



Costello, L. M., Scott-Samuel, N. E., Kjærnsmo, K., & Cuthill, I. C. (2020). False holes as camouflage. *Proceedings of the Royal Society B: Biological Sciences*, 287(1922), [20200126].
<https://doi.org/10.1098/rspb.2020.0126>

Peer reviewed version

Link to published version (if available):
[10.1098/rspb.2020.0126](https://doi.org/10.1098/rspb.2020.0126)

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False holes as camouflage

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Authors' accepted copy of ms in Proceedings of the Royal Society B

Acceptance date: 18/02/2020

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Abstract

Long noted by naturalists, leaf mimicry provides some of the most impressive examples of camouflage through masquerade. Many species of leaf-mimicking Lepidoptera also sport wing markings that closely resemble irregularly shaped holes caused by decay or insect damage. Despite proposals that such markings can either enhance resemblance to damaged leaves or act to disrupt surface appearance through false depth cues, no attempt has been made to establish exactly how these markings function, or even whether they confer a survival benefit to prey. Here, in two field experiments using artificial butterfly-like targets, we show that false hole markings provide significant survival benefits against avian predation. Furthermore, in a computer-based visual search experiment, we demonstrate that detection of such targets by humans is impeded in a similar fashion. Equally contrasting light marks do not have the same effect; indeed, they lead to increased detection. We conclude that the mechanism is disruption of the otherwise homogeneous wing surface ('surface disruptive camouflage') and that, by resembling the holes sometimes found in real leaves, the disruptive benefits are not offset by conspicuousness costs.

Keywords: protective coloration, camouflage, predation, surface disruption, leaf mimicry, depth perception.

52

53 **1. Introduction**

54 Leaf mimicry is a taxonomically widespread form of the camouflage strategy known as
55 masquerade: resemblance to an irrelevant background object [1-4]. This impressive
56 example of protective coloration has been discussed by naturalists and evolutionary
57 biologists for more than a century [5,6]; not only do many animals bear a remarkable
58 resemblance to the shape of a leaf but, in many cases, they also exhibit marks that look
59 like the blemishes of decay or products of attack by herbivores (figure 1). For
60 example, Alfred Russel Wallace describes this phenomenon first hand in his seminal
61 work on mimicry and other protective resemblances noting: "... we find
62 representations of leaves in every stage of decay, variously blotched and mildewed and
63 pierced with holes ..." ([7], p. 7). Striking examples of such markings can be seen in
64 several species of Anura and Lepidoptera, which closely resemble irregular holes in the
65 wing or body surface (figure 1). Although some are simply dark, contrasting, colour
66 patches, other markings are so convincing in apparent 3D relief (at least in a
67 photograph) that the holes look real. However, rather like another striking form of
68 defensive coloration, 'eye spots' [8], the term 'false hole' suggests a function that it is
69 dangerous to assume without evidence [9]. Until now, there have been no
70 investigations of whether false holes are even adaptive and, if so, by which
71 mechanism(s) would it be advantageous to bear patterns that resemble a hole.

72

73 Unless damaged leaves are the norm, it is not immediately obvious why mimicking a
74 leaf with holes would be a better disguise than mimicking an intact leaf. Indeed, there
75 is some evidence that insectivorous birds can use leaf damage as a cue to the presence
76 of caterpillar prey [10,11]: mimicking such a leaf would attract attention rather than
77 avoid it. Both Thayer [12] and Cott [13], pioneers of camouflage theory, instead

78 proposed that these markings are disruptive camouflage, either breaking up the wing
79 surface into apparent multiple planes using false depth cues, disguising shape through
80 the creation of false internal edges with higher contrast markings than the true wing
81 boundary, or simply distracting attention from the wing boundary. Today these putative
82 effects are recognised as different mechanisms [3,14] and, in different contexts, there is
83 evidence that each can be effective [1].

84
85 Here, we attempt to identify any survival advantage conferred by false hole markings,
86 and the possible mechanism(s) by which this benefit could be achieved. We carried out
87 three experiments using artificial butterfly-like targets: two in the field under bird
88 predation and a third, computer-based visual search task with humans as surrogate
89 predators. In the first field experiment, we investigated whether real holes in the wings
90 of leaf-like prey provide a survival advantage (without such an advantage, the benefits
91 of false holes must lie elsewhere), and whether this effect is background-dependent. In
92 the second field experiment, we assessed the degree to which false holes affect survival
93 relative to targets with real holes, and no holes, in the wings: real holes always look
94 like the surface underneath, whereas false holes only represent one generic
95 background. We also explored whether this benefit could be achieved by any high-
96 contrast surface marking: is mimicking a hole actually important, or is just breaking up
97 the surface with a contrasting pattern sufficient? In the third (computer-based)
98 experiment, we used humans to assess directly the effect of false holes on target
99 detectability, furthering our understanding of the similarities and differences in
100 organisation and performance of avian and human visual search.

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105 **2. Materials and Methods**

106 (a) Field experiments with avian predation

107 (i) Stimuli

108 Prey targets were coloured paper ‘wings’ attached to an edible mealworm ‘body’. A
109 stencil was used to create background-matching artificial butterfly wings that were the
110 average colour of bramble, based on calibrated digital photographs of a sample of 50
111 *Rubus fruticosus* leaves (following Stevens *et al.* [15]), in the colour space of a model
112 passerine bird, the blue tit *Cyanistes caeruleus* (following Stevens *et al.* [16]). The
113 targets were not intended to mimic any real species of butterfly (for which avian
114 predators might have pre-existing preferences or aversions) and bramble was chosen as
115 a substrate simply because it was common across the study site, and an easily matched
116 homogeneous green. Target wings were printed double-sided on to A4 waterproof paper
117 (Rite-in-the-Rain, J.L. Darling LLC, Tacoma, WA, US) using a calibrated Canon
118 imageRUNNER ADVANCE C5535i printer (Canon Inc., Tokyo, Japan). Printing
119 double-sided ensured that targets remained cryptic even if the wings separated from
120 each other (see below). Wings were scored and folded down the mid-line, and glued
121 together (Pritt original, Henkel Ltd, Germany) to replicate the appearance of a butterfly
122 in its natural resting position. To create holes (figure 2), a nominally flower-shaped
123 hole-punch (Woodware craft collection; Woodware, Skipton, UK) was used. This shape
124 was chosen as a low-salience convenient shape; a circle or other simple geometric shape
125 might have attracted attention, being rare in natural backgrounds [17].

126

127 A 30 mm x 0.5 mm dressmaking pin (PRYM, Stolberg, Germany) was inserted
128 approximately a third of the way down the wings (figure 2). A dead mealworm

129 (*Tenebrio molitor* larva frozen at -80°C) was threaded onto to the pin, which was then
130 attached to the background substrate. New targets were used for every block.

131
132 The first field experiment was designed to assess whether real holes in wings affected
133 predation rates using two treatments, ‘Intact wings’ and ‘Real holes’. The second field
134 experiment introduced wing markings. This experiment used four treatments: ‘Intact
135 wings’, ‘Real holes’, ‘False holes’, ‘Pale controls’. To create the False hole treatment, a
136 dark shade of grey matching the mean luminance of the background seen through
137 calibrated photographs of the Real hole targets *in situ* was used. The Pale control was a
138 shade of grey of equal luminance contrast to that of the False holes, with respect to the
139 ‘bramble green’ base colour of the wings. This treatment served to assess whether
140 contrast per se with the wings was responsible for a false (or real) hole’s effect on
141 predation risk, or whether that patch has to be darker than the rest of the wing surface.
142 In Cott’s [13] original formulation of his theory of ‘maximum disruptive contrast’, it
143 was the contrast with background-matching colours on the animal that aided
144 concealment, regardless of whether these colours were common in the background or
145 not [18]. The contrasts were based on the double-cone response of a Blue Tit *Cyanistes*
146 *caeruleus* [19], calculated as in Stevens *et al.* [16].

147

148 (ii) Protocol

149 The first field experiment was conducted on 15th-26th January 2018 and the second on
150 5th - 31st March 2018, both in Brandon Hill Nature Reserve, Bristol, UK (51.4541° N,
151 2.6065° W), a hilly and grassy 1.81-hectare urban parkland inhabited by a variety of
152 avian predators such as Blue Tits (*Cyanistes caeruleus*), Great Tits (*Parus major*),
153 Eurasian Wrens (*Troglodytes troglodytes*), Common Chaffinches (*Fringilla coelebs*),
154 Common Blackbirds (*Turdus merula*) and European Robins (*Erithacus rubecula*).

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The first experiment had a 2×2 factorial design: treatment (Intact wings, Real holes) and substrate (Bramble – pinned to the petiole of bramble leaves; and Twig – pinned to an exposed, leafless twig of young hazel (*Coryllus alevana*), ash (*Fraxinus excelsior*), elder (*Sambucus nigra*), or birch (*Betula* sp.). We expected survival to be lower on exposed twigs, as the targets were not surrounded by similarly coloured leaves. The goal was to determine whether any effect of a hole was background dependent. There were 15 targets of each treatment*substrate combination per block, with three blocks each at different locations within the study site. The second experiment had 30 targets per treatment per block with 10 blocks in different locations within the study site. The substrate was bramble.

In both experiments, plants to which individual targets were pinned were selected haphazardly, as was the position and orientation of the targets; but target selection for any one plant was random (pulled from a plastic sealable bag in which all targets for a block had been shuffled). In each block, targets were put out between 9am and 10am and checks for predation were completed after 3, 6, 24, 27, 30, 48, 51 and 54 h. A target was said to have been predated when the mealworm was absent; data were treated as censored if the target could not be relocated, the target was found on the ground with either the mealworm or wings missing, the mealworm was subject to invertebrate predation (mainly slugs, visible on the target or leaving the paper chewed), or if the target survived to the end of the three-day study period. Targets that were predated were removed and, at the end of a block, all remaining targets were collected.

(iii) Statistical analysis

180 To take account of censoring, in both avian experiments survival analysis of ‘time to
181 predation’ was by mixed effects Cox regression using the ‘*coxme*’ package [20] in R
182 3.5.3 (R Core Team 2019), with block as a random effect and the fixed factors
183 treatment and substrate for the first field experiment, and treatment for the second field
184 experiment. The proportional hazards assumption of the method was checked by visual
185 inspection of partial residual plots against the ranked survival time [20]. Where
186 interactions were not significant, main effects were estimated by refitting models
187 without the interaction. The primary hypotheses of *a priori* interest were pair-wise
188 comparisons with the Real holes treatment, with p-values unadjusted because the
189 number of tests did not exceed the degrees of freedom [21]. The package ‘*multcomp*’
190 [22] was used for subsequent pair-wise *post hoc* comparisons of secondary interest,
191 using the Bonferroni method to control for multiple testing. The ‘*survival*’ package [23]
192 and ‘*RColorBrewer*’ [24] were used for plotting.

193

194 (b) Lab experiment on human detection performance

195 (i) Stimuli

196 So that we could assess the effect of target pattern while holding everything else in a
197 given visual scene constant, we used a chroma-key (blue screen) technique. Blue-
198 printed butterfly targets were prepared as per the methods for the first field experiment
199 and photographed *in situ* on bramble plants in the same field site as used for the bird
200 predation experiments. A third of the targets were uniform blue, a third blue with a real
201 hole, and a third blue with a pink patch of the same size and shape as the false holes in
202 the second field experiment, to allow digital replacement with different types of false
203 hole (see below). A total of 150 photographs were taken with a Nikon D3100 digital
204 SLR camera (Nikon Corporation, Tokyo, Japan), including an X-rite ColourChecker

205 Passport (X-Rite, Grand Rapids, MI, USA) for standardising image colours. The
206 lighting conditions were clear skies and bright sunlight.

207
208 A custom MATLAB R2017 script (The Mathworks Inc., Natick, MA, USA) was used
209 to identify the blue butterflies in photographs and replace this hue with ‘bramble green’,
210 whilst retaining cast shadow, changing gradations of tone, and partial occlusion by
211 vegetation (figure 2). Using the respective photographs, Plain and Real hole treatments
212 were produced. To replicate the Dark False hole and Pale control treatments from the
213 second experiment, shades of grey from that experiment replaced the pink markings. To
214 create an additional false hole treatment (henceforth ‘synthetic’), digitally selected
215 patches of adjacent bramble background were pasted into the pink hole marking. If
216 hole-mimicry is the function of dark wing patches, we predicted that a pattern that
217 depicts background vegetation should be even more effective as camouflage. We
218 therefore had five treatments of 25 images each.

219
220 (ii) Participants and Procedures

221 The experiment was performed by 20 male and 20 female participants, and one
222 participant who did not wish to identify as either male or female. The experiment was
223 run after participants had read generic instructions (‘find the hidden butterfly’) and
224 completed a consent form in accordance with the Declaration of Helsinki. All
225 participants were either postgraduate students or staff from the University of Bristol,
226 and all were naïve to the design of the experiment. The experiment was carried out in a
227 dark room using a laptop computer (MacBook Pro; Apple Inc., Cupertino, CA, USA),
228 running a control program written in MATLAB using the Psychtoolbox library
229 (Psychophysics Toolbox Version 3; [25]; <http://psychtoolbox.org>). Participants were
230 seated approximately 50 cm from an external display screen, which was a linearized

231 (gamma-corrected), 22", 1024 x 768 pixel LaCie Electron 22Blue CRT monitor (LaCie
232 Ltd., London) with a refresh rate of 100 Hz and a mean luminance of 72 cdm⁻².

233
234 Five practice images were presented to each participant, one randomly selected from
235 each treatment. This practice stage was followed by five experimental blocks of 25
236 images. A mid-grey screen with a black fixation cross in the centre was displayed
237 before each trial to focus the attention of the participant. Once the target had been
238 selected using the trackpad's cursor, the next fixation cross and image was presented.
239 Each image had a 60 s time-out. The program presented images from the five treatments
240 to participants in an order separately randomised for each participant. Between blocks
241 participants had the option to take a short break, or to continue straight through to the
242 next block. None of the participants took breaks lasting more than 2 min.

243
244 (iii) Statistical Analysis
245 In the third experiment, accuracy was analysed by calculating the centre of a rectangle
246 enclosing the target; a 'hit' was classed as a trackpad click within 5% of the perimeter
247 of this rectangle. The percentage of misses, at just 2.6 % across all trials, was too low to
248 analyse (models did not converge). This indicates that almost all the variation in
249 performance was captured by the response times. Prior to analysing the latter, one
250 'impossible' value was removed (< 0.1 ms, the 'false start' criterion in an Olympic
251 sprint). Inverse transforming the times normalised residuals from Linear Mixed Models
252 fitted using the R package '*lme4*' [26], with fixed effect treatment and random effect
253 participant. Subsequent pair-wise comparisons used the Tukey method in the
254 '*multcomp*' package [22].

255

256 **3. Results**

257 (a) Field experiment 1

258 The presence of holes in the ‘wings’ of the targets significantly lowered mortality
259 compared to intact wings, irrespective of the background substrate (figure 3;
260 treatment*substrate interaction: $\chi^2 = 0.52$, d.f. = 1, $p = 0.470$; main effect of holes: odds
261 ratio = 0.65, $\chi^2 = 6.15$, d.f. = 1, $p = 0.013$). There was also an increased chance of
262 predation when attached to twigs versus brambles (odds ratio = 1.46, $\chi^2 = 4.78$, d.f. = 1,
263 $p = 0.029$).

264

265 (b) Field experiment 2

266 Treatments differed significantly (figure 3; $\chi^2 = 141.25$, d.f. = 3, $p < 0.001$) with the Real
267 hole treatment having lower mortality than the Intact (odds ratio 0.53, $z = 5.45$, $p <$
268 0.001) and Pale controls (odds ratio 0.30, $z = 10.68$, $p < 0.001$), but similar survival to
269 False holes (odds ratio 0.79, $z = 1.89$, $p = 0.207$). False holes had lower mortality (odds
270 ratio 0.67, $z = 3.61$, $p = 0.001$) and Pale controls higher (odds ratio 1.77, $z = 5.80$, $p <$
271 0.001) than Intact wings. Although there is no significant difference between Real and
272 False holes, the 95% confidence intervals for the odds ratio indicates that the survival
273 benefit conferred by False holes is between 62% worse and 1% better than Real holes.

274

275 (c) Lab experiment on human detection performance

276 Response times differed significantly (figure 4; $\chi^2 = 1185.1$, d.f. = 4, $p < 0.001$) with
277 significant differences in the mean response times of all treatments (Tukey tests, all $p <$
278 0.001), apart from synthetic vs real hole ($z = 1.35$, $p = 0.660$). The Real hole and
279 Synthetic hole treatments were the slowest to be detected, followed by Plain wings and
280 then Dark false holes, with Pale controls the most rapidly detected.

281

282 **4. Discussion**

283 Over a century after the first speculations about the function of false holes were made
284 by Poulton [6], we present the first empirical evidence that these types of markings
285 provide a significant survival advantage through reduced detectability. Our model
286 ‘butterflies’ were not modelled on a real species but, if they had been, any reduced
287 predation on real and false hole treatments could have been due to dietary conservatism
288 [28]. This is still a possibility, although rendered less likely by the fact that the Pale
289 control treatment was readily consumed. There are no bramble-green butterflies with
290 light colour patches in the Bristol region [28].

291
292 The first field experiment indicates that real holes in the wings of background matching
293 butterfly-like prey reduce predation by approximately 35% and although,
294 unsurprisingly, an exposed position increased predation risk compared to location
295 among brambles, holes had similar effects on both substrates. Clearly, real holes in a
296 butterfly’s wing would negatively affect flight, but the second experiment demonstrates
297 that false holes are almost as effective when it comes to reducing predation. We next
298 discuss possible mechanisms behind this effect, and compare the results from avian and
299 human experiments.

300
301 The second field experiment showed that real holes and dark patches of the same shape
302 and location led to reduced mortality compared to plain intact wings, whereas pale
303 patches led to increased mortality. This suggests that false holes are not effective by
304 virtue of contrast with the green base colour alone, as might be the case if the
305 mechanism was attraction of attention and distraction from the true outline or shape of
306 the target [13,17,29-31]. Instead, a parsimonious explanation is that false, and real,
307 holes act as surface disruptive coloration, disguising the wing surface continuity
308 through creation of false internal edges [13,32]. In principle, contrasting pale holes

309 could act this way too, through maximum disruptive contrast [13], lateral inhibition or
310 contour capture [30] but, as has been shown for edge-disrupting camouflage [18,33],
311 this would be undermined if the disruptive colour patches themselves attracted attention
312 by virtue of being colours rare in the background.

313
314 The term ‘false holes’ might imply that false depth cues are important. Such cues break
315 up the continuity of the wing surface into multiple depth planes, encouraging incorrect
316 perceptual segregation [13,30,34]. However our results do not allow such an inference.
317 Manipulations such as edge-enhancement around the false hole [13,34,35] would be
318 informative here because, like Cott [13], we consider surface disruption to be the most
319 plausible explanation for the anti-predation benefits of false holes of the type
320 investigated here. Masquerade is another possible function of false holes when
321 combined with leaf mimicry, and the likelihood would increase if damaged leaves were
322 either more common than undamaged or, for other reasons, birds classified damaged
323 leaves as less likely to be leaf-mimicking insects than intact leaf-like objects [4].
324 However, as there is some evidence that birds use leaf damage as a cue for the presence
325 of insects [10,11], this would be a cost rather than a benefit of hole-mimicry.

326
327 When comparing the results of the computer-based search task using human
328 participants and the second avian predation field experiment, we observe some
329 differences in the relative survival of treatments. In both sets of experiments the
330 presence of real holes conferred significant survival benefit relative to targets with
331 intact wings, and pale control markings in the wings led to the highest levels of
332 predation and detection. However, in the computer experiment, while ‘false holes’ in
333 terms of the ‘synthetic’ treatment (cutting and pasting of background elements into the
334 ‘hole’) were as effective as real holes, dark false holes were not (despite being highly

335 effective in the avian predation experiments). The differences seen in the results most
336 likely reflect the differences in the tasks: whilst the human experiments solely measured
337 detection under focused attention for a narrow range of target types, the avian predators
338 were seeking multiple prey types. Participants in the human experiments, on debriefing,
339 reported that they found themselves “looking for the hole”, as 80% of presented images
340 possessed the ‘hole’ shape (dark, pale, real or synthetic hole treatments) and only in the
341 intact wings treatment was this shape absent. While the background seen through real
342 holes, and the background pasted into synthetic holes, differed for every single
343 replicate, all dark false holes had identical homogeneous coloration, so this pattern was
344 easier to learn in the, highly constrained, human experiment. Birds, seeking multiple
345 prey types (most of which were unlike our targets), and with multiple interruptions to
346 foraging, would not have had the same opportunity to learn such tactics. Conversely,
347 unlike humans in the computer experiment, birds in the field may have additional cues
348 to depth, from parallax and stereopsis, which would limit the effectiveness of false
349 holes at close range.

350
351 Empirical research of disruptive theory has previously focused on marginal markings,
352 with much less investigation into the protective benefits that can be provided by
353 internally placed markings [32,36]. Although false holes remain logically distinct from
354 other centrally placed markings, e.g. eye spots and distractive markings [8,17,31], our
355 results add weight to the support of Stevens *et al.* [32] for Cott’s [13] proposition that
356 other non-marginal markings can also achieve a significant disruptive effect. This
357 remains true whether ‘false holes’ are perceived by birds as holes or not, something that
358 awaits further investigation.

359

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363 **Ethics**

364 Experiments approved by the University of Bristol Animal Welfare and Ethical Review

365 Body (birds) and the University of Bristol Faculty of Science Research Ethics

366 Committee (humans).

367

368 **Data accessibility**

369 Raw data can be accessed from the Dryad data repository at [[doi to be added](#)].

370

371 **Authors' contributions**

372 ICC and LMC conceived the project; ICC, NSS and LMC designed the experiments;

373 ICC and LMC produced the stimuli; NSS and ICC wrote the programs for the blue-

374 screening and human experiment; LMC carried out the experiments, with the help of

375 ICC and KK. LMC wrote the first draft of the ms, with contributions from all authors.

376 All authors gave final approval for publication and agreed to be accountable for all

377 aspects of the content therein.

378

379 **Competing interests**

380 We have no competing interests.

381

382 **Funding**

383 This research was supported by the Engineering & Physical Sciences Research Council

384 UK, grant EP/M006905/1 to NSS, ICC and R.J. Baddeley.

385 **Acknowledgments**

386 Thanks to Benito Wainwright and Kelly Ray for help during field experiments, and to
387 CamoLab for useful discussion. John Skelhorn and two other, anonymous, referees
388 provided many constructive comments that helped improve the manuscript.

389

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- 466

Figures



468

469 **Figure 1** Examples of false holes found in Lepidoptera and Anura respectively. Top Left:

470 *Siculodes aurorula* (Thyrididae) © Photo courtesy of Marcos Cesar Campis, Morro

471 Agudo, Brazil. Bottom Left: *Siculodes aurorula* (Thyrididae) © Photo courtesy of Pavel

472 Kirillov, Comadre, Limon, Costa Rica; Top and Bottom Right: *Rhinella margaritifera*,

473 Crested Forest Toad, © Photo courtesy of John Sullivan/Ribbit Photography, Madre Selva

474 Biological Station, Loreto, Peru.

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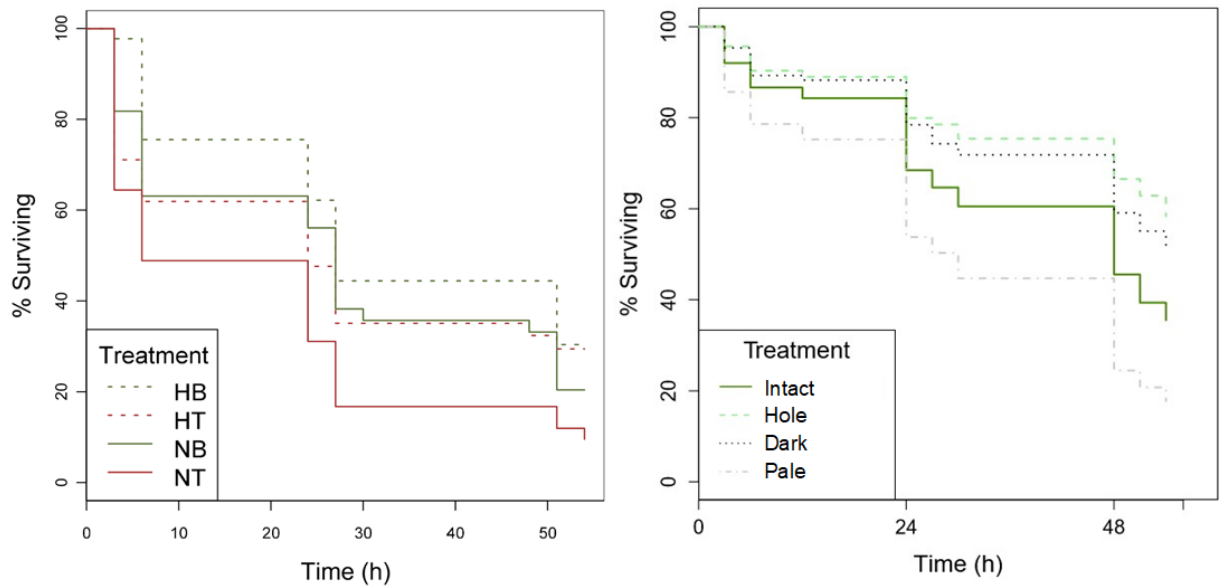


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478 **Figure 2** Left: target dimensions, illustrated with a Pale control treatment; the holes were
 479 absent for the intact wings treatment. The approximate point of pin insertion is indicated
 480 (•) on the midline. Distances A (between centre points of each hole) and B (between the
 481 centre point of each hole to the midline) were always consistent. Right: (a) Blue target in
 482 situ; (b) blue replaced with ‘bramble green’ by means of chroma-key to form an Intact
 483 treatment; (c) Real hole; (d) Pale control; (e) dark false hole; (f) Synthetic false hole.
 484 Panels (c) to (f) are close-ups; the image size in the human experiment was as in (b).

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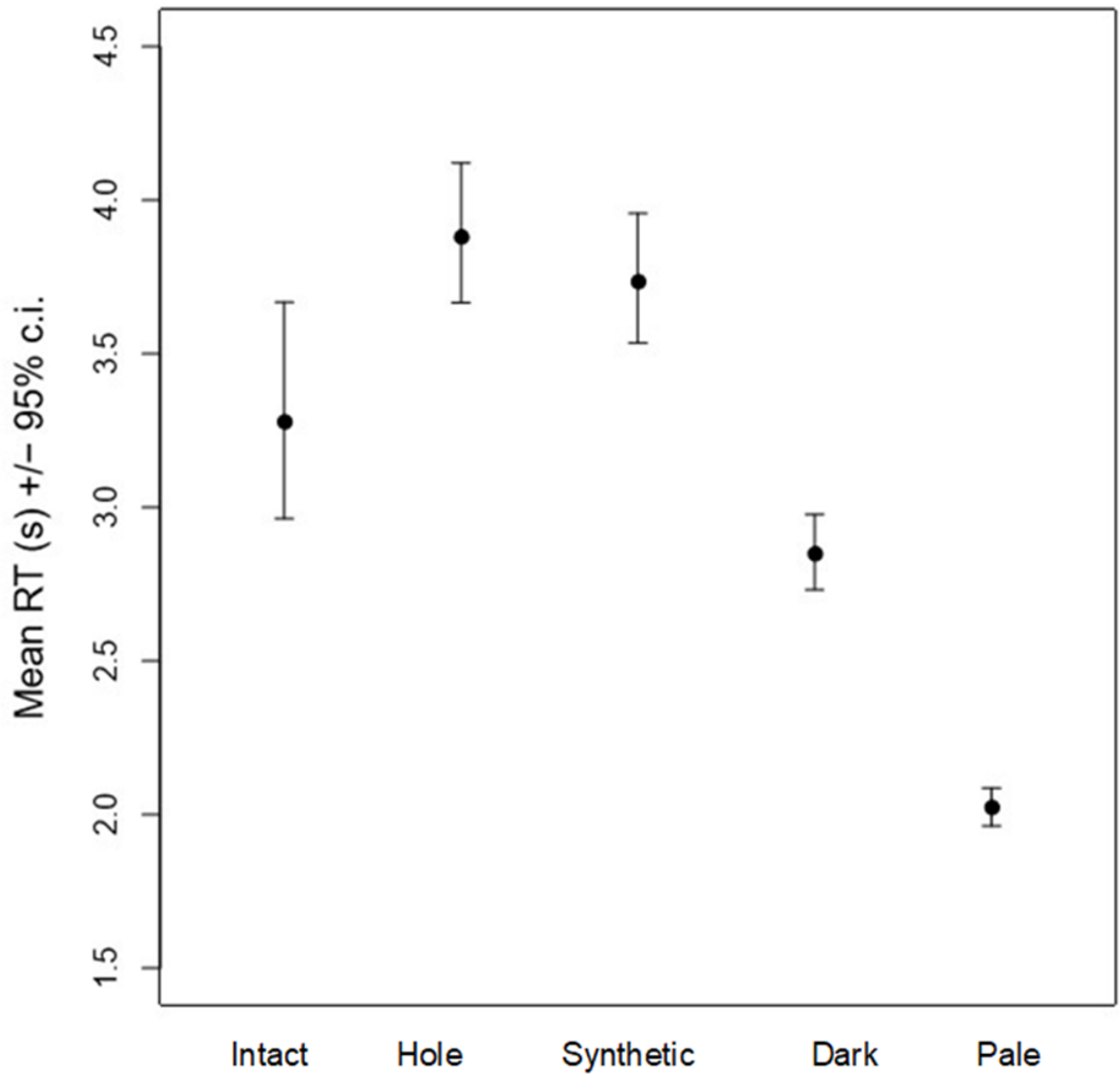


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488 **Figure 3** The left-hand plot shows, for the first field experiment, survival on each
 489 substrate (top to bottom: wings with holes on bramble (HB), wings with holes on twigs
 490 (HT), intact wings on bramble (NB), and intact wings on twigs (NT)). The right-hand
 491 plot shows survival in the second field experiment, for the four treatments (Intact wings,
 492 Real holes, Dark false hole, and Pale false holes) on a bramble substrate. The curves
 493 indicate the probability of avoiding bird predation as a function of time over a three-day
 494 period (54 h), based on Kaplan–Meier estimates to account for incomplete data due to
 495 censoring. Long periods of stasis (8+ h) with no changes in survival probability
 496 corresponds to hours of darkness when targets were not checked.

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500 **Figure 4** Mean (\pm 95% c.i., based on fitted GLMMs) reaction times (in seconds) by
501 human participants in the lab experiment. Greater reaction times indicate increased
502 difficulty of detection and hence more effective target camouflage.

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