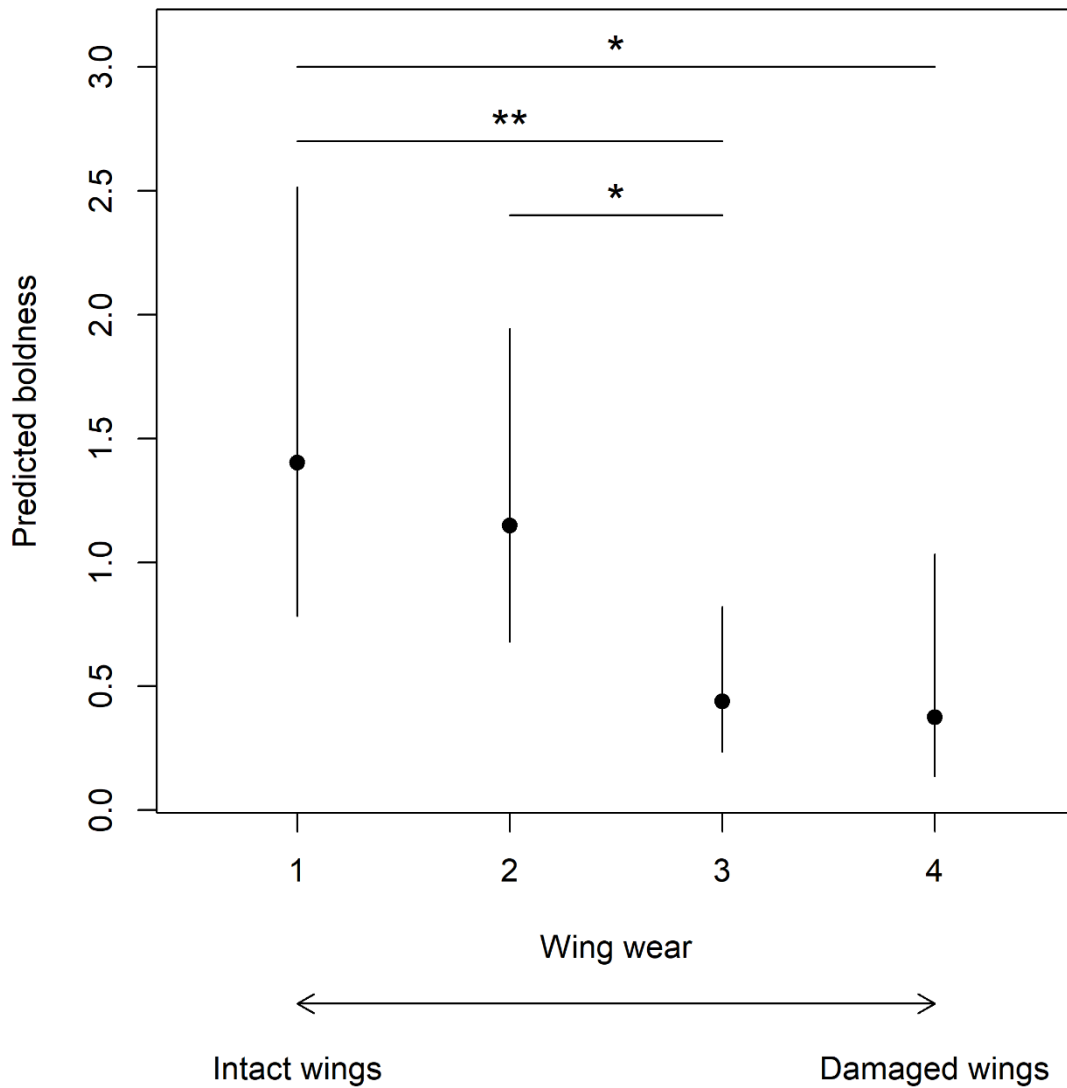
486 Figure 1: Relation between ambient and thoracic temperatures. The dotted line refers to the
487 isothermal condition (1:1 relationship); the solid line represents the regression line based on the
488 model output.



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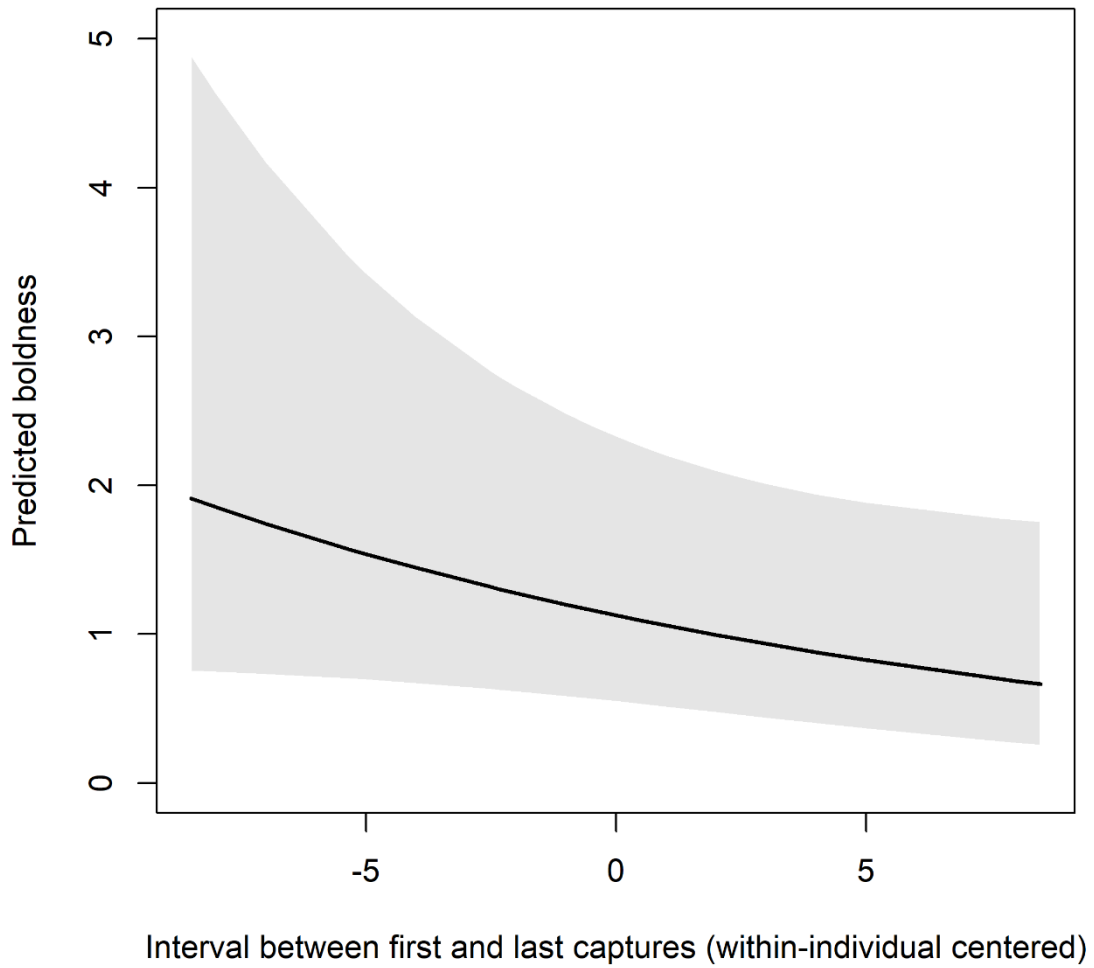
491 Figure 2: Effect of wing wear (used as a proxy for age) on butterfly boldness. We show the
492 predicted values (means and 95% confidence intervals) based on the model output. Asterisks
493 show significant differences among age classes (after adjustment for multiple comparisons; *P
494 < 0.05; **P < 0.01).



495

496

497 Figure 3: Within-individual change in boldness for recaptured males. The solid line shows the
498 predicted boldness based on the model output; the grey area shows the credible interval.



499