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1 **Transparency improves concealment in cryptically coloured moths**

2

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9 **Running title**

10 Transparency enhances terrestrial camouflage

11 **Abstract**

12 Predation is a ubiquitous and strong selective pressure on living organisms. Transparency is a
13 predation defence widespread in water but rare on land. Some Lepidoptera display transparent
14 patches combined with already cryptic opaque patches. A recent study showed that transparency
15 reduced detectability of aposematic prey with conspicuous patches. However, whether transparency
16 has any effect at reducing detectability of already cryptic prey is still unknown. We conducted field
17 predation experiments with free avian predators where we monitored and compared survival of a
18 fully opaque grey artificial form (cryptic), a form including transparent windows and a wingless
19 artificial butterfly body. Survival of the transparent forms was similar to that of wingless bodies and
20 higher than that of fully opaque forms, suggesting a reduction of detectability conferred by
21 transparency. This is the first evidence that transparency decreases detectability in cryptic terrestrial
22 prey. Future studies should explore the organisation of transparent and opaque patches in animals
23 and their interplay on survival, as well as the costs and other potential benefits associated to
24 transparency on land.

25 **Keywords**

26 Predation, communication, vision, butterfly, camouflage

27

28 Introduction

29 Predation is ubiquitous and exerts a strong selection on living organisms. Often, prey sport
30 cryptic colour patterns that reduce detectability by visual predators, rendering prey hardly
31 distinguishable from their background. Crypsis is achieved if colour patterns represent random
32 samples of background colouration (Endler, 1981). This is challenging, as backgrounds are often
33 complex combinations of elements that can move and that vary in colour and pattern (Ruxton *et al.*,
34 2004). Background matching is efficient only if sufficient number of aspects perceived by predators
35 (e.g., colour, brightness, polarization) are matched (Endler, 1978; Ruxton *et al.*, 2004). Moreover,
36 perception of prey coloration can vary between predators with different visual systems as suggested
37 by the different colours displayed by the dwarf chameleon *Bradypodion transvaalense* when hiding
38 from snakes or from birds (Stuart-Fox *et al.*, 2006). Given the intimate dependence between prey
39 survival and background colouration, cryptic colourations constrain prey movements, and potentially
40 hinder “risky” activities such as foraging, which are associated to an increase in predation risk (Stamp
41 & Wilkens, 1993; Bernays, 1997; Gotthard, 2000). By contrast, dynamic colour changes (Hanlon *et al.*,
42 1999) or transparency (Johnsen, 2014) can free prey from background dependency, improve survival
43 in visually heterogeneous environments, and foster vital activities such as foraging. Notably,
44 transparency can minimize detectability against virtually any background (Johnsen, 2014).

45 Transparency maximises light transmission, minimising reflection and absorption at all angles
46 and for all wavelengths seen by predators. Transparency is rare on land, with the notable exception
47 of insect wings. Among insects, Lepidoptera (moths and butterflies) typically have opaque wings
48 covered by coloured scales involved in intraspecific communication (Jiggins *et al.*, 2004), and
49 antipredator defences such as aposematism (i.e. advertisement of unpalatability, Mallet & Singer,
50 1987), masquerade (i.e. imitation of inedible objects, Suzuki *et al.*, 2014) and camouflage (Stevens &
51 Cuthill, 2006). Yet, wing transparency has evolved independently in multiple Lepidoptera families
52 often in combination with opaque elements. By comparing detection of four real species of

53 aposematic butterflies by predators, Arias *et al* (2019) recently showed that even if all offered high
54 visual contrast and were conspicuous to predators, fully opaque species were more detectable than
55 species with transparent elements. In this case, transparency may help reducing detection in the first
56 place, but if detected, butterflies may benefit from advertising their unpalatability with highly
57 contrasting patches (McClure *et al.*, 2019). However, in many species, transparency has evolved in
58 already cryptic butterflies, as in the Neotropical moth *Neocarnegia basirei* (Saturniidae) or the
59 Malaysian *Carriola ecnomoda* (Erebidae), where transparent wing areas are surrounded by brownish
60 patches frequent in their visual background. Whether transparency can decrease detectability of
61 already cryptically coloured prey remains unknown. We here test for the first time whether
62 transparency decreases detectability on already cryptic terrestrial prey, by conducting field predation
63 experiments by free avian predators and using artificial moths.

64

65 **Materials and Methods**

66 Field experiments

67 We performed predation experiments in May 2018 in southern France, in La Rouvière forest,
68 (43.65°N, 3.64°E) for one 1-week session and at the Montpellier zoo (43.64°N, 3.87°E) for the
69 subsequent two 1-week sessions. According to the local bird-watcher website www.faune-lr.org
70 insectivorous species reported for the zoo and its surroundings are more numerous. However,
71 predator communities are rather similar between sites in spring (Table S2). Great tits (*Parus major*)
72 and blue tits (*Cyanistes caeruleus*), predators of artificial prey in previous similar studies (Rowland *et*
73 *al.*, 2008; Stevens *et al.*, 2008), were seen every morning while monitoring artificial prey at both
74 locations. Additionally, diurnal insectivorous birds such as the Eurasian jay (*Garrulus glandarius*), the
75 common chaffinch (*Fringilla coelebs*), the golden oriole (*Oriolus oriolus*) and the European robin
76 (*Erithacus rubecula*) have also been seen in both localities. We followed the previously validated
77 protocol (Rowland *et al.*, 2008; Stevens *et al.*, 2008) for monitoring artificial prey survival from

78 predation by bird communities. Artificial prey (body and wings) were pinned on green oak *Quercus*
79 *ilex* tree trunks (>10cm in diameter, with few or no moss cover), every 10m in the forest cover. To
80 minimise ant attacks, artificial prey were one centimetre away from the trunk. Additionally, this
81 space was covered by 0.4 cm of Vaseline and 0.6 cm of sticky double-faced transparent tape.
82 Vaseline and tape could be seen from the side, but not when facing the artificial moth. We randomly
83 placed artificial moths with edible body, and three types of wings: fully opaque grey wings (C form),
84 wings with grey contour and large transparent windows (T form), and no wings (B form) as a control
85 of body attractiveness (Fig. S1). Prey were disposed vertically to the ground and mostly facing north
86 to reduce direct sunlight reflection. We monitored prey survival once per day for the following four
87 consecutive days after placing them on trunks, and removed them afterwards.

88 Artificial moths

89 As in other similar experiments (Cuthill *et al.*, 2005; Stevens *et al.*, 2006, 2008), artificial moths
90 consisted of paper wings and an edible body, made of flour and lard in this case. Triangular shaped
91 moths (triangle 25x36mm, surface of 450mm²) did not mimic any real local species, but resembled a
92 generic resting moth (examples in Fig. S1). We designed moths that bore a constant crypsis level by
93 displaying poor visual contrast (chromatic and achromatic) against the average trunk colouration of
94 the highly abundant green oaks.

95 First, we took reflectance spectra of green oak trunk colouration (Fig. S2) and laminated grey
96 paper. We then computed colour and brightness contrasts between paper and trunk as perceived by
97 birds, by using Vorobyev and Osorio's discriminability model (Vorobyev & Osorio, 1998). This model
98 reconstructs the difference in colour and brightness between two colour patches (here butterfly and
99 trunk), as seen by a predator under a given light environment. Contrasts are expressed in JNDs (just
100 noticeable differences) and 1 JND is commonly assumed as the threshold below which two colours
101 are indistinguishable. We found that Grey155 (i. e., in a RGB scale (Red, Green, Blue) from 0 (black) to
102 255 (white), R=G=B=155), printed with a HP officejet pro 6230 printer on Canson® sketch paper, was

103 chromatically indistinguishable but lighter than oak trunks (Table S1), and was chosen as it allowed
104 us testing transparency as a crypsis enhancer on moths bearing a colour that conferred the same
105 imperfect level of crypsis to all artificial prey (see ESM for contrast calculation details). We built the
106 “T” form by cutting two triangular windows (total area of 234 mm²) in the laminated grey triangle,
107 and putting a transparent film (3M for inkjet, chosen for its high transparency even in the UV range
108 see ESM, Fig S2) underneath the remaining parts. On top of moth wings, we added an artificial body
109 made from pastry dough (428g flour, 250g lard, and 36g water, following Carrol & Sherratt (2013)),
110 dyed grey by mixing yellow, red and blue food dyes (spectrum in Fig. S2, contrast values in Table S1).
111 Such malleable mixture allowed us to register and distinguish marks made by bird beaks from insect
112 jaws. We finally computed the visual contrasts produced in the eyes of bird predators (for details see
113 ESM extended materials and methods): C was cryptic (chromatic contrast < 1JND, achromatic
114 contrast ≤ 1.64 JND) and more conspicuous than T and B forms (Table S1).

115 Data collection and analysis

116 We hereafter report all measures, conditions and data exclusions of our experiment, as well as how
117 we determined our sample sizes. As it has been done in previous similar studies, prey were
118 considered as attacked only when artificial moths showed V-shaped or U-shaped marks on their
119 body, or when a prey was missing without signals of invertebrate attacks (i.e. no body scraps left on
120 wings or around the butterfly on the trunk, Carroll & Sherratt, 2013; Hossie *et al.*, 2015). We
121 monitored hundreds of prey models within a few hours and decided as a group whether marks we
122 observed on these models represented valid attacks. Because the observers were aware of the
123 hypothesis, there was the opportunity for bias in the interpretation of marks on models. However,
124 we believe this bias was minimized because we made decisions as a group, most marks were
125 unambiguously attributable or not attributable to birds, and we were focused on the more difficult
126 task of finding models in the field and thus were distracted from the hypothesis when assessing
127 marks on models. We removed all remains of artificial moths attacked by birds, but replaced them

128 when attacked by invertebrates or fully missing. Non-attacked prey were considered as censored
129 data. We started with a sample size of 100 prey items per treatment, as reported on similar studies
130 (Schaefer & Stobbe, 2006; Stevens, 2007). We increased the experimental effort until statistical
131 clarity was reached while keeping similar sample sizes per treatment (see Amrhein *et al.*, 2019 and
132 Dushoff *et al.*, 2019 for discussion on statistical clarity versus statistical significance). One hundred
133 and fifty artificial moths placed in a frequently visited zone of the zoo were excluded from the
134 experiment dataset. In this zone too many moths were completely removed (body, wing, and pin)
135 and it was impossible to determine whether birds as magpies or humans took them. Therefore, all
136 artificial prey from this zone (those that disappeared and those that had not) were removed from the
137 analyses. We analysed prey survival using Cox proportional hazard regression (Cox, 1972), with type
138 of prey, week and their interaction as explanatory variables. By including “week”, the first contrast
139 tests for time and place (by comparing week 1 at La Rouvière, and weeks 2 and 3 at the zoo), while
140 the second contrast test for ‘time’ at the zoo (Table 1). Overall significance was measured using a
141 Wald test. Statistical analyses were performed in R (R Foundation for Statistical Computing, 2014)
142 using *survival* package (Therneau & Lumley, 2009).

143 **Results**

144 492 artificial moths including 165 C moths, 163 T moths and 169 B moths were analysed. 70 of these
145 moths were attacked (predation rate: 14.08%, see Fig. S3 for an example of an attacked prey).
146 Survival strongly differed between forms (Wald test =24.35, df = 8, p = 0.002): wingless bodies and
147 butterflies with transparent windows were similarly attacked (z = 1.51, p = 0.13) and both were less
148 attacked than opaque butterflies (z = 3.98, p < 0.001, Fig. 1, Table 1). Differences between attacks
149 registered at La Rouvière (where 151 moths were displayed on week 1) and attacks at the zoo
150 appeared small (hazard ratio = 0.96) and statistically unclear (pooling weeks 2 and 3 together, z = -
151 0.04, p = 0.71, Table 1). At the zoo, more attacks were registered on week 2 (with 154 analysed
152 moths and closer to blue and great tit reproduction peak) than on week 3 (with 192 analysed moths,

153 $z = 0.55$, $p = 0.003$). No statistically clear interaction between prey form and time or prey form and
154 place was detected (Table 1).

155 **Discussion**

156 Using artificial prey mimicking resting moths with and without transparent elements, exposed to a
157 natural community of avian predators, we show for the first time that transparency confers survival
158 benefits in already cryptically-coloured terrestrial prey. Transparent butterflies were attacked as little
159 as wingless bodies and less than opaque butterflies, suggesting that transparent windows reduce
160 detection. This study is the first to investigate the benefit value of transparency in cryptic terrestrial
161 prey, and to experimentally isolate the effect of transparency from other aspects (as patch colour or
162 patch size). Whether the position and the size of transparent windows, as well as the intrinsic optical
163 properties of the transparent surface (levels of transmission and reflection briefly explored by Arias
164 *et al* (2019) and McClure *et al* (2019)) and its interaction with the ambient light (Johnsen & Widder,
165 1999) influence transparency efficiency also remains untested for terrestrial prey.

166 Although repeatedly proven useful to evaluate predation pressure in the wild (Cuthill *et al.*, 2005;
167 Stevens *et al.*, 2006; Merrill *et al.*, 2012; Carroll & Sherratt, 2013), artificial prey experiments as ours
168 have several limitations (Irschick & Reznick, 2009). Those include the lack of predator species
169 identification, sampling a subset of all possible interactions between prey and predators (i.e. prey
170 detection but not attack, attack of the same prey by different predators), and excluding prey
171 movement, a feature that can facilitate detectability by predators. Camera traps have been useful to
172 get more information on artificial prey predation (Akcali *et al.*, 2019). However, they have provided
173 little information when studying artificial insect predation so far (Low *et al.*, 2014; Ho *et al.*, 2016),
174 most likely because camera traps are less efficient at capturing birds than other predators such as
175 mammals (Ho *et al.*, 2016; Akcali *et al.*, 2019). Other options as DNA analyses on preyed items could
176 be of better help at identifying avian predator species in future studies (Rößler *et al.*, 2018).

177 Crypsis can incur costs related to thermoregulation (Carrascal *et al.*, 2001), intraspecific
178 communication (Dunham & Tierney, 1983), and, more importantly, mobility (Stamp & Wilkens, 1993;
179 Ruxton *et al.*, 2004), thereby hindering foraging and looking for mates. While costs of transparency in
180 terms of thermoregulation and communication have been unexplored so far, transparency can
181 potentially reduce detectability in virtually all backgrounds, reducing the mobility costs associated to
182 crypsis, and enlarging habitat exploitation as reported for the transparent form of the *Hippolyte*
183 *obliquimanus* shrimp (Duarte *et al.*, 2016). However, if camouflage is maximal when including
184 transparency and offers additional benefits in terms of mobility, the low representation of
185 transparency in land, especially in Lepidoptera, is puzzling. As it has been hypothesised for benthic
186 habitats, transparency may be more costly than pigmentation (Johnsen, 2001). In Lepidoptera, scales
187 are involved in several physiological adaptations (communication, water repellency,
188 thermoregulation) (Miaoulis & Heilman, 1998; Jiggins *et al.*, 2004; Wanasekara & Chalivendra, 2011).
189 Whether transparent wings may incur communication, hydrophobic or thermal costs remains to be
190 studied to better understand the costs associated with the evolution of transparency on land and
191 explain its rarity.

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200 **Competing interests**

201 Authors have no conflict of interest to declare.

202 **Ethical statement**

203 No animal was intentionally harmed during this experiment and most artificial prey were found and
204 collected, avoiding leaving wastes in the forest.

205

206 **References**

207 Akcali, C.K., Pérez-Mendoza, H.A., Salazar-Valenzuela, D., Kikuchi, D.W., Guayasamin, J.M. & Pfennig,
208 D.W. 2019. Evaluating the utility of camera traps in field studies of predation. *PeerJ* **7**: e6487.

209 Amrhein, V., Trafimow, D. & Greenland, S. 2019. Inferential Statistics as Descriptive Statistics: There
210 Is No Replication Crisis if We Don't Expect Replication. *Am. Stat.* **73**: 262–270.

211 Arias, M., Mappes, J., Desbois, C., Gordon, S., McClure, M., Elias, M., *et al.* 2019. Transparency
212 reduces predator detection in mimetic clearwing butterflies. *Funct. Ecol.*

213 Bernays, E. 1997. Feeding by lepidopteran larvae is dangerous. *Ecol. Entomol.* **22**: 121–123.

214 Carrascal, L.M., Díaz, J.A., Huertas, D.L. & Mozetich, I. 2001. Behavioral thermoregulation by
215 treecreepers: trade-off between saving energy and reducing crypsis. *Ecology* **82**: 1642–1654.

216 Carroll, J. & Sherratt, T. 2013. A direct comparison of the effectiveness of two anti-predator
217 strategies under field conditions. *J. Zool.* **291**: 279–285.

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

219 Cuthill, I.C., Stevens, M., Sheppard, J., Maddocks, T., Párraga, C.A. & Troscianko, T.S. 2005. Disruptive
220 coloration and background pattern matching. *Nature* **434**: 72.

221 Duarte, R.C., Stevens, M. & Flores, A.A. 2016. Shape, colour plasticity, and habitat use indicate
222 morph-specific camouflage strategies in a marine shrimp. *BMC Evol. Biol.* **16**: 218.

223 Dunham, D. & Tierney, A.J. 1983. The communicative cost of crypsis in a hermit crab *Pagurus marshi*.
224 *Anim. Behav.* **31**: 783–787.

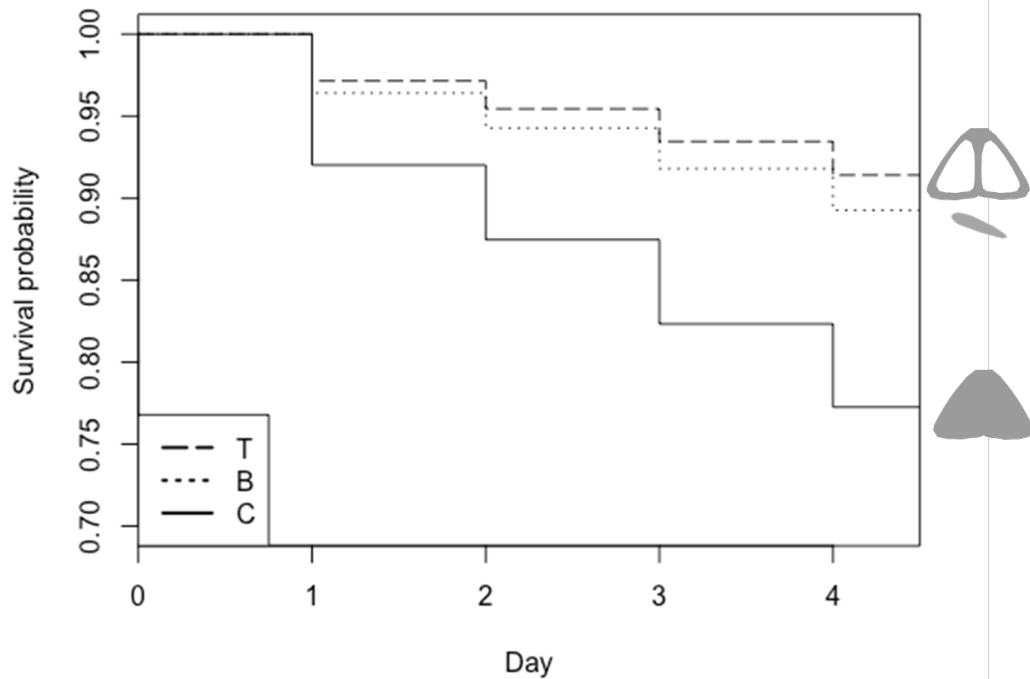
225 Dushoff, J., Kain, M.P. & Bolker, B.M. 2019. I can see clearly now: reinterpreting statistical
226 significance. *Methods Ecol. Evol.* **10**: 756–759.

227 Endler, J.A. 1978. A predator's view of animal color patterns. In: *Evolutionary biology*, pp. 319–364.
228 Springer.

229 Endler, J.A. 1981. An overview of the relationships between mimicry and crypsis. *Biol. J. Linn. Soc.* **16**:
230 25–31.

- 231 Gotthard, K. 2000. Increased risk of predation as a cost of high growth rate: an experimental test in a
232 butterfly. *J. Anim. Ecol.* **69**: 896–902.
- 233 Hanlon, R.T., Forsythe, J.W. & Joneschild, D.E. 1999. Crypsis, conspicuousness, mimicry and
234 polyphenism as antipredator defences of foraging octopuses on Indo-Pacific coral reefs, with
235 a method of quantifying crypsis from video tapes. *Biol. J. Linn. Soc.* **66**: 1–22.
- 236 Ho, S., Schachat, S.R., Piel, W.H. & Monteiro, A. 2016. Attack risk for butterflies changes with eyespot
237 number and size. *R. Soc. Open Sci.* **3**: 150614.
- 238 Hossie, T.J., Skelhorn, J., Breinholt, J.W., Kawahara, A.Y. & Sherratt, T.N. 2015. Body size affects the
239 evolution of eyespots in caterpillars. *Proc. Natl. Acad. Sci.* **112**: 6664–6669.
- 240 Irschick, D.J. & Reznick, D. 2009. Field experiments, introductions, and experimental evolution. *Exp.*
241 *Evol. Concepts Methods Appl. Sel. Exp.* 173–193.
- 242 Jiggins, C.D., Estrada, C. & Rodrigues, A. 2004. Mimicry and the evolution of premating isolation in
243 *Heliconius melpomene* Linnaeus. *J. Evol. Biol.* **17**: 680–691.
- 244 Johnsen, S. 2001. Hidden in Plain Sight: The Ecology and Physiology of Organismal Transparency. *Biol.*
245 *Bull.* **201**: 301–318.
- 246 Johnsen, S. 2014. Hide and seek in the open sea: pelagic camouflage and visual countermeasures.
247 *Annu. Rev. Mar. Sci.* **6**: 369–392.
- 248 Johnsen, S. & Widder, E.A. 1999. The physical basis of transparency in biological tissue: ultrastructure
249 and the minimization of light scattering. *J. Theor. Biol.* **199**: 181–198.
- 250 Low, P.A., Sam, K., McArthur, C., Posa, M.R.C. & Hochuli, D.F. 2014. Determining predator identity
251 from attack marks left in model caterpillars: guidelines for best practice. *Entomol. Exp. Appl.*
252 **152**: 120–126.
- 253 Mallet, J. & Singer, M.C. 1987. Individual selection, kin selection, and the shifting balance in the
254 evolution of warning colours: the evidence from butterflies. *Biol. J. Linn. Soc.* **32**: 337–350.
- 255 McClure, M., Clerc, C., Desbois, C., Meichanetzoglou, A., Cau, M., Bastin-Héline, L., *et al.* 2019. Why
256 has transparency evolved in aposematic butterflies? Insights from the largest radiation of
257 aposematic butterflies, the Ithomiini.
- 258 Merrill, R.M., Wallbank, R.W., Bull, V., Salazar, P.C., Mallet, J., Stevens, M., *et al.* 2012. Disruptive
259 ecological selection on a mating cue. *Proc. R. Soc. B-Biol. Sci.* **17**: 17.
- 260 Miaoulis, I.N. & Heilman, B.D. 1998. Butterfly thin films serve as solar collectors. *Ann. Entomol. Soc.*
261 *Am.* **91**: 122–127.
- 262 R Foundation for Statistical Computing, R.C. 2014. *R: A language and environment for statistical*
263 *computing*. Vienna, Austria.
- 264 Rößler, D.C., Pröhl, H. & Lötters, S. 2018. The future of clay model studies. *BMC Zool.* **3**: 6.
- 265 Rowland, H.M., Cuthill, I.C., Harvey, I.F., Speed, M.P. & Ruxton, G.D. 2008. Can't tell the caterpillars
266 from the trees: countershading enhances survival in a woodland. *Proc. R. Soc. Lond. B Biol.*
267 *Sci.* **275**: 2539–2545.

- 268 Ruxton, G.D., Sherratt, T.N. & Speed, M.P. 2004. *Avoiding attack*. Oxford University Press.
- 269 Schaefer, H.M. & Stobbe, N. 2006. Disruptive coloration provides camouflage independent of
270 background matching. *Proc. R. Soc. Lond. B Biol. Sci.* **273**: 2427–2432.
- 271 Stamp, N.E. & Wilkens, R.T. 1993. On the cryptic side of life: being unapparent to enemies and the
272 consequences for foraging and growth of caterpillars. In: *Caterpillars: ecological and*
273 *evolutionary constraints on foraging*, pp. 283–330. Chapman & Hall, New York.
- 274 Stevens, M. 2007. Predator perception and the interrelation between different forms of protective
275 coloration. *Proc. R. Soc. B Biol. Sci.* **274**: 1457–1464.
- 276 Stevens, M. & Cuthill, I.C. 2006. Disruptive coloration, crypsis and edge detection in early visual
277 processing. *Proc. R. Soc. B Biol. Sci.* **273**: 2141.
- 278 Stevens, M., Cuthill, I.C., Windsor, A.M. & Walker, H.J. 2006. Disruptive contrast in animal
279 camouflage. *Proc. R. Soc. Lond. B Biol. Sci.* **273**: 2433–2438.
- 280 Stevens, M., Hardman, C.J. & Stubbins, C.L. 2008. Conspicuousness, not eye mimicry, makes
281 “eyespot” effective antipredator signals. *Behav. Ecol.* **19**: 525–531.
- 282 Stuart-Fox, D., Whiting, M.J. & Moussalli, A. 2006. Camouflage and colour change: antipredator
283 responses to bird and snake predators across multiple populations in a dwarf chameleon.
284 *Biol. J. Linn. Soc.* **88**: 437–446.
- 285 Suzuki, T.K., Tomita, S. & Sezutsu, H. 2014. Gradual and contingent evolutionary emergence of leaf
286 mimicry in butterfly wing patterns. *BMC Evol. Biol.* **14**: 229.
- 287 Therneau, T. & Lumley, T. 2009. Survival: Survival analysis, including penalised likelihood. R package
288 version 2.35-7. *R Found. Stat. Comput.*
- 289 Vorobyev, M. & Osorio, D. 1998. Receptor noise as a determinant of colour thresholds. *Proc. R. Soc.*
290 *B-Biol. Sci.* **265**: 351–8.
- 291 Wanasekara, N.D. & Chalivendra, V.B. 2011. Role of surface roughness on wettability and coefficient
292 of restitution in butterfly wings. *Soft Matter* **7**: 373–379.
- 293
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296

297 Figure 1. Survival of artificial prey with (T) transparent elements on their wings, (B) bodies without
 298 wings, and (C) fully coloured opaque butterflies. Artificial butterflies were placed on tree trunks and
 299 monitored for their 'survival' every day for 4 days. Data from the three weeks during which the
 300 experiment was conducted are pooled together.

301

302 Table 1. Cox regression analyses for attacks on artificial butterflies.

	Coefficient	Exp. Coef	SE	z	p
Form. C > T +B	-0.34	0.71	0.09	-3.98	<0.001***
Form. B > T	-0.01	0.99	0.20	-0.03	0.9750
Rouvière w1 < Zoo w2 & w3	-0.04	0.96	0.10	-0.38	0.7061
Zoo w2 > Zoo w3	0.55	1.73	0.18	3.01	0.003**
Form C > T +B: Rouvière w1 < Zoo w2 & w3	-0.04	0.96	0.06	-0.63	0.5289
Form. B > T : Rouvière w1 < Zoo w2 & w3	0.01	1.01	0.14	0.06	0.9505
Form. C > T +B: Zoo w2 > Zoo w3	0.11	1.11	0.11	0.99	0.3219
Form. B > T: Zoo w2 > Zoo w3	-0.35	0.71	0.26	-1.36	0.1729

303

304 Explanatory variables are: form (fully coloured ‘C’, with transparent windows ‘T’, and wingless bodies
 305 ‘B’), week (w1, w2, w3), place (Rouvière and zoo) and their interactions. Notice that the experiment
 306 was performed only at Rouvière on w1 and only at the zoo on w2 and w3. Therefore, the contrast “
 307 Rouvière w1 < Zoo w2 & w3 ” tests both time and place simultaneously. z corresponds to the values
 308 from the Wald z test used to test for factor significance, Exp. Coeff. to exponentiated coefficients or
 309 hazard ratios and SE to standard errors. Symbols: ** $p < 0.01$, *** $p < 0.001$.

310

311