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► To cite this version:

Mónica Arias, Lucie Leroy, Clément Madec, Louane Matos, Cynthia Tedore, et al.. Partial wing transparency works better when disrupting wing edges: evidence from a field experiment. *Journal of Evolutionary Biology*, 2021, 10.1111/jeb.13943 . hal-03373157

HAL Id: hal-03373157

<https://hal.science/hal-03373157>

Submitted on 20 Oct 2021

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Title: Partial wing transparency works better when disrupting wing edges: evidence from a field experiment

Running title: transparency works better when disruptive

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Acknowledgements: Authors thank Julien Renoult and Charles Perrier for comments on a previous version of this manuscript. This work was funded by Clearwing ANR project (ANR-16-CE02-0012), HFSP project on transparency (RGP0014/2016). With the support of LabEx CeMEB, an ANR "Investissements d'avenir" program (ANR-10-LABX-04-01).

Author contribution section: MA, DG and ME designed the study; MA, LL, CM, LM acquired field data, CT and MA analysed the data, MA, CT, DG and ME contributed to manuscript writing.

Conflict of Interest Statement: The authors have no conflict of interest to declare

1 **Abstract**

2 Lepidoptera – a group of insects in which wing transparency has arisen multiple
3 times - exhibit much variation in the size and position of transparent wing zones.
4 However, little is known as to how this variability affects detectability. Here, we test
5 how the size and position of transparent elements affect predation of artificial moths
6 by wild birds in the field. Morphs with transparent elements touching wing borders
7 showed a reduced predation risk, with the effect being the same regardless of the
8 number of wing borders being touched. By contrast, transparent element size had
9 little to no effect on predation risk. Overall, this experiment shows for the first time
10 that transparency offers higher protection when it disrupts prey contour in terrestrial
11 habitats.

12 **Keywords**

13 background matching, disruptive coloration, transparency, wild bird predators,
14 artificial prey

15

16 **Introduction**

17 Predator evasion has promoted some of the most striking adaptations in the living
18 world, including lures, mimicry and camouflage in prey (Ruxton *et al.*, 2004). High
19 transparency (with minimal reflection and absorption at any angle or wavelength)
20 constitutes, by definition, the most effective mechanism of background matching
21 against all types of backgrounds. Transparency is more common in pelagic
22 environments, where there is no place to hide, than in terrestrial environments
23 (Johnsen, 2001), because: 1) small differences in refractive index between water and
24 biological tissues limit reflections that would betray the presence of a prey, 2) UV
25 absorbing pigments are not necessary in the depths of oceans because UV radiation
26 is filtered out by water and 3) often tissues on land need to be thick and/or dense to
27 keep an animal's physical structure in place despite gravity, counteracted by buoyant
28 forces in water but not on land. Contrary to aquatic species, in which animals' entire
29 bodies are often transparent, transparency on land has only evolved as "elements"
30 (i.e. parts of the body). It is currently unknown which visual configurations of
31 transparent and opaque elements are more efficient at reducing prey detectability on
32 land.

33 On land, a handful of terrestrial groups have evolved transparency, a trait
34 largely represented in insect wings. In Lepidoptera, most species display wings
35 covered by opaque scales. However, transparency has evolved independently
36 several times in butterflies and moths (Gomez *et al.*, 2021). According to recent
37 experimental evidence, translucency (low level of transparency with high amount of
38 light diffusion) can smoothen and blur the animal-environment transition, and reduce
39 body outline detectability in glass frogs (Barnett *et al.*, 2020). The presence of well-
40 defined transparent windows, often found in Lepidoptera exhibiting transparency,
41 reduces detectability in both conspicuous (Arias *et al.*, 2019) and cryptic (Arias *et al.*,
42 2020) butterflies and moths. However, wing transparency can occur in different forms
43 (Figure 1): as small windows (e.g., as in the moths *Attacus atlas*, or *Carriola*

44 *ecnomoda*) or as large windows (e.g., as in the sphinx *Hemaris fuciformis*) delimited
45 by brownish elements or conspicuous wing borders (e.g., as in the Ithomiini tribe).
46 Wing transparency can also be associated with discontinuous borders, touching prey
47 edges (e.g., as in moths of the genus *Bertholdia*). Whether the size of transparent
48 windows or their disruption of contour have any effect on prey detectability remains
49 to be studied.

50 This diversity of forms suggests that including transparent elements can
51 reduce detectability by different mechanisms. For example, a transparent window
52 surrounded by an opaque border could reduce detectability by increasing
53 background resemblance. The larger the transparent area, the larger the proportion
54 of the prey's surface area that matches its background ("background matching
55 hypothesis"). On the other hand, transparent elements in contact with the prey
56 outline can hamper detection as a form of disruptive coloration. In disruptively
57 coloured prey, colours that imitate the background are combined with contrasting
58 elements that are located on the prey border, breaking its visual edges and making it
59 difficult to detect ("disruptive coloration hypothesis") (Cuthill *et al.*, 2005; Stevens &
60 Cuthill, 2006). Broken edges have been shown to work better than background
61 matching (Cuthill *et al.*, 2005), especially when low and intermediate colour contrast
62 elements are included (Stobbe & Schaefer, 2008). Additionally, transparent elements
63 touching prey edges can make the prey appear to be of smaller size than it actually
64 is, reducing its perceived profitability and its risk of being attacked, as predation rate
65 is directly correlated with prey size (Berger *et al.*, 2006). To understand the relative
66 importance of these different mechanisms in partially transparent terrestrial prey, we
67 need to investigate the effects of the size and position of transparent elements.

68 Here, we explored the perceptual mechanisms by which transparent wing
69 windows decrease predation, using wild avian predators of artificial moths, naïve to
70 transparent butterflies and moths. Field experiments with artificial prey models are a
71 common way to explore the behaviour of natural predators in response to the visual

72 characteristics of prey and thus to infer the perceptual mechanisms of predation
73 avoidance (Cuthill *et al.*, 2005, 2006; Stevens *et al.*, 2013). We carried out field
74 experiments to analyse the effect of different sizes and positions of transparent
75 “windows” on the attack of prey by avian predators. We predicted that larger
76 transparent windows would decrease prey detectability by background matching, and
77 that transparent windows touching prey outlines would make prey more difficult to
78 detect, presumably *via* disruptive coloration. Hence, large transparent windows
79 touching wing edges should produce the maximal protection against visual predators.

80

81 **Material and methods**

82 Field experiments

83 We followed an experimental design similar to that described in Arias *et al* (2020).
84 Briefly, we performed predation experiments in April and May 2019 in two forests in
85 southern France with evergreen and white oaks as predominant tree vegetation: La
86 Rouvière forest (43.65°N, 3.64°E) and a large natural wooded area of the Montpellier
87 Zoological Park (43.64°N, 3.87°E), for three 1-week sessions at each place. We
88 monitored artificial prey survival from predation by bird local communities once per
89 day for four consecutive days after placing them on trunks, and removed them
90 afterwards. Common birds at each site included great tits (*Parus major*), blue tits
91 (*Cyanistes caeruleus*), Eurasian jays (*Garrulus glandarius*), common chaffinches
92 (*Fringilla coelebs*), golden orioles (*Oriolus oriolus*) and European robins (*Erithacus*
93 *rubecula*). Artificial prey (body and wings) were pinned on evergreen oak (*Quercus*
94 *illex*) tree trunks (>10cm in diameter, with little or no moss cover) every 10m. To deter
95 ant attacks, we applied Vaseline and double-sided transparent tape between the
96 wings and the trunk. Prey were placed perpendicularly to the ground and mostly on
97 the north-facing side of tree trunks to reduce direct sunlight reflection that could

98 facilitate their detection. We monitored prey survival once per day for the following
99 four consecutive days after placing them on trunks, and removed them afterwards.

100 Artificial moths

101 Artificial moths consisted of paper wings and an edible body, as described by Arias
102 *et al* (2020), and similar to other experiments (Cuthill *et al.*, 2005; Stevens & Cuthill,
103 2006). Wings consisted of paper right triangles resembling resting generic moths
104 (i.e., not representing any one particular species). Each triangle was 25mm high by
105 36mm wide, giving a surface area of 450mm². In choosing a printed-colour and paper
106 combination for the wings, we sought paper that would bear low chromatic and
107 achromatic contrasts with the oak trunk for birds regardless of whether they had the
108 UVS or VS visual system. To choose it, we performed reflectance measurements of
109 evergreen oak trunk colouration (120 measurements on 6 trunks) and we also
110 measured reflectance from laminated grey paper of a range of grey levels. For that
111 purpose, we used a deuterium halogen lamp (Avalight DHS) emitting over the 300-
112 700 nm range, including UV to which birds are sensitive (Chen & Goldsmith, 1986), a
113 spectrophotometer (Starline Avaspec-2048 L), an optical probe (including both
114 illumination and measurement fiber optics) with its tip cut at 45° (FC-UV200-2-1.5 x
115 100, Avantes), and a white diffuse reference (spectralon, WS2). We then calculated
116 colour and brightness contrasts between paper and trunk as potentially seen by birds
117 by applying the Vorobyev and Osorio discriminability model (Vorobyev & Osorio,
118 1998) using the *pavo* package of R software (Maia *et al.*, 2013). We calculated
119 discriminability for both UVS vision (blue tit, (Hart *et al.*, 2000)) and VS vision
120 (shearwater, (Hart, 2001)). We used a forest shade light environment (Gomez &
121 Théry, 2007). Single photoreceptor noise was 0.1 and cone numbers corresponded
122 to 1:1.7:2.5:3 (U/V:S:M:L) (Hart, 2001; Kram *et al.*, 2010; Rahman *et al.*, 2010;
123 Baumhardt *et al.*, 2014; Ensminger & Fernández-Juricic, 2014). A Weber fraction of
124 0.2 was used for the brightness response (as the average reported values for known
125 bird species (Lind *et al.*, 2013)). Within the range of printed grey papers, we found

126 that colour Grey155 (R=G=B=155), printed on Canson® sketch paper with a HP
127 officejet pro 6230 printer, was chromatically indistinguishable from trunk coloration
128 (chromatic contrast of 0.47 ± 0.16 JND for UVS vision and of 0.41 ± 0.14 JND for VS
129 vision), and marginally lighter than oak trunks (achromatic contrast of 1.65 ± 0.69
130 JND for UVS vision and of 1.65 ± 0.68 JND for VS vision). The brightness mismatch
131 ensured that opaque uniformly coloured prey were detectable enough to be predated
132 upon at high enough rates to be able to test for differences among treatments. Since
133 achromatic vision is involved in object detection while in motion (Schaerer &
134 Neumeyer, 1996), it was important that the mismatch occurred on brightness (see
135 Figure 1 for pictures of the different morphs against their natural background during
136 the experiment). This design thus enabled us to explore the effect of transparent
137 windows and their spatial configuration on reducing detectability of imperfectly cryptic
138 prey.

139 We tested five types of artificial grey moth morphs with different wing
140 characteristics (Figure 1): an opaque morph (O), a morph with small transparent
141 windows (SW), a morph with large transparent windows (LW), a morph with large
142 transparent windows touching the bottom edge of the wing (BE), and a morph with
143 large transparent windows touching all three wing edges (B3E). Morphs that included
144 transparent elements were built by cutting two right triangular windows out of the
145 laminated grey triangle. Dimensions for each triangular window were 10 mm high by
146 7 mm wide (transparency occupying 70 mm²; thus 15% of the original grey surface)
147 for the SW morph, and 18 mm high by 14 mm wide for the LW, BE and B3E morphs
148 (transparency occupying 252 mm²; thus 56% of the original grey surface). To

149 simulate transparent wing surfaces, we then added a transparent film (3M for inkjet,
150 chosen for its high transparency even in the UV range; see ESM, Figure S1)
151 underneath the remaining parts. On top of the moth wings, we added an artificial
152 body made from pastry dough (428g flour, 250g lard, and 36g water, following
153 (Carroll & Sherratt, 2013)), dyed grey by mixing yellow, red and blue food dyes
154 (spectrum in Figure S1). This malleable mixture allowed us to make small bodies on
155 which we could record marks made by bird beaks and distinguish them from those
156 made by insects. Morphs were randomised in blocks of 25 artificial moths.

157 Data collection and analysis

158 During monitoring, we considered artificial moths as attacked by birds when their
159 body showed V-shaped or U-shaped marks, or when the body was missing without
160 signs of invertebrate attacks (i.e. no body scraps left on the wings or around the moth
161 on the trunk). We removed all remains of artificial moths attacked by birds, and
162 replaced them when attacked by invertebrates or when the entire artificial prey
163 (wings, body, and pin) was missing, as we could not exclude that the prey item fell
164 down or was blown away by the wind. Non-attacked prey items were treated as
165 censored data in the analyses (i.e. prey that survived at least until the end of the
166 experiment). We analysed prey survival, applying mixed effects and hierarchical (with
167 block nested within location) Cox Proportional Hazards models (Cox, 1972) using the
168 *coxme* package (Therneau, 2020) in R (R Foundation for Statistical Computing,
169 2014). We tested four models, each of which included different ways of describing
170 morph visual characteristics as explanatory variables: 1) the morph (O, SW, LW, BE,
171 B3E, Model 1), 2) the number of borders touched by transparent windows
172 (continuous variable with 0 in O, SW, and LW, 1 border in BE, and 3 borders in B3E,
173 Model 2), and 3) the transparent window size (continuous variable describing the
174 relative surface area of the transparent windows altogether (0 for O, 0.14 for SW and
175 0.57 for LW, BE and B3E), Model 3), and 4) a model including both transparent
176 window size and the number of borders touched by transparent windows (Model 4).

177 We used the AICc criterion to compare them. We fitted two additional models to two
178 subsets of our data. The first included only morphs that had the same transparent
179 surface area (LW, BE and B3E) in order to evaluate the effect of the number of
180 borders touched while holding transparent window size constant (Model 5). The
181 second included only complete border morphs (O, SW and LW) in order to evaluate
182 the effect of transparent window size while holding the continuity of the border
183 constant (Model 6). Continuous explanatory variables were scaled for all models.

184 **Results**

185 A total of 618 artificial moths were attacked out of the 1733 used in the field
186 experiment (35.7% attack rate). The model with border characteristics as the
187 explanatory variable (Model 2) had the lowest AICc value, followed by the model
188 including both border and surface area characteristics (Model 4), followed by the
189 model with only surface area characteristics (Model 3, Table S1). The model using
190 morphs as the explanatory variable was not among the best models according to the
191 AICc criterion (Model 1, Table S1).

192 Prey with transparent windows touching the borders (morphs BE and B3E)
193 survived slightly better than morphs with unbroken borders (survival: 68% for morphs
194 touching the borders versus 62% for morphs with unbroken borders; Model 2: Cox
195 mixed-effects model coefficient = -0.09 ± 0.04 , $z = -2.2$, $p = 0.03$, Table S2 and
196 Figure 2), suggesting that this characteristic rendered morphs less detectable.
197 However, this difference did not hold when restricting the dataset to morphs with
198 large transparent windows (Model 5, Cox mixed-effects model coefficient = -
199 0.08 ± 0.05 , $z = -1.49$, $p = 0.14$ for a restricted dataset with 1039 prey and 355
200 attacks).

201 In model 3, morphs sporting large transparent windows had a marginally
202 higher survival compared to the other morphs (morphs LW, BE, B3E (66% of
203 survival) as compared to the morph SW (63% of survival) and the morph and C
204 (61.4% of survival); Model 3: Cox mixed-effects model coefficient = 0.07 ± 0.04 , $z =$

205 1.84, $p = 0.07$). However, the survival of morphs with different transparent surface
206 areas was not significantly different when restricting the dataset to the morphs with
207 unbroken borders (Model 6: Cox mixed-effects model coefficient = -0.03 ± 0.05 , $z = -$
208 0.54 , $p = 0.59$, Table S2 for a restricted dataset with 1040 prey and 393 attacks).

209

210 **Discussion**

211 The position of transparent elements was the key visual characteristic that
212 affected moth survival in our experiment. However, the role of transparent window
213 size was less clear. Model 2, which included only border characteristics, had the
214 lowest AICc and also the only significant effect out of all of the statistical models.
215 Adding an effect of transparent window size (Model 4) did not improve model fit.
216 Including only an effect of window size (Model 3) yielded a marginally significant
217 effect. This marginally significant effect was likely a spurious effect driven by border
218 characteristics, however, as two of the three morphs with large windows also had
219 broken borders, whereas the morphs with small (SW) and non-existent (O)
220 transparent windows had complete borders. The fact that SW morphs had slightly
221 higher survival than LW morphs (Fig. 2) further supports the conclusion that the
222 marginally significant effect of window size in model 3 was spurious. It is puzzling
223 that subsetting the dataset to include only morphs with the same transparent window
224 size (LW, BE, B3E) yielded no significant effect of border (Model 5). Our best
225 explanation is that this reduced dataset lacked statistical power due to the lower
226 sample size. However, the lack of significance in this reduced dataset prevents us
227 from completely excluding the possibility that transparent window size had an effect
228 on the results of model 2. Further experiments producing larger datasets are needed
229 to clarify the importance of transparent window size on prey survival.

230 In aquatic organisms, increased camouflage effect for transparency touching
231 animal edges has been suggested, but never tested experimentally. Bagge *et al*
232 (2016) have found in several hyperiid species (Amphipods, Crustacea) that their

233 transparent appendages – which facilitate prey detection when visible - have more
234 efficient antireflective nanostructures than the rest of the body, probably due to a
235 stronger selective pressure for camouflage on body contour elements. In terrestrial
236 organisms, Barnett et al (2020) have explored the effect of translucent elements (low
237 transparency and high reflection levels) in glass frogs, which smoothen the animal-
238 environment transition by increasing environmental reflections around the animal
239 contour. In our experiment, morphs with broken contours had higher survival than
240 morphs with complete contours. We thus provide the first experimental evidence that
241 transparency (high transmission and reduced reflection) can function better when
242 disrupting animal edges. As found in opaque species (Cuthill *et al.*, 2005; Schaefer &
243 Stobbe, 2006; Fraser *et al.*, 2007), our results suggest that breaking the body outline
244 is more efficient at reducing prey detectability than matching the background while
245 keeping all borders intact. It would be interesting to test whether the advantage of
246 transparent windows disrupting wing edges would remain if the opaque portions of
247 the wings more closely matched bark brightness or had patterns mimicking the
248 heterogeneous visual texture of real tree bark.

249 Despite the fact that several Lepidoptera species show transparent elements
250 breaking prey edges, including the cossid *Zeuzera pyrina*, the noctuid *Gaujonia*
251 *arboisi* and the erebids *Hypercompe robusta*, *Perina nuda* and *Senecauxia coraliae*,
252 the disruption of wing outline is actually rather uncommon in butterflies and moths
253 exhibiting transparent wing elements. Transparency in wings is sometimes combined
254 with highly visible wing edges as in several bee/wasp mimics, such as the hawk-
255 moth *Hemaris fuciformis* as well as in the unpalatable Ithomiini tribe. Transparent
256 elements in these latter species may reduce prey detectability as they are large
257 transparent zones that one would expect to enhance background matching (Arias *et*
258 *al.*, 2019; McClure *et al.*, 2019). However, transparency in these species could also
259 potentially function as a means of visual communication such as mimicry (Pinna *et*
260 *al.*, 2021). It is also possible that in the relatively large-winged Lepidoptera, evolving

261 transparent areas touching wing edges is constrained by factors linked to wing
262 strength or flight dynamics. Whether transparent zones not surrounded by opaque
263 borders are indeed more fragile or more sensitive to wind and/or water than opaque
264 patches remains an open question.

265 However, in contrast to the recent findings reported by Arias *et al* (2020), we
266 did not find that the mere presence of transparent elements decreases detectability
267 in imperfectly uniformly coloured cryptic prey (no significant survival difference
268 between morphs “O”, “SW” and “LW” in Model 3 and Figure 2). Perhaps the overall
269 attack rate in our field experiment was too high to see differences in predation rates
270 among morphs. The attack rate in this experiment was over double that of the study
271 by Arias *et al* (2020) study carried out under similar conditions (35.1% in the current
272 study vs. 14.08% in (Arias *et al.*, 2020)). Under strong predation pressure, once the
273 most detectable prey morphs in a given area have already been attacked, less
274 detectable prey are more likely to be attacked. This could potentially have led to a
275 homogenization of attack rates among morphs. Another difference between our
276 study and that of Arias *et al.* (2020) was the number of morphs simultaneously
277 available to predators. Instead of three prey types, including two moth-like types as in
278 Arias *et al.* (2020), the present study included five moth-like forms with fewer
279 phenotypic differences among them, which may have elicited less divergent predator
280 reactions to each of them. Certain levels of phenotypic similarity, such as that
281 exhibited by imperfect mimics, is often enough to trigger predator generalization and
282 a similar response to distinct phenotypes (Ruxton *et al.*, 2008; Kikuchi & Pfennig,
283 2010; Arias *et al.*, 2016). Additionally, feeding on many instead of a small number of
284 prey types affects detection of changes in predator foraging behavior. For instance,
285 theoretical approaches suggest that prey switching (i.e. when a given prey becomes
286 relatively more abundant in predators’ diet (Murdoch, 1969)) is less marked and
287 more difficult to detect when predators feed on a greater diversity of prey items (van
288 Leeuwen *et al.*, 2013).

289 Overall, according to the results of our fieldwork experiment, having transparent
 290 elements breaking at least one prey border seems to be the most effective
 291 mechanism for reducing detectability of prey and subsequent predation.

292 **Data Availability Statement**

293 Field experiment data is available in Dryad (doi:10.5061/dryad.3n5tb2rjb)

294 **References**

295

296 Arias, M., Elias, M., Andraud, C., Berthier, S. & Gomez, D. 2020. Transparency
 297 improves concealment in cryptically coloured moths. *Journal of Evolutionary*
 298 *Biology* **33**: 247–252. Wiley Online Library.

299 Arias, M., le Poul, Y., Chouteau, M., Boisseau, R., Rosser, N., Théry, M., *et al.* 2016.
 300 Crossing fitness valleys: empirical estimation of a fitness landscape
 301 associated with polymorphic mimicry. *Proc. R. Soc. B* **283**: 20160391.

302 Arias, M., Mappes, J., Desbois, C., Gordon, S., McClure, M., Elias, M., *et al.* 2019.
 303 Transparency reduces predator detection in mimetic clearwing butterflies.
 304 *Functional Ecology* **33**: 1110–1119. Wiley Online Library.

305 Bagge, L.E., Osborn, K.J. & Johnsen, S. 2016. Nanostructures and monolayers of
 306 spheres reduce surface reflections in hyperiid amphipods. *Current Biology* **26**:
 307 3071–3076. Elsevier.

308 Barnett, J.B., Michalis, C., Anderson, H.M., McEwen, B.L., Yeager, J., Pruitt, J.N., *et*
 309 *al.* 2020. Imperfect transparency and camouflage in glass frogs. *Proceedings*
 310 *of the National Academy of Sciences* **117**: 12885–12890. National Acad
 311 Sciences.

312 Baumhardt, P.E., Moore, B.A., Doppler, M. & Fernández-Juricic, E. 2014. Do
 313 American goldfinches see their world like passive prey foragers? A study on
 314 visual fields, retinal topography, and sensitivity of photoreceptors. *Brain,*
 315 *Behavior and Evolution* **83**: 181–198. Karger Publishers.

316 Berger, D., Walters, R. & Gotthard, K. 2006. What keeps insects small?—Size
 317 dependent predation on two species of butterfly larvae. *Evolutionary Ecology*
 318 **20**: 575. Springer.

319 Carroll, J. & Sherratt, T. 2013. A direct comparison of the effectiveness of two
 320 anti-predator strategies under field conditions. *Journal of Zoology* **291**: 279–
 321 285.

322 Chen, D.-M. & Goldsmith, T.H. 1986. Four spectral classes of cone in the retinas of
 323 birds. *Journal of Comparative Physiology A* **159**: 473–479.

324 Cox, D.R. 1972. Models and life-tables regression. *JR Stat. Soc. Ser. B* **34**: 187–220.

- 325 Cuthill, I.C., Stevens, M., Sheppard, J., Maddocks, T., Párraga, C.A. & Troscianko,
326 T.S. 2005. Disruptive coloration and background pattern matching. *Nature*
327 **434**: 72.
- 328 Cuthill, I.C., Stevens, M., Windsor, A.M. & Walker, H.J. 2006. The effects of pattern
329 symmetry on detection of disruptive and background-matching coloration.
330 *Behavioral Ecology* **17**: 828–832. Oxford University Press.
- 331 Ensminger, A.L. & Fernández-Juricic, E. 2014. Individual variation in cone
332 photoreceptor density in house sparrows: implications for between-individual
333 differences in visual resolution and chromatic contrast. *Plos One* **9**: e111854.
334 Public Library of Science.
- 335 Fraser, S., Callahan, A., Klassen, D. & Sherratt, T.N. 2007. Empirical tests of the role
336 of disruptive coloration in reducing detectability. *Proceedings of the Royal*
337 *Society of London B: Biological Sciences* **274**: 1325–1331.
- 338 Gomez, D., Pinna, C., Pairraire, J., Arias, M., Barbut, J., Pomerantz, A., *et al.* 2021.
339 Wing transparency in butterflies and moths: structural diversity, optical
340 properties, and ecological relevance. *Ecological Monographs* e01475. Wiley
341 Online Library.
- 342 Gomez, D. & Théry, M. 2007. Simultaneous crypsis and conspicuousness in color
343 patterns: comparative analysis of a neotropical rainforest bird community. *the*
344 *american naturalist* **169**: S42–S61.
- 345 Hart, N., Partridge, J., Cuthill, I. & Bennett, A.T. 2000. Visual pigments, oil droplets,
346 ocular media and cone photoreceptor distribution in two species of passerine
347 bird: the blue tit (*Parus caeruleus* L.) and the blackbird (*Turdus merula* L.).
348 *Journal of Comparative Physiology A* **186**: 375–387.
- 349 Hart, N.S. 2001. Variations in cone photoreceptor abundance and the visual ecology
350 of birds. *Journal of comparative physiology. A, Sensory, neural, and*
351 *behavioral physiology* **187**: 685–697.
- 352 Johnsen, S. 2001. Hidden in Plain Sight: The Ecology and Physiology of Organismal
353 Transparency. *The Biological Bulletin* **201**: 301–318.
- 354 Kikuchi, D.W. & Pfennig, D.W. 2010. Predator cognition permits imperfect coral
355 snake mimicry. *The American Naturalist* **176**: 830–834.
- 356 Kram, Y.A., Mantey, S. & Corbo, J.C. 2010. Avian cone photoreceptors tile the retina
357 as five independent, self-organizing mosaics. *PloS one* **5**: e8992. Public
358 Library of Science.
- 359 Lind, O., Karlsson, S. & Kelber, A. 2013. Brightness discrimination in budgerigars
360 (*Melopsittacus undulatus*). *PLoS One* **8**: e54650.
- 361 Maia, R., Eliason, C.M., Bitton, P., Doucet, S.M. & Shawkey, M.D. 2013. pavo: an R
362 package for the analysis, visualization and organization of spectral data.
363 *Methods in Ecology and Evolution* **4**: 906–913.
- 364 McClure, M., Clerc, C., Desbois, C., Meichanetzoglou, A., Cau, M., Bastin-Héline, L.,
365 *et al.* 2019. Why has transparency evolved in aposematic butterflies? Insights

- 366 from the largest radiation of aposematic butterflies, the Ithomiini. *Proceedings*
367 *of the Royal Society B* **286**: 20182769. The Royal Society.
- 368 Murdoch, W.W. 1969. Switching in general predators: experiments on predator
369 specificity and stability of prey populations. *Ecological monographs* **39**: 335–
370 354. Wiley Online Library.
- 371 Pinna, C., Vilbert, M., Borenztajn, S., de Marcillac, W.D., Piron-Prunier, F.,
372 Pomerantz, A., *et al.* 2021. Mimicry drives convergence in structural and light
373 transmission features of transparent wings in Lepidoptera. *bioRxiv*
374 2020.06.30.180612.
- 375 R Foundation for Statistical Computing, R.C. 2014. *R: A language and environment*
376 *for statistical computing*. Vienna, Austria.
- 377 Rahman, M.L., Yoshida, K., Maeda, I., Tanaka, H. & Sugita, S. 2010. Distribution of
378 retinal cone photoreceptor oil droplets, and identification of associated
379 carotenoids in crow (*Corvus macrorhynchos*). *Zoological science* **27**: 514–
380 521. BioOne.
- 381 Ruxton, G.D., Franks, D.W., Balogh, A.C.V. & Leimar, O. 2008. Evolutionary
382 implications of the form of predator generalization for aposematic signals and
383 mimicry in prey. *Evolution* **62**: 2913–2921.
- 384 Ruxton, G.D., Sherratt, T.N. & Speed, M.P. 2004. *Avoiding attack*. Oxford University
385 Press.
- 386 Schaefer, H.M. & Stobbe, N. 2006. Disruptive coloration provides camouflage
387 independent of background matching. *Proceedings of the Royal Society of*
388 *London B: Biological Sciences* **273**: 2427–2432.
- 389 Schaerer, S. & Neumeyer, C. 1996. Motion detection in goldfish investigated with the
390 optomotor response is “color blind.” *Vision research* **36**: 4025–4034. Elsevier.
- 391 Stevens, M. & Cuthill, I.C. 2006. Disruptive coloration, crypsis and edge detection in
392 early visual processing. *Proc Biol Sci* **273**: 2141.
- 393 Stevens, M., Marshall, K.L., Troscianko, J., Finlay, S., Burnand, D. & Chadwick, S.L.
394 2013. Revealed by conspicuousness: distractive markings reduce
395 camouflage. *Behavioral Ecology* **24**: 213–222. Oxford University Press UK.
- 396 Stobbe, N. & Schaefer, H.M. 2008. Enhancement of chromatic contrast increases
397 predation risk for striped butterflies. *Proceedings of the Royal Society B:*
398 *Biological Sciences* **275**: 1535–1541. The Royal Society London.
- 399 Therneau, T.M. 2020. Mixed Effects Cox Models [R package coxme version 2.2-16].
400 Comprehensive R Archive Network (CRAN).
- 401 van Leeuwen, E., Brännström, Å., Jansen, V.A., Dieckmann, U. & Rossberg, A.G.
402 2013. A generalized functional response for predators that switch between
403 multiple prey species. *Journal of theoretical biology* **328**: 89–98. Elsevier.
- 404 Vorobyev, M. & Osorio, D. 1998. Receptor noise as a determinant of colour
405 thresholds. *Proceedings of the Royal Society B-Biological Sciences* **265**:
406 351–8.

407

408

409 **Figure Legends**

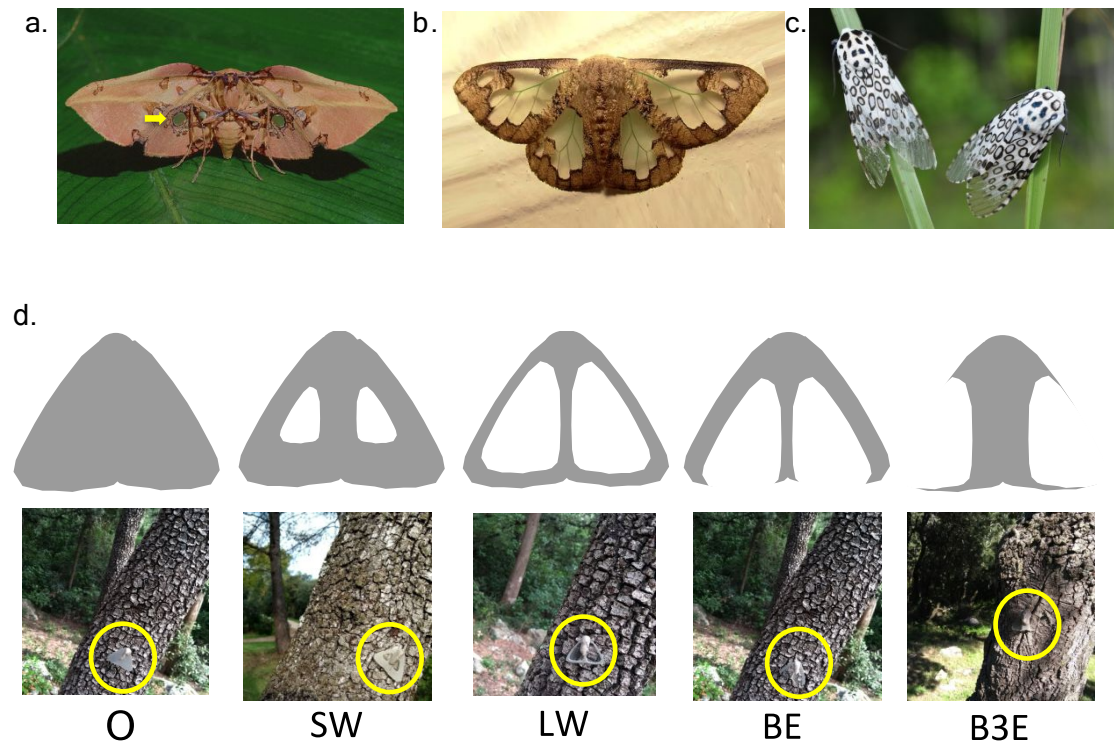
410

411 Figure 1. Examples of the diversity of position and size of transparent elements in
412 butterflies and moths. a. The thyridid *Siculodes aurorula* shows small windows
413 (indicated by the yellow arrow, photo: © Adrian Hoskins), b. The erebid *Carriola*
414 *ecnomoda* shows large windows (wingspan ~ 40mm, photo: © Ann van Wijgerden
415 via projectnoah.org), c. The erebid *Hypercompe scribonia* shows windows breaking
416 the bottom edge (wingspan 76 mm, photo: © Green Futures). d. the 5 artificial moths
417 used in this study (25mm high by 36mm wide) against a white background and
418 against the natural background used during the experiment.

419

420 Figure 2. Survival of artificial prey without transparent elements (O-opaque), with
421 small (SW) and large (LW) transparent elements touching none, one (B1E) or three
422 prey edges (B3E). Artificial butterflies were placed on tree trunks and monitored for
423 their 'survival' every day for 4 days. Data from the six weeks during which the
424 experiment was conducted are pooled together.

425



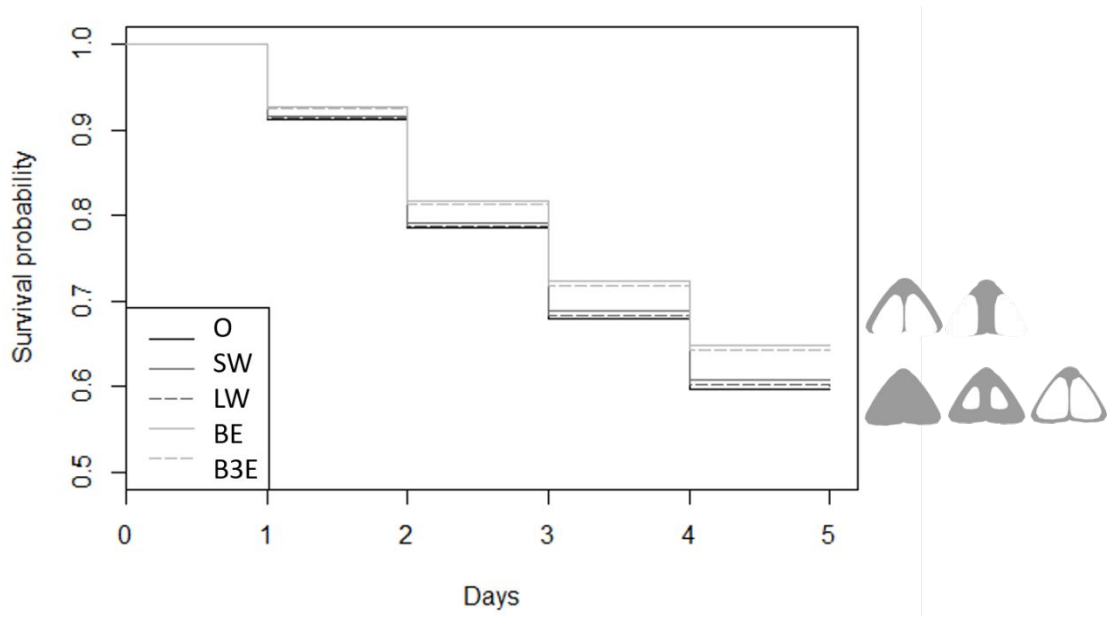


Figure 2

Electronic supplementary material

Partial wing transparency works better when disrupting wing edges: evidence from a field experiment

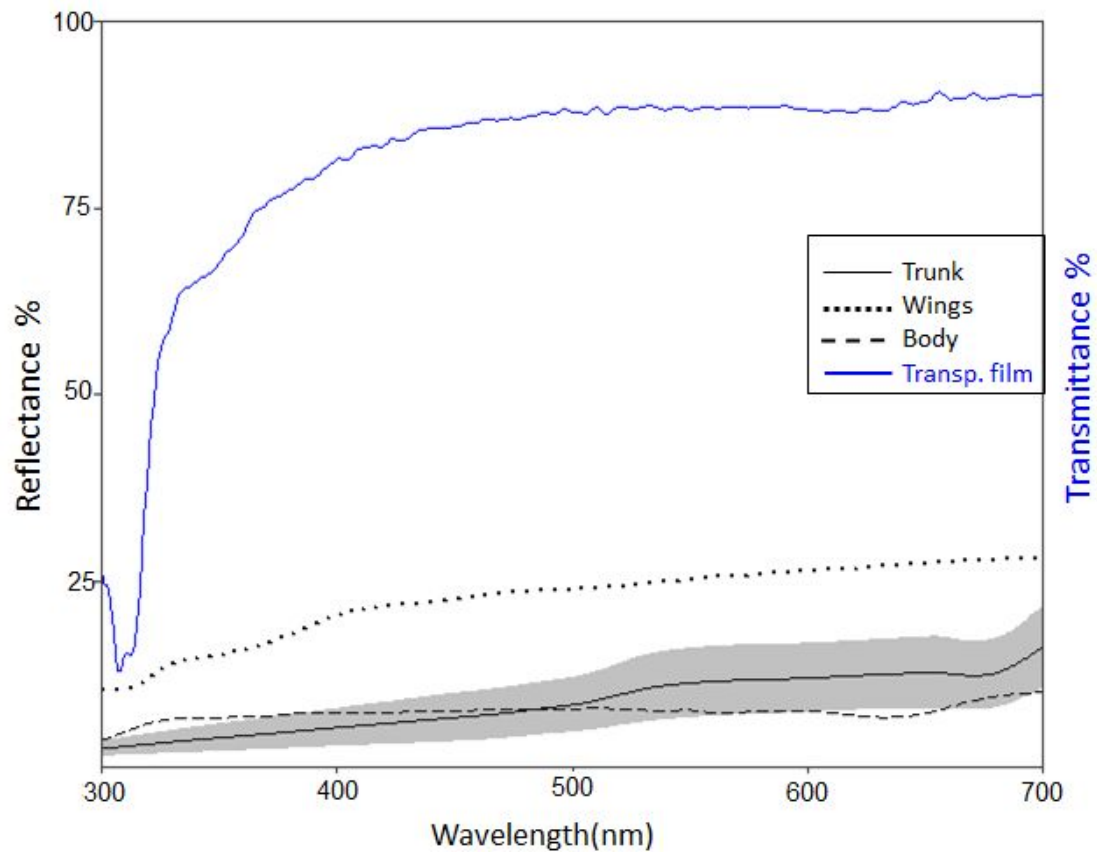


Figure S1. Reflectance spectra of the background (oak tree trunks in solid black line with a confidence interval of ± 1 standard deviation) and opaque areas: body (dashed line) and opaque wings (dotted line), and transmittance of the transparent film (solid blue line).

Table S1. AICc of of mixed effect and hierarchical (with block nested within location) Cox Proportional Hazards models on morph attack. Models are ranked according to their AICc values, from lowest (best fit) to highest. K stands for the number of parameters and delta AICc for the difference in AICc with the best model.

Model	Number of prey	Number of attacks	Exp. variables	K	AICc	Delta AICc
2	1733	618	Border	3	8571.15	0
4	1733	618	Border+Surface	4	8572.66	1.50
3	1733	618	Surface	3	8572.85	1.69
1	1733	618	Morph	6	8576.59	5.44

Table S2. Results from different mixed effect and hierarchical (always with block nested within location) Cox Proportional Hazards model on morph attack

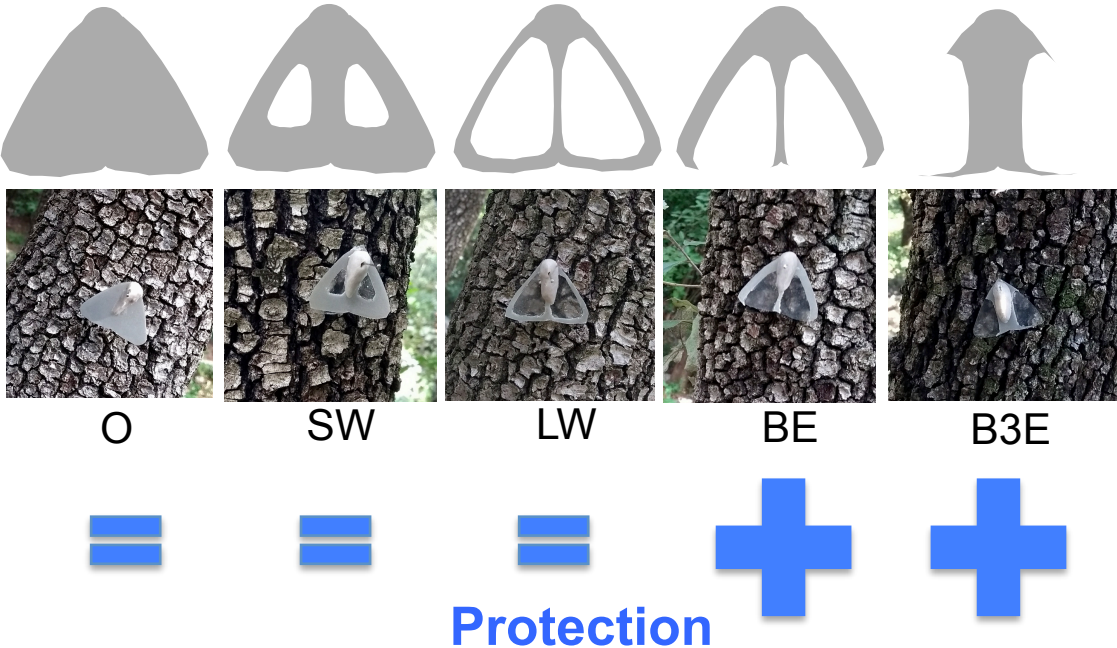
	Number of prey	Number of attacks	Morphs included	Variable	Coef. \pm SE	<i>z</i>	<i>p-value</i>
Model 2	1733	618	All	Border	-0.09 \pm 0.04	-2.2	0.03
Model 4	1733	618	All	Border	-0.07 \pm 0.05	-1.47	0.14
				Surface	0.03 \pm 0.05	0.71	0.48
Model 3	1733	618	All	Surface	0.07 \pm 0.04	1.84	0.07
Model 5	1039	355	Large windows	Border	-0.08 \pm 0.05	-1.49	0.14
Model 6	1040	393	Unbroken edges	Surface	-0.03 \pm 0.05	-0.54	0.59

Each row shows the explanatory variable used in each model and the results obtained. Models 2-4 were fitted using the entire dataset and are the best models according to the AIC criteria (Table S1). Model 5 explored the survival variation explained by border characteristics between LW (0 broken edges), BE (1 broken edge) and B3E (3 broken edges) in morphs with a constant transparent surface area. Model 6 explored survival variation explained by transparent surface area between O (0 transparent surface), SW (15% of the original opaque surface) and LW (56% of the original opaque surface) thus, only including morphs with unbroken edges.

Transparent elements of different sizes and positions can be found on insect prey. Do these elements confer similar protection against visual predators?



We performed field experiments with 5 artificial forms varying in surface area and position of their transparent elements.



We found that transparent elements are most effective when disrupting wing edges