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1 Evidence of attack deflection suggests adaptive evolution of wing 2 tails in butterflies

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16
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22
23

24 **Abstract**

25 Predation is a powerful selective force shaping many behavioural and morphological traits in
26 prey species. The deflection of predator attacks from vital parts of the prey usually involves
27 the coordinated evolution of prey body shape and colour. Here, we test the deflection effect of
28 hindwing tails in the swallowtail butterfly *Iphiclides podalirius*. In this species, hindwings
29 display long tails associated with a conspicuous colour pattern. By surveying the wings within
30 a wild population of *I. podalirius*, we observed that wing damage was much more frequent on
31 the tails. We then used a standardised behavioural assay employing dummy butterflies with
32 real *I. podalirius* wings to study the location of attacks by great tits *Parus major*. Wing tails
33 and conspicuous coloration of the hindwings were struck more often than the rest of the body
34 by birds. Finally, we characterised the mechanical properties of fresh wings and found that the
35 tail vein was more fragile than the others, suggesting facilitated escape ability of butterflies
36 attacked at this location. Our results clearly support the deflective effect of hindwing tails and
37 suggest that predation is an important selective driver of the evolution of wing tails and colour
38 pattern in butterflies.

39

40 **Keywords:** Attack deflection, *Papilionidae*, butterfly tails, adaptive evolution, wing damage,
41 mechanical resistance of wings

42 Introduction

43

44 Predation often affects the evolution of multiple morphological and behavioural traits
45 in prey species. While many traits limiting predator attacks evolve, traits increasing survival
46 after an attack have also been repeatedly promoted by natural selection [1]. Traits enhancing
47 attack deflection, by attracting strikes towards a conspicuous body part, indeed limit damage
48 to vital parts and increase escape probability [2]. The conspicuous coloration on the tails of
49 some lizard species has been suggested to promote attacks on the tails, therefore limiting
50 wounds on other parts of the body ([3],[4]). The attraction towards conspicuous tails can also
51 be reinforced by striped body coloration, directing the attention of predators towards the tail
52 [5]. In salamanders, defensive posture increases tail conspicuousness [6], suggesting that both
53 body shape and colour, as well as behaviour, may contribute to the deflecting effect. The
54 emergence of a deflecting effect may thus result from a joint evolution of several morphological
55 and behavioural traits (reviewed in [7] for lizards). In butterflies, the joint evolution of
56 hindwing tails and specific behaviour enhancing attack deflection has been shown in
57 *Lycaenidae*. In these butterflies, the hindwings frequently display tiny tails, conspicuous colour
58 patterns and a specific behaviour involving tails movements, hypothesised to mimic a head
59 with moving antennae (the “false head effect”, [8],[9]). The ‘false-head’ tails of *Lycaenidae*
60 are likely to deflect attacks away from vital parts [8]. Laboratory experiments with spiders
61 indeed showed that *Calycopis cecrops* butterflies, displaying false-head hindwings, escaped
62 more frequently than butterflies from other species where hindwings do not display such false-
63 heads [10]. In Museum collections, the prevalence of individuals with symmetrically damaged
64 hindwings, interpreted as beak marks of failed predator attacks, has been shown to be higher
65 in *Lycaenidae* species with wing tails, as compared to species without a tail or with a less
66 conspicuous colour pattern [11]. This suggests that the deflecting effect associated with
67 hindwing tails might rely on the joint evolution of wing shape, colour pattern, and behaviour,
68 promoted by the attack behaviour of predators relying on visual cues.

69 Such a deflecting effect may lead to the loss of the attacked body part, but with limited
70 effect on survival. In lizards and salamanders, tails can be detached without severely impacting
71 survival of the attacked animal (*i.e.* autotomy [12]; [13]). In butterflies, wing margins
72 displaying eyespots are preferentially attacked (e.g. in *Bicyclus anynana* [14], in *Lopinga*
73 *achine* [15]). The loss of wing margins and especially hindwing margins has a low impact on
74 butterflies flying abilities [16] and may therefore have a limited impact on survival. Butterflies
75 are indeed commonly observed flying in the wild with such wing damage [17]. The escape
76 from predators after an attack might also be facilitated by enhanced fragility of the attacked
77 parts of the wings. In *Pierella* butterflies for instance, Hill and Vaca (2004) [18] showed that
78 the conspicuous areas of the hindwings are associated with increased fragility, which may
79 facilitate the escape after a predation attempt directed at this specific wing area. Similarly, in
80 small passerine bird species, the feathers located in the zone most prone to the predator attacks
81 are easier to remove [19]. The evolution of specific body parts with increased fragility might
82 thus be promoted by predation pressure, because they enhance prey survival after an attack.

83 The repeated evolution of hindwing tails in *Lepidoptera* could result from the selection
84 exerted by predators on the evolution of traits that enhance deflection. The long, twisted wing
85 tails of some *Saturniidae* moths have indeed been shown to divert bats from attacking moth

86 bodies [20]. During flapping flight, the spinning tails indeed confuse the echolocation signal
87 perceived by predators, thus diminishing strike efficiency [21]. The evolution of wing tails in
88 moths is thus likely to be promoted by the sensory system of their nocturnal predators. The
89 deflecting effect of wing tails has also been suggested in day-flying butterflies facing diurnal
90 predators relying on visual cues, but has been tested only in the very specific case of the false-
91 head wing tail of *Lycaenidae*.

92 A large number of other butterfly species with diurnal activities nevertheless display
93 hindwing tails. Swallowtail butterflies are particularly well-known for their conspicuous,
94 highly diversified hindwing tails [22], but the selection exerted by predators on the repeated
95 evolution of these tails has never been formally investigated. Here, we tested whether the
96 evolution of tails might be promoted by attack deflection, using the swallowtail species
97 *Iphioides podalirius* (Linné, 1758 *Lepidoptera*, *Papilionidae*) as a case-study. *I. podalirius* is
98 a large palearctic butterfly with hindwings displaying long tails associated with a salient colour
99 pattern: an orange eyespot and four blue lunules with strong UV reflectance [23]. The
100 combination of hindwing tail and colour pattern is therefore very conspicuous (Figure 3), and
101 especially for predators sensitive to UV reflection, such as songbirds [24]. Moreover, the four
102 wings exhibit convergent black stripes over a pale background, contiguous between forewings
103 and hindwings in resting position, pointing towards the anal edge. This may enhance the
104 attraction of a predator to the posterior part of the hindwing [8]. To test whether the evolution
105 of wing tails in this species may stem from selection promoting traits enhancing attack
106 deflection, we performed a series of three complementary experiments.

107 First, we characterised the amount and location of damage on the wings of wild
108 butterflies to test whether tails are more frequently lacking in surviving butterflies, possibly
109 indicative of failed predation attempts. Second, we conducted experimental behavioural assays
110 in captivity using an avian generalist predator, the Great tit *Parus major*, and dummy butterflies
111 made with real *I. podalirius* wings, in order to investigate the location of attacks. We
112 specifically tested whether attacks are more frequently directed towards the hindwing tails and
113 associated colour pattern as compared to the rest of the butterfly body. Finally, we used a
114 specific experimental set up to estimate the force needed to tear wings at different locations.
115 Preferentially-attacked body parts are predicted to be more easily detached, as it would enhance
116 the probability of escape of the butterfly after an attack [18]. This combination of experiments
117 in controlled and under natural conditions provides a test for the role of predator deflection in
118 the adaptive evolution of wing shape, wing colour pattern and wing resistance in swallowtail
119 butterflies.

120

121

122 **Materials and Methods**

123

124 **Field sampling**

125 Field sampling of *I. podalirius* was performed in Ariege (France) during the summer of
126 2020 (Collection sites: 43°04'17.86"N, 01° 21'58.88"E; ca. 400 m a.s.l., and 43°03'50.94"N,
127 01° 20'40.95"E; ca. 400 m a.s.l.). We sampled a total of 138 wild individuals, with a large
128 majority of males (132 males/6 females), likely reflecting the patrolling behaviour displayed

129 by males (hill topping). After their capture, butterflies were euthanized by hypothermia and
130 their wings stretched out and dried.

131

132 **Assessing the distribution of wing damage in the wild**

133 The dorsal side of the forewings (FWs) and hindwings (HWs) of the field-sampled
134 individuals was photographed in controlled LED light conditions (Nikon D90, Camera lens:
135 AF-S Micro Nikkor 60 mm 1:2.8G ED). Out of the 138 wild butterflies collected, 65 exhibited
136 wing damage. We studied the location of missing wing areas, distinguishing damage occurring
137 on HW and FW, and reported the asymmetry of different types of damage (left and right
138 damage with visually similar areas and positions were considered symmetric). A Pearson's Chi-
139 squared test with Yates' continuity correction was used to test whether (1) damage was more
140 often observed on hindwings than on forewings, and (2) damage on hindwings was more often
141 asymmetric than damage on forewings.

142 To finely quantify the distribution of missing wing areas, we then digitised the wing
143 outlines of the 65 damaged butterflies and 10 intact individuals as references. We defined 300
144 semi-landmarks equally spaced along the outline of both the left- and right-reflected FWs and
145 HWs, using TpsDig2 [25]. The average shape of intact butterflies was obtained with TpsRelw,
146 [25]), using a geometric morphometric approach ([26]; [27]). The wing outline of each
147 damaged individual was then manually superimposed on the average shape of intact butterflies,
148 in order to characterise the missing area of each damaged wing. A heat map was then obtained
149 by summing up the occurrences of missing areas at each pixel throughout the sample of
150 damaged individuals, using EImage (R package; [28]), following [16]. The heat map was
151 then plotted with autoimage (R package; [29]).

152

153 **Behavioural experiment with birds**

154 We conducted an experiment to determine the location of attacks by birds on *I.*
155 *podalirius* wings between October 2020 and January 2021 at the Station d'Ecologie Théorique
156 et Expérimentale du CNRS, France (near the collection sites). Great tits were caught in mist-
157 nets in the vicinity of the research station, ringed, and housed in individual indoor/outdoor
158 cages (5m x 1m x 3m) and fed *ad libitum* with mealworms and sunflower seeds. After 2 days
159 of habituation to captivity, we conducted behavioural experiments on two consecutive days
160 during the three hours after sunrise while birds did not have access to sources of food other
161 than dummy butterflies. The whole experiment was repeated three times using new birds for a
162 total of 72 different birds tested. Capture of wild birds was performed under permits from the
163 French ringing office (CRBPO, permit 13619 to A. Chaine). Capture and holding of birds from
164 the wild was approved by the Région Midi-Pyrénées (DIREN, n°2019-s-09) in the Moulis
165 experimental aviaries (Préfecture de l'Ariège, institutional permit n°SA-12-MC-054;
166 Préfecture de l'Ariège, Certificat de Capacité, n°09-321 to A. Chaine).

167 We built 95 dummy butterflies, using actual wings of *I. podalirius* butterflies collected
168 in the wild, glued on an artificial black cardboard body. The position of the glued wings
169 corresponded to the natural position of butterflies at rest (Figure 1). A dummy was placed in
170 each bird cage, about 1.5 m off the ground, using a wire fixed to the cage wall. This setting
171 thus allowed the dummy to gently “flutter” in the middle of the cage, far enough from any
172 perching site, to prevent close inspection by resting birds. The birds thus had to approach and

173 potentially strike dummy butterflies while flying. Each cage was equipped with a camera
174 filming continuously (Figure 1, S2). Two observers also monitored the 24 experimental cages:
175 damaged dummies were replaced as soon as noticed by the observers, to maximise the number
176 of attacks on intact butterflies. After each experimental session, the birds were fed *ad libitum*
177 until nightfall to minimise the stress generated by the experiment. The whole experiment was
178 repeated for 2 consecutive days.

179 Analyses of videos recorded during the experiments were used to count the exact
180 number of strikes performed by each bird on each dummy butterfly. Each strike was defined
181 as a single touch of the beak on the dummy butterfly. The films were also used to assess the
182 precise location of each strike on the butterfly body. Five categories of strike location were
183 defined: body, coastal part of the forewing, distal part of the forewing, hindwing colour pattern
184 and hindwing tail (see Figure 1). In some cases, the strike affected several locations at once.
185 These “combined” locations were considered as separate categories, leading to a total of 8
186 possible targeted locations (see Figure 3). Because a dummy could be attacked several times
187 before it was replaced, we also recorded the order of each strike performed by the tested bird
188 on the given dummy.

189 We first tested whether strikes occurred more often on the hindwings than on the
190 forewings, using a Pearson Chi-squared test with Yates' continuity correction. To test whether
191 the different parts of the wings were equally prone to attack, we applied a generalised binomial
192 regression model for the probability of attack, using strike location and strike rank order as
193 effects and considering all specimens and sessions (including birds that did not attack). An
194 analysis of variance was then applied (ANOVA type II, function “Anova” package “car”, [30]).
195 To perform pairwise comparisons on the location categories, we finally performed a series of
196 post hoc tests (function “tukey_hsd” package “rstatix”, [31]).

197
198

199 **Mechanical resistance of the wings**

200 **Experimental sample:** We tested mechanical resistance of the different wing parts on
201 28 fresh *I. podalirius* butterflies (21 females and 7 males) obtained as pupae from a commercial
202 supplier (Worldwide Butterflies Ltd). After emergence, individuals were placed in individual
203 cages to allow proper unfolding and drying of the wings, then placed in entomological
204 envelopes to avoid wing damage. The butterflies were fed once a day with a mixture of water
205 and honey, and maintained for 11 to 20 days depending on the time between emergence and
206 the start of the experiments. Experiments were performed on freshly-killed individuals to limit
207 the effect of wing drying on mechanical properties [32]. In order to test whether the tails are
208 more fragile, we compared the mechanical resistance of different regions of the wings (Figure
209 2). Specifically, we contrasted the vein located within the hindwing tail (M3H vein), with
210 another hindwing vein located outside the colour pattern area (R5H vein). We also included
211 the two developmentally-homologous veins on the forewing (M3F and R5F; [33]). For each
212 butterfly, the experiment was conducted on one hindwing and one forewing. The four veins
213 were measured in a randomised order to avoid any bias caused by the deformation of the wings
214 due to previous tearing.

215

216 **Experimental setup:** As wing parts involved in predator deflection are expected to be
217 particularly fragile, we designed a custom experimental set-up adapted from Hill and Vaca
218 (2004) [18] and De Vries (2002) [34] to specifically estimate the mechanical resistance of
219 different parts of the wings. When a bird catches the wing of a butterfly, the force exerted by
220 the beak and the opposed escape movement of the butterfly likely induce tensile stresses on the
221 wing. We thus compared the mechanical response of the different wing veins to a tensile force
222 exerted in the direction of the vein, away from the body (see Figure 2). Our set up was
223 composed of a fixed part holding the wing and of a mobile part exerting traction on the wing
224 (Figure 2, S3). This mobile part was connected to the wing using a flattened and filed alligator
225 clip with a squared 9 mm² piece of rubber ensuring a soft and standardised contact with the
226 wing. For each measurement, the clip was fixed at 3mm from the edge of the wing. This clip
227 was then connected to a piezo-electric force transducer (Kistler 9217A type 9207 Serian
228 number: 1275844), connected to a charge amplifier (Kistler type 5011). The force was fixed
229 on a linear table controlled by a motor (RS PRO, 12V dc, 2400 gcm), allowing constant
230 traction. The charge from the force transducer was measured by the amplifier and sent to a
231 Biopac AD unit. Forces were captured and analysed using AcqKnowledge software (version
232 4.1, BIOPAC Systems, Inc.).

233 The variation of the force through time, from the onset of the motor to the total rupture of the
234 wing was recorded for each trial. These response curves were first smoothed using a lowpass
235 filter set at 20HZ. Five summary variables were extracted from the response curve (Figure 2):
236 (1) the maximum force exerted on the vein (estimating the maximum strength of the vein, noted
237 F_{max}), (2) the time to the first break (T_1 ; shown by the first abrupt decrease in force), (3) the
238 time to the complete rupture of the vein (T_{max} ; when the force returns to zero), (4) the slope (S)
239 of the curve between the beginning of the pull and the point of maximum force (estimating the
240 stiffness of the wing - see Supplementary materials S1) and (5) the impulse required for the
241 complete rupture of the vein (J_{max}), assessed by the area under the curve. The forces were
242 measured in Newtons (N) - note the force takes negative values since we measured a tensile
243 force.

244
245 **Statistical analysis** - The five mechanical parameters measured on the different veins
246 were then compared using linear mixed models using wing (forewing vs. hindwing) and vein
247 (M3 vs. R5) as fixed effects, while butterfly ID, sex and the date of measurement session were
248 set as random variables (function “lmer”, package “lmerTest”, [35]). The date of measurement
249 session was added to account for potential differences in heat and humidity across session
250 possibly affecting the wing mechanical properties. For J_{max} , there was some evidence that the
251 wing and vein effects interacted. We thus modified the model to directly account for the four
252 modalities of the vein effect (R5F, M3F, R5H, M3H). We analysed all models with a type III
253 analysis of variance. All statistical analyses were carried out in R version 4.0.3 (R Core Team
254 2020).

255

256

257 **Results**

258

259 **Wing damage mostly affects the tails**

260 We hypothesised that a deflection effect should result in a higher proportion of wing
261 damage on the deflecting wing areas in the wild. To test this hypothesis, we studied the location
262 of wing damage in a natural population of *I. podalirius*. Among all wild individuals collected,
263 47.1% had wing damage. Forewings were less often damaged than hindwings (22.31% and
264 85.38% respectively; $\chi^2 = 101.54$, $df = 1$, $P < 0.001$). The frequency of individuals with missing
265 hindwing tails in the wild was especially high: all 65 damaged individuals had at least one tail
266 damaged (out of 130 wings tested, 82.3% had tail damaged). This result is illustrated by the
267 heatmap (Figure 5). Furthermore, damage on the hindwings were more often asymmetrical
268 (78.46%) than damage on the forewings (24.62%) ($\chi^2 = 35.603$, $df = 1$, $P < 0.001$).

269 Behavioural experiments with birds reveal preferential attacks on hindwing tail and 270 colour pattern

271 Using the behavioural assays carried out with great tits, we investigated whether the
272 attacks on dummy butterflies were directed towards the posterior part of the hindwings (Figure
273 3), as expected under the hypothesis of a deflecting effect induced by the butterfly morphology.
274 Among the 72 birds tested, only 17 attacked the dummy butterflies, resulting in 65 recorded
275 strikes. Because some strikes occurred outside of the field of view of the camera, the targeted
276 part of the dummy could be determined in only 59 of these strikes. The hindwings were more
277 often targeted by the birds (43 strikes; 72.9%) than the forewings (16 strikes; 27.1%)
278 ($\chi^2 = 12.36$, $df = 1$, $P < 0.001$). The probability of attack strongly depended on the wing
279 location ($LR \chi^2 = 141.21$, $df = 8$, $p < 0.001$): there was strong evidence that strikes jointly
280 targeting the tail and the colour pattern of the hindwings (23 attacks; 39%) were more frequent
281 than strikes on any other body part (see detailed statistical tests in Table 1). In contrast, no
282 evidence for an effect of the attack ranking on attack probability was found (see detailed
283 statistical tests in Supplementary table 1).

284 285 Hindwings and in particular hindwing tails are more easily damaged

286 We then tested whether the hindwing region with the tail and conspicuous colour
287 patterns is more fragile than the rest of both wings, as expected if they are involved in a
288 deflecting effect. There was a strong evidence that time to first rupture (T_l) and the time to total
289 rupture (T_{max}) were lower in hindwings veins than forewing veins (Figure 4, see statistical tests
290 in Table 2). J_{max} , the impulse required to fully rupture the vein (as assessed by the area under
291 the response curve; Figure 2) was smaller for the hindwing tail vein (M3H) than for any other
292 veins (M5H: $t = -2.42$; $P = 0.019$; M3F: $t = -2.48$; $P = 0.016$; M5F: $t = -1.88$, $P = 0.06$). The
293 slope of the force profile, S , reflects the stiffness of the wing: the greater the slope, the stiffer
294 the veins (equations in Supplementary materials S1). There was strong evidence that hindwing
295 veins had higher force profile slopes than forewing veins (Figure 4, details in Table 2),
296 indicating that they are stiffer. Finally, a weak evidence for a lower F_{max} (maximum force
297 applied to the vein) in the hindwings than in the forewings was found ($F = 3.11$; $P = 0.082$,
298 Table 2).

299 300 Discussion 301

302 Our multi-pronged approach combining behavioural experiments, biomechanical
303 measurements and survey in natural population provide strong evidence of a deflecting effect
304 of hindwing tails in *I. podalirius*, opening new research avenues on the predation pressures
305 involved in the evolution of tails in butterflies.

306

307 *Adaptive evolution of hindwing tails promoted by predator behaviour*

308 Our behavioural trials showed that attacks by great tits on *I. podalirius* are highly biased
309 towards the hindwing tails and colour pattern. This provides strong support for a deflective
310 effect generated by both colour pattern and tail on predators. Interestingly, only a small fraction
311 of the tested birds actually attacked the dummies. This could suggest that *I. podalirius*
312 butterflies are not the usual prey consumed by great tits [36], especially during the season when
313 the tests were carried out (late fall and winter), where they mostly rely on seeds rather than on
314 insects. Our behavioural experiments are thus relevant for the behaviour of generalist predators
315 that are probably naïve to the phenotypes of the tested butterflies, a likely situation in nature,
316 as no specialist predator is known for *I. podalirius*. Some of the birds nevertheless repeatedly
317 attacked the posterior area of the hindwings, consecutively targeting the two tails, showing a
318 particularly strong interest for this location (see Supplementary movie 1).

319 Birds typically flew above the butterflies, patrolling the cage at 3m from the ground and
320 dummies had their tails oriented towards the ground about 1.5m from the ground. The high
321 frequency of attacks on the tails therefore did not result from an easier access to the tails due
322 to a positional bias. To the contrary, birds adjusted their trajectory to attack from below (see
323 Supplementary materials S4; Supplementary movie 2), suggesting they were specifically
324 targeting the tails. The combination of tails and associated conspicuous colour patterns is thus
325 probably very attractive to predators, inducing the observed pattern of attack locations. Given
326 the tested birds preferentially attacked the distal area of the hindwing, we would expect that
327 this wing area should be easier to tear off. Such enhanced fragility would facilitate the butterfly
328 escape and may thus be promoted by natural selection generated by the behaviour of birds.

329 Our analysis of the mechanical resistance of wing veins indeed shows that hindwing
330 veins, and especially the vein located within the tail, are less resistant to the application of a
331 tensile force and break sooner than forewing veins. Whether the measured difference in
332 strength would have a significant impact during a predator attack is unknown but the forces
333 tested are relevant to the type of strikes observed in our behavioural experiment. The enhanced
334 fragility of the hindwing vein located within the tail is thus consistent with the deflection
335 hypothesis. It should increase escape probability, while preserving the integrity of the wing and
336 reducing aerodynamic costs. Interestingly, in *Pierella* butterflies, the conspicuous white patch
337 of the hindwing found to have an increased fragility by Hill & Vaca (2004) [18] contains the
338 M3H vein, *i.e.* the vein located within the tail in *I. podalirius*, that was found to be the stiffest
339 and to break the earliest in our study. The M3H vein could have an enhanced fragility in many
340 butterfly species, therefore promoting the evolution of conspicuousness in these wing areas,
341 enhancing survival after an attack. The evolution of such association should especially be
342 favoured if butterflies missing such wing area still survive in the wild.

343 The large abundance of tailless *I. podalirius* flying in the wild indeed testifies to the
344 limited aerodynamic consequences of such damage. Tail loss does not prevent these damaged
345 butterflies from performing their typical hill-topping behaviour and is thus likely to have a

346 limited impact on their fitness. The distribution of damage across the wings in the natural
347 population of *I. podalirius* also confirms that hindwing tails are more prone to attack than any
348 other part of the wing (Figure 5). Inferring predation from butterfly wing damage alone can be
349 misleading because damage can stem from a diversity of sources, including interactions with
350 conspecifics ([37]; [38]) or collision with obstacles ([39]; [16]). However, the pattern we found
351 is still consistent with an increased attack rate on hindwing tails. While damage due to
352 collisions should be symmetrical as seen on forewings, the prevalence of asymmetric damage
353 on the tails of *I. podalirius* matches the hypothesis of predator attacks during flight or when
354 butterflies are at rest, typically perching on high branches with their wings wide open (Figure
355 1). This also suggests that symmetry in the tail is not critical for aerodynamics. Our survey in
356 natural population thus reinforces the evidence for the adaptive evolution of tail and colour
357 pattern in *I. podalirius*, where the benefits in terms of escape ability may exceed the costs of
358 wing damage.

359 Considered together, (1) the strong prevalence of the attacks on the hindwing tails and
360 associated colour patterns, (2) the reduced strength or the corresponding parts of the wings and
361 (3) the very high incidence of natural wing damage on the tails, provide evidence for the
362 adaptive evolution of hindwings tails in *I. podalirius* via a deflecting effect of predator attacks.
363 The effect of attack deflection on the evolution of wing tails in day-flying butterflies has only
364 been demonstrated in the peculiar case of false head morphology in *Lycaenidae* ([8]; [9]). Our
365 study suggests that predation can be a major selective pressure involved in the evolution of
366 hindwing tails in butterflies. Hindwing tails have evolved multiple independent times
367 throughout the diversification of butterflies and are associated with an important diversity of
368 colour patterns ([40]). Our results thus open the question of the evolution of different traits
369 involved in predator deflection, namely hindwing shape, fragility and colour patterns, as well
370 as behaviour, jointly forming an adaptive syndrome.

371

372 *Adaptive syndrome of predation deflection*

373 In our experiments with birds, tails alone were targeted in a large proportion of the
374 trials, but most attacks involved a combination of the tails and associated colour pattern. This
375 strongly suggests that the visual effect triggering attack deflection in *I. podalirius* is jointly
376 induced by the tails and the colour pattern, including the blue marks and the orange eyespots
377 on the hindwing, and possibly the black stripes pointing at the tails. The deflection effect
378 therefore probably relies on the evolution of a series of traits, including wing shape, wing
379 colour pattern and wing mechanical resistance. The joint vs. sequential nature of the evolution
380 of these different traits is largely unknown and might depend on the developmental and genetic
381 bases of the traits involved in deflective syndromes, as well as the different selection pressures
382 acting on each of those traits.

383 Associations between hindwing tails and peculiar colour patterns promoted by
384 predation pressure have been described for butterfly species involved in Batesian mimicry. In
385 *Papilio memnon*, for instance, some females display hindwing tails and red coloration
386 resembling the toxic species *Pachliopta coon* on the Malay peninsula while other females have
387 no tail and an alternative yellow colour pattern mimicking *Troides helena* in Northern Borneo
388 [41]. These two traits are controlled by different loci and the linkage disequilibrium between
389 these loci might have been promoted by the selective advantages brought by mimicry [42].

390 Nevertheless, the association between well-developed tails and conspicuous colour elements is
391 not universal in Papilionidae: for example, *Papilio ulysseus* tails and surrounding wing parts are
392 completely black, while in *Papilio demodocus*, conspicuous distal eyespots are observed in
393 tailless hindwings. Shared developmental pathways in wing shape and colour pattern might
394 promote their joint evolution, so that the emergence of deflective syndromes can be facilitated
395 in some lineage. Alternatively, species ecology might trigger strong selection promoting
396 linkage disequilibrium between loci controlling traits enhancing deflection.

397 The combined evolution of traits limiting predation also frequently extends to
398 behaviour. Whether the behaviour emerges before or after the evolution of morphological traits
399 involved in deflection is an open question. In *I. podalirius*, the perching position with wings
400 wide open possibly enhances the deflecting effect provided by hindwing tails but might have
401 been promoted for its effect on thermoregulation [43] before the evolution of tails. Adaptive
402 syndromes involving the evolution of both morphological and behavioural traits promoted by
403 predator behaviour have been observed in other *Lepidoptera*. In some species, hidden
404 conspicuous coloration can be suddenly uncovered when threatened by a predator, inducing a
405 startling effect (e.g. *Catocala nupta*, [44]). The evolutionary sequence of these behavioural and
406 morphological traits has been investigated experimentally by testing the deterring effect of both
407 traits independently. These experiments suggest that behavioural changes might have preceded
408 the evolution of conspicuous coloration, because sudden movements can be sufficient to induce
409 strong deterrence ([45]). Whether a similar ‘behaviour first’ evolutionary sequence is involved
410 in the evolution of deflective syndromes should be investigated.

411 Important selective trade-offs between predator deflection and flight abilities might also
412 influence the evolution of deflective syndromes in *Lepidoptera*, therefore constraining wing
413 areas involved in such syndromes. Anteromotorism being a shared characteristic of butterflies
414 [46], hindwing fragility might be ancestral, and conspicuous marks might have secondarily
415 been favoured on these weaker wings. In Papilionidae, hindwing shape is indeed strikingly
416 more diversified than forewing shape [22] in agreement with lower aerodynamic constraints
417 on the hindwings. The study of aerodynamic forces applied to an artificial model of a butterfly
418 with tails suggests that hindwing tails increase the lift of the butterfly during gliding [47].
419 Preservation of flight capacity through the maintenance of tail integrity, and in particular a
420 sufficient strength to withstand the pressure forces applied during flapping, could act as an
421 evolutionary trade-off with the selection of mechanical weakness. The selective pressures
422 acting on each of the traits involved in these deflective syndromes should now be studied
423 independently and compared in species with contrasted ecologies and levels of phylogenetic
424 proximity to determine the evolutionary forces involved in the emergence of deflective
425 syndromes.

426

427 **Conclusions**

428 The diversity of wing tails observed in *Lepidoptera* suggests they have evolved multiple
429 times, therefore raising the question of the selective pressures involved. Based on our combined
430 analysis of natural wing damage, biomechanical resistance of the wings, and behavioural
431 interactions with bird in the species *I. podalirius*, we provide evidence for an effect of natural
432 selection exerted by predators on hindwing tail evolution, promoting traits enhancing attack
433 deflection away from the vital body parts. Our study therefore opens up new research avenues

434 on the relative effect of predation pressure vs. other selective forces involved in the evolution
435 of hindwing tails in butterflies. We also highlight that such a deflective effect may have
436 emerged from a sequential evolution of a suite of traits, including wing shape, wing colour
437 patterns, and wing mechanical properties. These questions should stimulate new research on
438 the developmental and selective origin of the traits involved in deflective syndromes in various
439 butterfly species.

440

441

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573
574

575 Legends

576

577 **Figure 1: Experimental setup for behavioural assay with wild-caught great tits.** (a) Each
578 experimental cage (5m x 1m x 3m) was equipped with a video camera filming continuously. A
579 butterfly dummy was fixed to the wall at about 1.5 m off the ground using a wire far enough
580 from any perching site to prevent close inspection by the birds not in flight. (b) Picture of a
581 butterfly dummy struck by a bird. (c) Schematic of a dummy butterfly composed of four real
582 wings glued on an artificial black cardboard body. Five locations could be targeted by birds:
583 Body, FW coastal, FW distal, Colour pattern, and Tail. Photograph of the setup in
584 Supplementary materials S2.

585

586 **Figure 2: Experimental setup designed to estimate the strength needed to break wings at**
587 **different locations.** (a) A custom setup was built, composed of a mobile part (clip + force
588 transducer + linear table) exerting traction on the wing and a fixed part, holding the wing. (b)
589 Summary variables derived from force profile: F_{max} (the maximum force exerted on the vein),

590 T_l (the time to the first break), T_{max} (the time to the complete rupture of the vein), S the slope
591 of the curve (estimating the stiffness of the wing) and the area under the curve J_{max} (indicating
592 the impulse). (c) Locations of the four measured points with attachment on a vein at 3mm from
593 the edge of the wings. Hindwing tail resistance is measured at the point M3H. Photograph of
594 the setup in Supplementary materials S3.

595

596 **Figure 3: Locations of bird strikes on the dummy butterflies**, recorded during six
597 experimental sessions on 72 captured *Parus major* using butterfly dummies built with real
598 wings of *I. podalirius*. A total of 59 strikes were recorded. Each category is defined by the
599 location targeted by a bird in a single strike and represented in orange on each associated
600 butterfly scheme. Only essential statistical comparisons are represented; see details in Table
601 1. Video in Supplementary movies 1-2.

602

603 **Figure 4: Variation in mechanical resistance in different areas of the forewing and**
604 **hindwings of fresh *I podalirius* samples (n=28)**. On each of the 28 butterflies, four locations
605 were studied, corresponding to four different veins (R5F, M3F, R5H, M3H). Means and
606 standard errors are indicated as well as significant differences between locations. Three
607 mechanical variables per wing location are reported (a) T_{max} (the time to the complete rupture
608 of the vein). (b) S , the slope of the curve (estimating the stiffness of the wing) and (c) J_{max} ,
609 the area under the curve (a measure of impulse).

610

611 **Figure 5: Heatmap describing the spatial distribution of wing damage on a sample of**
612 **wild *I. podalirius***. Left: Photograph of *I. podalirius* wings. Right: Proportion of naturally
613 damaged wing locations. Data for left and right wings were pooled for each pair of wings (65
614 individuals, so 130 forewings and 130 hindwings). The most frequently damaged areas are
615 shown in red, while intact areas are shown in blue (see colour scale).

616

617 **Table 1: Post Hoc comparisons of bird strike numbers on the dummy butterflies**
618 **between attack locations**. Eight categories of location were defined: Body, FW coastal, FW
619 distal, Colour pattern, Tail, FW coastal + Body, Tail + Colour pattern, Tail + Colour pattern +
620 FW distal.

621

622 **Table 2: Summary of the linear mixed-effects models** describing the effect of Wing
623 (forewing/hindwing) and Vein (M3/R5) on the five mechanical parameters measured during
624 the mechanical resistance experiment in different areas of the forewing and hindwings of
625 fresh *I podalirius* samples (n=28): F_{max} (the maximum force exerted on the vein), T_l (the time
626 to the first break), T_{max} (the time to the complete rupture of the vein), S (estimating the
627 stiffness of the wing), J_{max} (the impulse required for the complete rupture of the vein). These
628 five models were analysed with a type III analysis of variance.

629

630 **Supplementary table 1: Post Hoc comparisons of bird strike numbers on the dummy**
631 **butterflies between rank order of attacks**. Each strike was characterised by its rank order,
632 from 1 to 7.

633

634 **Supplementary materials S1: Physical characterisation** of the tensile strength of the wing
635 (from [48]).

636

637 **Supplementary materials S2: Photograph of the experimental setup** for behavioural assay
638 with wild-caught great tits.

639

640 **Supplementary materials S3: Photograph of the experimental setup** to estimate the force
641 needed to tear the wings at different locations.

642

643 **Supplementary materials S4: Strike trajectories of birds (n=59).** We tested whether
644 strikes occurred more often with a bottom-up trajectory than a top-down trajectory using a
645 Pearson Chi-squared test. Bottom-up trajectories (n=33) are more frequent than top-down
646 (n=19) ($\chi^2 = 6.3333$, $df = 1$, $P = 0.012$).

647

648 **Supplementary movie 1: Video of three sequential strikes** performed by a great tit on a
649 dummy butterfly. Strikes are shown at normal speed then slowed down 10 times.

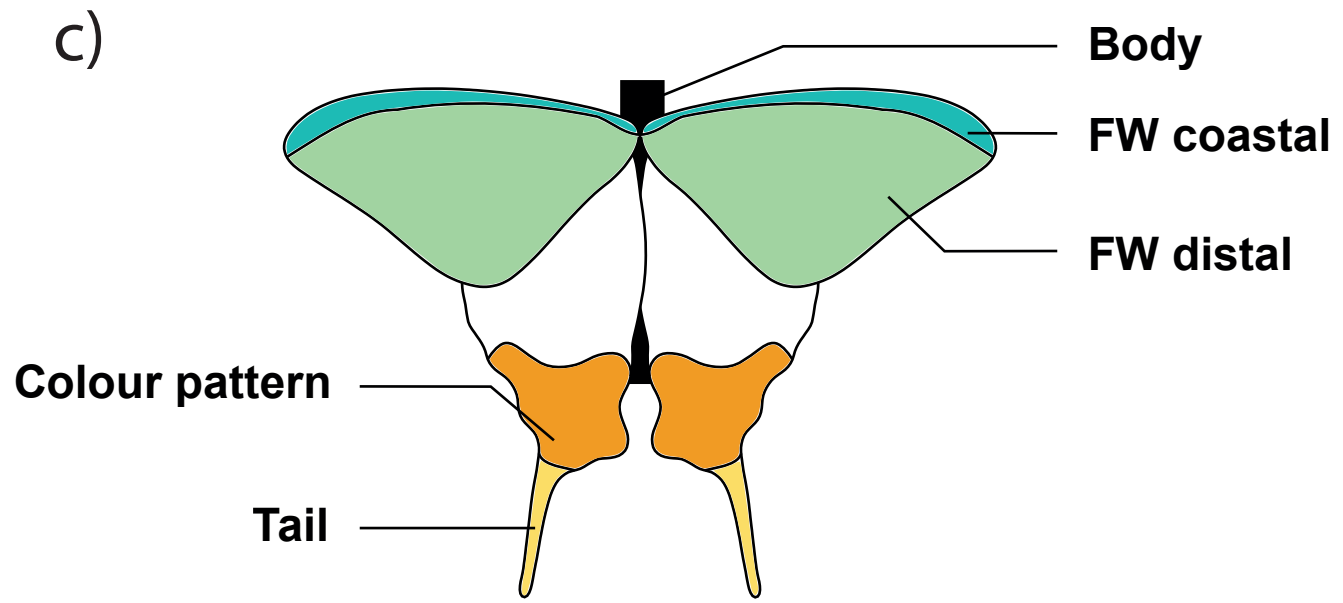
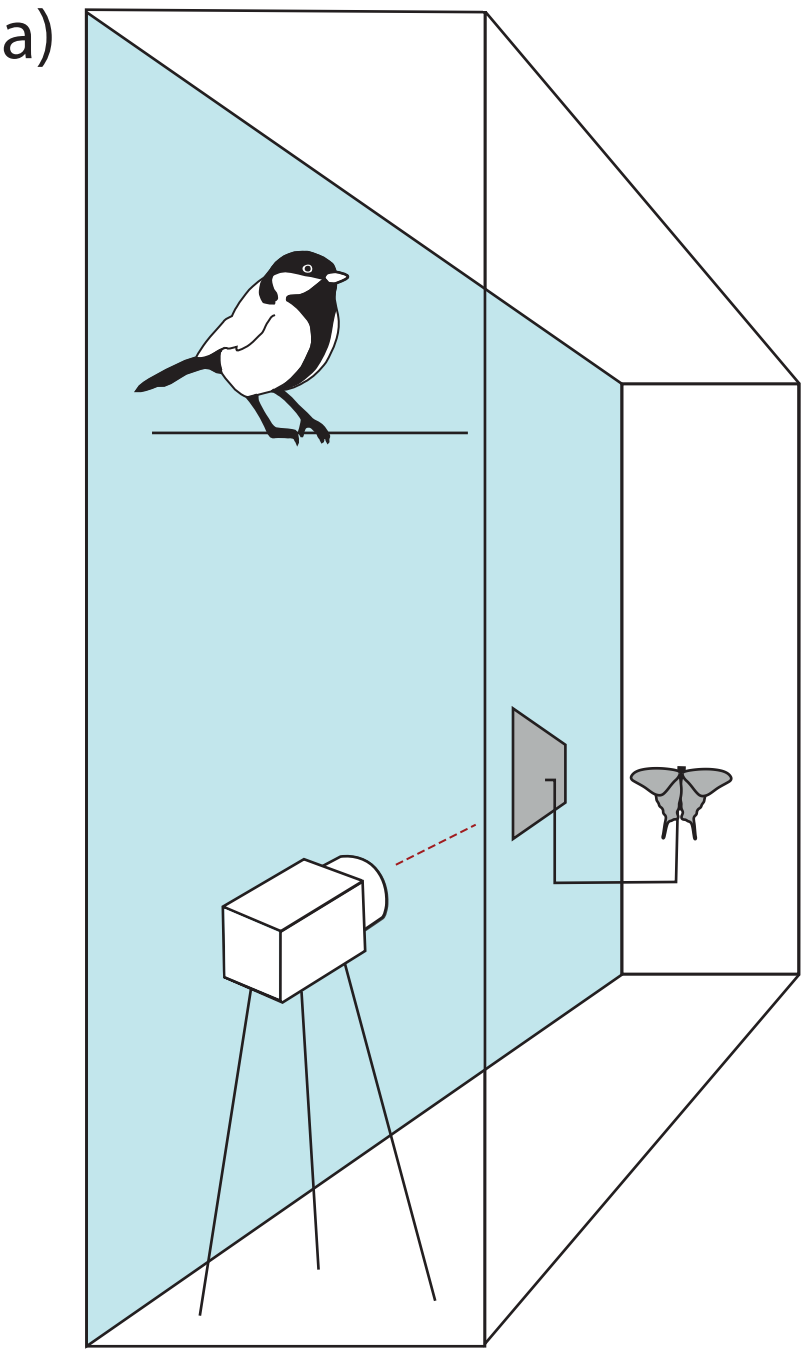
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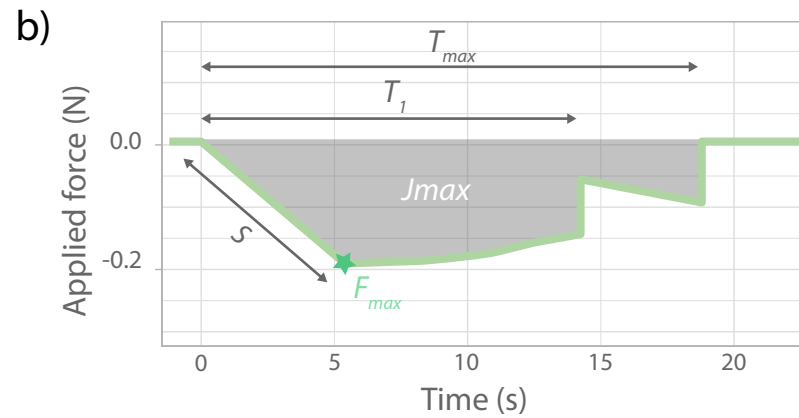
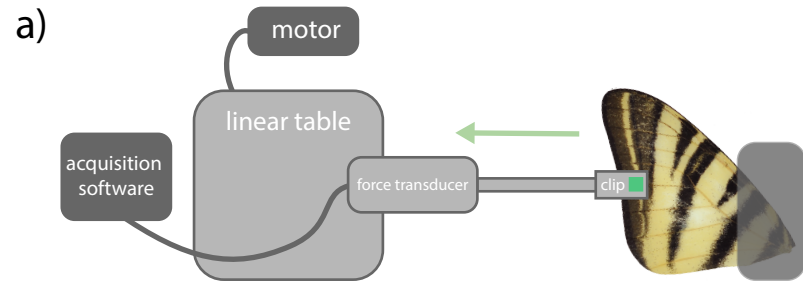
651 **Supplementary movie 2: Video of one strike** performed by a great tit on a dummy butterfly.
652 Strike is shown at normal speed then slowed down 10 times.

653

654

655

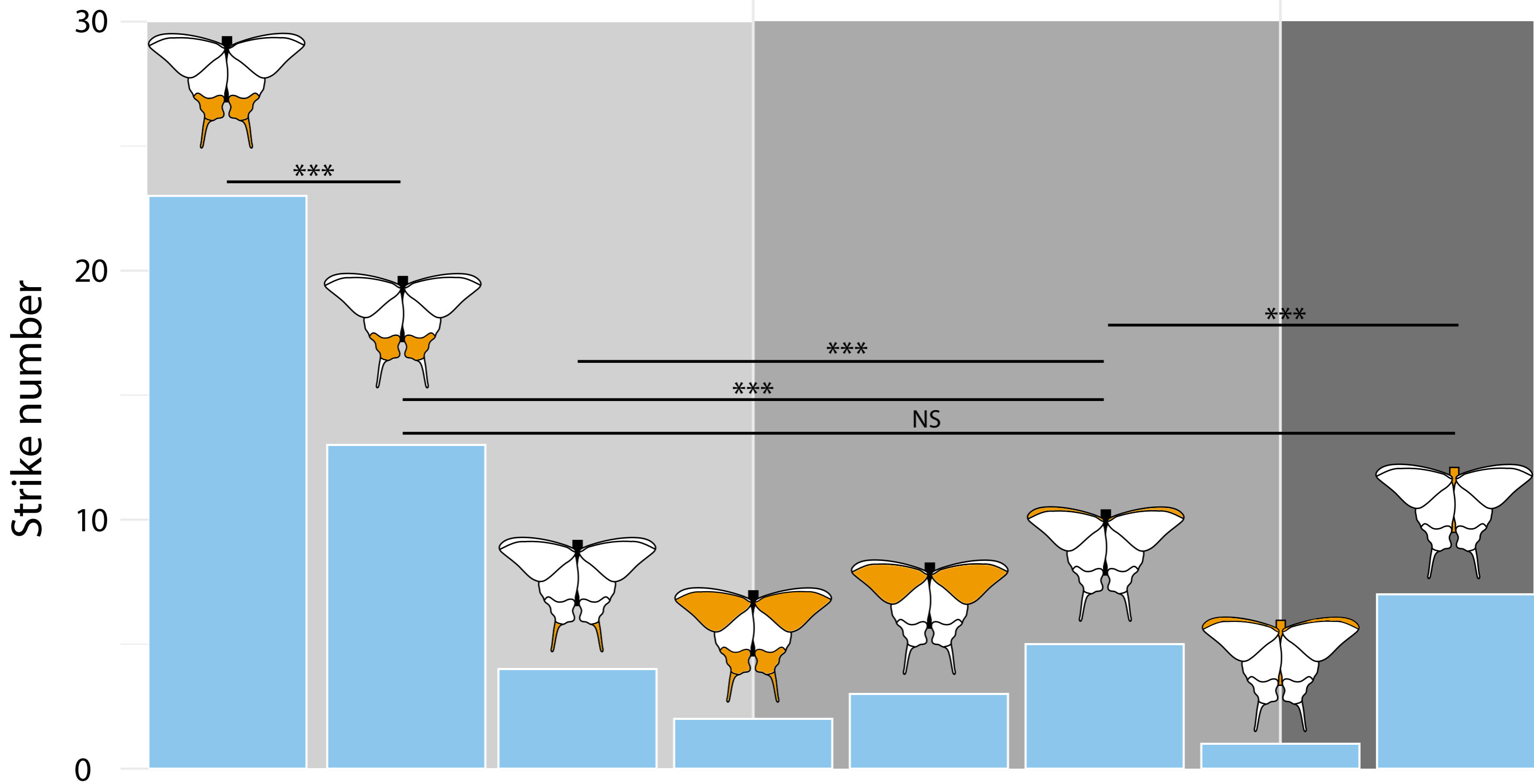


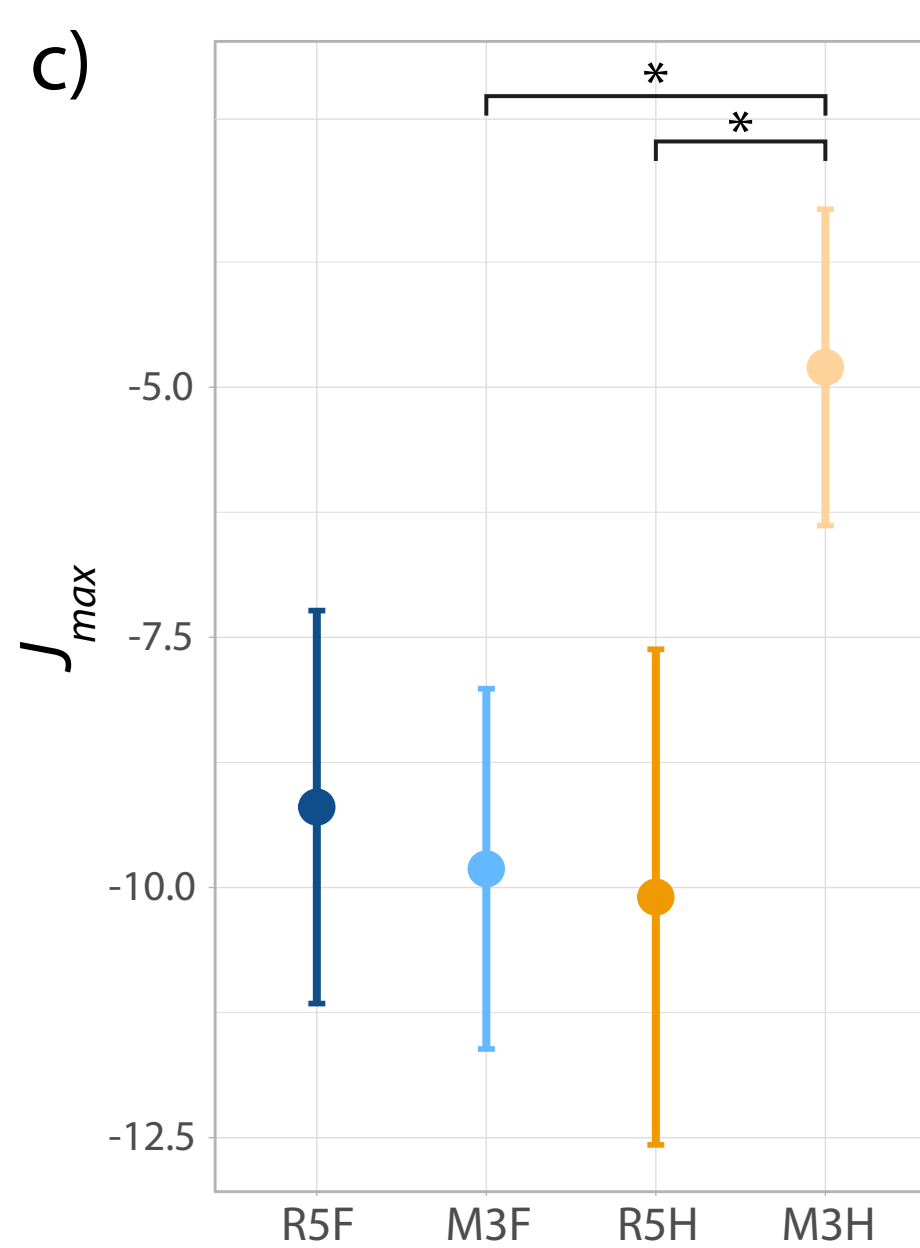
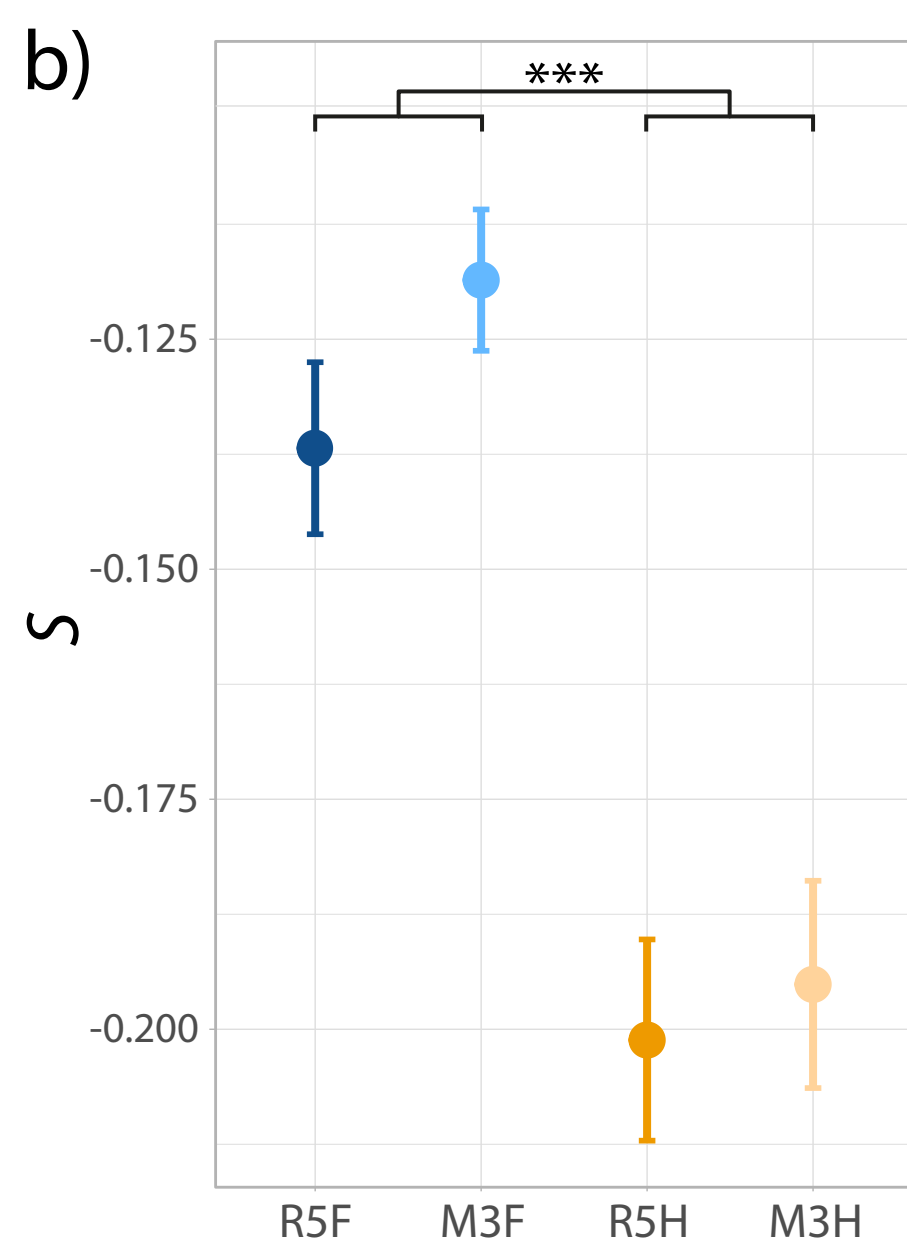
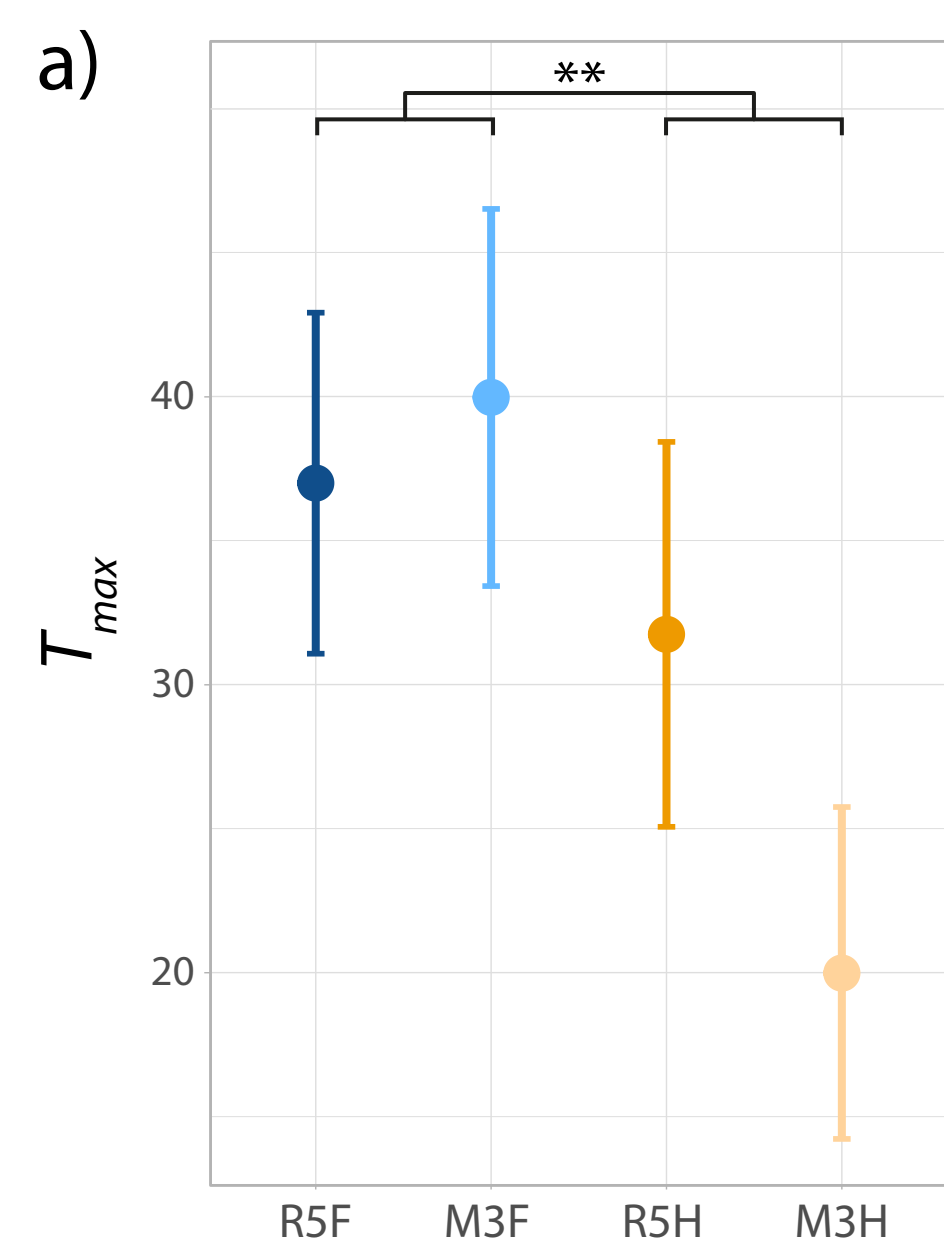


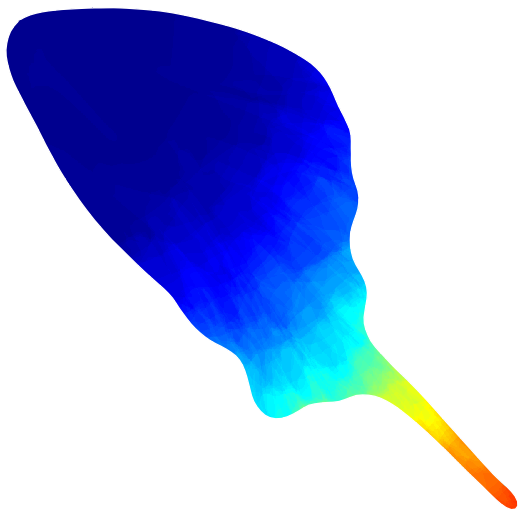
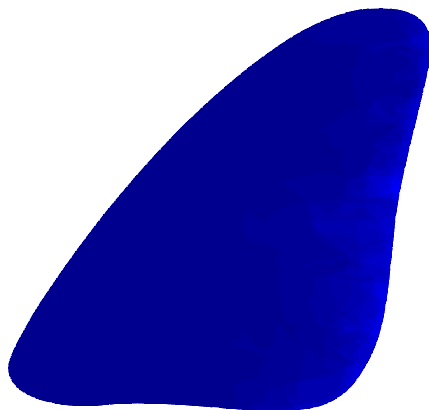
Hindwing

Forewing

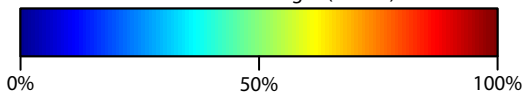
Body







Percent of damages (n=130)



	Wing			Vein			Wing:Vein		
	<i>df</i>	<i>F-value</i>	<i>p-value</i>	<i>df</i>	<i>F-value</i>	<i>p-value</i>	<i>df</i>	<i>F-value</i>	<i>p-value</i>
F_{max}	75.8500	3.1006	0.0823	75.6680	0.0180	0.8937	75.791	1.3071	0.2565
T_1	44.4160	17.7794	< 0.001 ***	44.1520	0.8624	0.3581	44.793	2.7123	0.1066
T_{max}	67.7270	7.9865	0.0062 **	64.3680	1.1973	0.2779	63.458	2.1050	0.1517
S	69.0870	60.4044	< 0.001 ***	68.9320	1.3691	0.2460	70.49	0.3050	0.5825
E_{max}	64.036	1.8635	0.1770	58.537	2.0436	0.1582	57.844	4.1549	0.04609 *