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1 **AUTHORS' ACCEPTED COPY**

2
3 **Background complexity can mitigate poor camouflage**

4
5 Zeke W. Rowe^{1*}, Daniel J. D. Austin¹, Nicol Chippington¹, William Flynn¹, Finn Starkey¹,
6 Edward J. Wightman¹, Nicholas E. Scott-Samuel² and Innes C. Cuthill¹

7
8 ¹ School of Biological Sciences, University of Bristol, Life Sciences Building, 24 Tyndall
9 Avenue, Bristol BS8 1TQ, United Kingdom

10 ² School of Psychological Science, University of Bristol, 12A Priory Avenue, Bristol BS8 1TU,
11 United Kingdom

12 * Corresponding author: zr17137@bristol.ac.uk

13
14 ORCID: ZWR: 0000-0002-9617-5539

15 NESS: 0000-0002-8270-8437

16 ICC: 0000-0002-5007-8856

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28 **Abstract**

29 Avoiding detection through camouflage is often key to survival. However, an animal's
30 appearance is not the only factor affecting conspicuousness: background complexity also
31 alters detectability. This has been experimentally demonstrated for both artificially
32 patterned backgrounds in the lab and natural backgrounds in the wild, but only for targets
33 that already match the background well. Do habitats of high visual complexity provide
34 concealment to even relatively poorly-camouflaged animals? Using artificial prey which
35 differed in their degrees of background matching to tree bark, we were able to determine
36 their survival, under bird predation, with respect to the natural complexity of the
37 background. The latter was quantified using low-level vision metrics of feature congestion
38 (or 'visual clutter') adapted for bird vision. Higher background orientation clutter (edges
39 with varying orientation) reduced the detectability of all but the poorest background-
40 matching camouflaged treatments; higher background luminance clutter (varying
41 achromatic lightness) reduced average mortality for all treatments. Our results suggest that
42 poorer camouflage can be mitigated by more complex backgrounds, with implications for
43 both camouflage evolution and habitat preferences.

44

45 **Key words:** background complexity, camouflage, detectability, visual search, protective
46 coloration, visual clutter

47

48 **1. Introduction**

49 Remaining undetected is frequently important for a number of reasons, including predator-
50 prey interactions, avoiding social harassment, and seeking sneak mating opportunities [1].
51 Camouflage is the most widespread means of achieving concealment 'in plain sight',
52 arguably the most critical factor being the similarity of the object's colour and pattern to
53 that of its immediate background [2-5]. However, a factor extrinsic to the camouflaged
54 object also affects its concealment: background complexity [6-10]. Merilaita [6] argued,
55 based on results from neural network models, that the visual complexity of the background
56 is a key determinant of detectability, and that higher background complexity relaxes the
57 requirement for precise background matching. He proposed that this is because more
58 complex backgrounds impose higher information-processing costs, and that predators are
59 limited in their processing capacity; we return to this issue in the Discussion. Analogously,
60 the effect of many, highly salient, visual features in the background, known as 'visual
61 clutter', has been investigated in humans in applied contexts such as visual display design
62 [11, 12], and also in a few other species. First, by monitoring predation on artificially
63 patterned backgrounds by birds or fish [7-9] and second, by measuring wild avian predation,
64 and human visual search, for artificial targets against natural backgrounds [10]. Although
65 these studies demonstrate a detrimental effect of background complexity on detection,
66 they do not tell us how important it is relative to matching the background. Somewhat
67 surprisingly, Xiao & Cuthill's [10] experiment suggested that, for birds, background

68 complexity was far more important than matching the immediate background. A key
69 limitation of Xiao & Cuthill [10] is that the effect of background complexity was
70 demonstrated for only a single target colour: that of the average background. This leaves
71 open the question of whether the benefits of background complexity for concealment are
72 independent of background matching, as Merilaita [6] suggested, or whether some level of
73 background matching is required. Murali et al. [13] have addressed this question using
74 humans searching on artificial backgrounds, concluding that background heterogeneity aids
75 concealment, but not when the targets fail to match the background. However, whether
76 such effects apply to non-human predators in the field, and the sort of complexity variation
77 seen in natural backgrounds, need to be addressed. Our present study fills that gap, by
78 systematically varying the degree of background matching and establishing the limits of
79 background complexity's ability to impede detection by wild predators searching on natural
80 backgrounds in the field.

81 Here, we determine the extent to which background complexity can mitigate poor
82 camouflage. Understanding the interaction between conspicuousness and background
83 complexity is important for two main reasons: the first is to understand what pattern of
84 camouflage evolution will be favoured in different habitats [6]; the second is to understand
85 which habitats animals prefer if complexity does indeed decrease detection [9]. Most
86 habitats are heterogenous in colour and pattern, and many animals move between visually
87 different habitats. So an open question is whether it is better to have coloration that is a
88 compromise between different backgrounds, or specialised to one [6, 14-16]. Modelling
89 suggests that a critical factor is the trade-off between improved survival on one background
90 and reduced survival on another [15, 17]. Background complexity will affect that trade-off if
91 it mitigates any mismatch of specialist camouflage to alternative backgrounds, and of
92 compromise strategies to all backgrounds. Furthermore, animals benefiting from
93 concealment could potentially select backgrounds with higher complexity [9] and those
94 benefiting from salience (for signalling) could select habitats with lower complexity [18].

95 By monitoring the survival of artificial prey 'moths' in natural woodland, we examined the
96 effect of natural levels of background complexity ([as in 10]) on the survival of different
97 degrees of background matching ([as in 19]). By recording the frequency of colours across a
98 large sample of European oak tree (*Quercus robur*) bark within the woodland, we produced
99 treatments which spanned the background luminance frequency distribution. This allowed
100 us to test whether higher background complexity interferes with detection of all targets
101 regardless of how well they match the background, or whether complexity cannot mitigate
102 poor camouflage. We predicted that high background complexity would only reduce
103 detectability for targets that already match the background well. By manipulating one
104 simple feature, the average luminance or achromatic lightness, that is known to influence
105 the salience of camouflaged objects in our experimental paradigm [20], we sought to
106 determine just how mismatched the target needs to be to the background for complexity to
107 cease to affect detectability. Whether the effect is sudden or continuous is an empirical
108 question that our experiment should help address. To measure background complexity we
109 used feature congestion [11, 12], which is based on features from the early stages of visual
110 processing, namely variation in luminance, colour and edge orientation. It has been shown

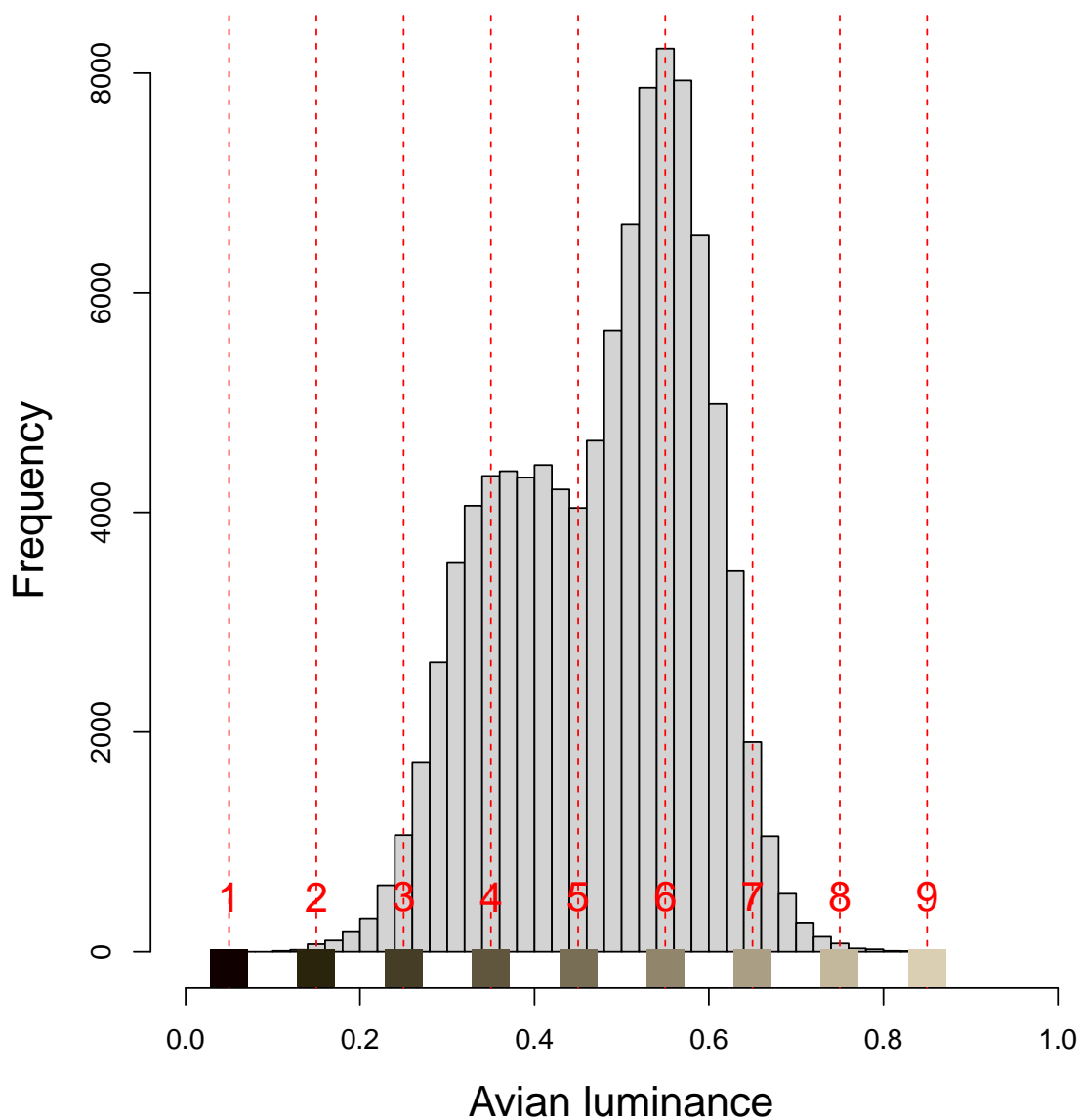
111 to predict interference in both human and bird search [10, 11]. For avian colour vision, we
112 used Xiao & Cuthill's [10] adaptation of the model of Rosenholtz *et al.* [11, 12].

113

114 **2. Material and methods**

115 **(a) Stimuli**

116 The targets were designed to resemble a non-specific Lepidopteran: right-angle triangles at
117 45 mm wide × 32 mm high. Nine treatments were produced, all having the average hue of
118 oak bark but varying in achromatic lightness. The colour information was derived from 1000
119 calibrated photographs of oak tree bark, taken in the same woods as the experiment was
120 carried out in (Leigh Woods National Nature Reserve, North Somerset, UK, 2°38.6' W,
121 51°27.8' N) the previous year. Photographs were taken at head height, approximately one
122 metre away from the oak trees, of areas of bark that were free from lichen and not in direct
123 sunlight. The camera was a Nikon D3200 DSLR camera with 35 mm Nikon AF-S DX NIKKOR
124 f/1.8G lens (Nikon Corp., Tokyo, Japan), set at ISO 1600, f8 and automatic integration time.
125 A colour standard, Colorchecker Passport (XRite, Grand Rapids, Michigan, USA), was pinned
126 to the trees in the bottom left-hand corner of the frame for later calibration (as in [21, 22]).
127 These photographs were linearised and normalised to control for variation in light intensity
128 and colour balance, and then mapped to the cone photon-capture colour space of a typical
129 passerine predator, using cone spectral sensitivity data for the blue tit (*Cyanistes caeruleus*)
130 [23]. The procedures were carried out using custom MATLAB scripts (MATLAB 2019b, The
131 MathWorks, Natick, MA, USA), using the same procedures as described in [22, 24] and see
132 Supplementary Material. One hundred random target-sized samples were taken from each
133 photograph (the xy coordinates being pairs of random numbers drawn from a uniform
134 distribution), and the average colour for each was calculated. The measure of lightness was
135 the photon catch of the avian double cones [25], scaled from 0 (black) to 1 (white), and two
136 opponent channels to represent the relevant variation in hue: red-green (the contrast
137 between mediumwave- and longwave-sensitive cones) and blue-yellow (the contrast
138 between shortwave- and the average of mediumwave- and longwave-sensitive cones), both
139 also scaled to lie between 0 and 1 ([for further details see 10]). Neither oak bark nor the
140 printed targets reflected ultraviolet, so this component of avian colour could be ignored [for
141 bark reflectance spectra see 26]. The 'avian luminance' of the 100,000 samples ranged
142 between 0.07 and 0.85, and had two modes (Figure 1). The treatments of 0.05, 0.15, 0.25,
143 0.35, 0.45, 0.55, 0.65, 0.75, 0.85 luminance units were chosen to span the range from
144 exceedingly rare and dark to exceedingly rare and light, with treatments also approximating
145 the two peaks and the trough between them (Figure 1). Validation of the intended
146 manipulation of target-background contrast is provided in the Supplementary Material. All
147 treatments had the same red-green and blue-yellow contrasts (0.013 and -0.155
148 respectively), matching the average of the 100,000 bark samples, so they varied in
149 tone/lightness but not hue. These targets were printed on waterproof paper (Rite-in-the-
150 Rain, J.L. Darling LLC, Tacoma, WA, USA) using a calibrated printer (Canon imageRUNNER
151 ADVANCE C5535i; Canon Inc., Tokyo, Japan).



152

153 **Figure 1-** A histogram showing the frequency of the avian luminance of 100,000 oak tree
 154 (*Quercus robur*) bark samples. The red dotted lines show where on the distribution the
 155 treatment luminance values fall, with the darkest designated as treatment 1 and the lightest
 156 as 9.

157 **(b) Procedure**

158 The experiments were run from October to December 2020. The general experimental
 159 protocol followed that of Cuthill *et al.* [27], with the artificial ‘moths’ pinned to mature oak
 160 trees along non-linear transects with a dead mealworm (*Tenebrio molitor*) larva frozen at
 161 -80°C then thawed) underneath the ‘wings’, with a small portion showing. Each transect
 162 comprised a block within an overall randomised block design. The transects varied in length
 163 from ca 500 to 1000 m, according to variation in oak tree density within different areas of
 164 the woodland. The meandering nature of the transects would make them hard to define in
 165 terms of area, but they did not overlap each other. Younger oak trees (trunk circumference

166 at head height < 0.9 m) were avoided, with no more than one target per tree, pinned at
167 roughly head-height, facing away from paths to minimise interference from the public. Once
168 pinned, a photograph was taken of the target and its respective background; four mobile
169 phones were used, two of which were iPhones (iPhone 8 and 11, Apple Inc., Cupertino, CA,
170 USA) and two of which were Samsungs (Samsung SM-A405FN and SM-G970F, Samsung
171 Group, Seoul, South Korea). The known size and reflectance of the target, coupled with
172 calibrations based on photographs of a colour chart (Colorchecker Passport; X-Rite, Grand
173 Rapids, MI, USA), were used to normalise and linearise the photographs, then map them to
174 avian colour space. These photos were then used to extract the same measures of
175 background complexity as in Xiao & Cuthill [10], using Rosenholtz's principles of feature
176 congestion [11, 12]. The calculations were carried out using the custom MATLAB scripts
177 described and explained in [24], based on the original Matlab functions of Rosenholtz and
178 colleagues (<https://dspace.mit.edu/handle/1721.1/37593>). Rosenholtz *et al.*'s "feature
179 congestion" can be thought of as a perceptual measure of the variation in three
180 components of a visual scene: luminance, colour and edge orientation. A scene with high
181 levels of local contrast in brightness will score highly on the luminance clutter measure;
182 analogously, spatial variation in colour contributes to the colour clutter metric, and variation
183 in the orientation of edges (lines) contributes to the orientation clutter metric. "Local
184 contrast" is in fact calculated at three spatial resolutions (i.e. capturing variation in each of
185 coarse, medium, and fine detail) and summed to provide a single measure of each of what
186 Rosenholtz *et al.* [11, 12] call contrast (luminance), colour and edge orientation 'clutter'. The
187 feature congestion metric is a weighted sum of the three, based on empirically derived
188 estimates of the contribution of each to perceived differences. Xiao & Cuthill [10] showed
189 that the orientation clutter measure of perceived image complexity, and an equivalent for
190 avian vision, predicted the detectability of triangular (notionally moth-shaped) targets on
191 natural bark backgrounds, for humans and birds respectively. The supplementary material
192 of Xiao & Cuthill [10, 24] has a figure that, in a simple intuitive way, demonstrates how the
193 Rosenholtz *et al.* clutter metrics relate to image features.

194 Targets were checked at 24, 48, 72 and 96 h, with disappearance of all or most of the
195 mealworm being marked as avian predation, and predation by invertebrates (spiders, slugs,
196 wasps) and 'survival' up to 96 h being marked as 'censored'. Invertebrate predation was
197 determined by either direct observation (one instance of a wasp), a hollowed-out
198 exoskeleton (spiders) or the presence of mucus near the target (slugs). The large sample size
199 that our method allows precludes direct observation of most predation events, so we
200 cannot be certain that birds were responsible for all events scored as bird predation.
201 However, one would expect birds to be the predominant visual predator for such prey in
202 winter in UK woodland, and non-visual predators would only add noise to our data. In each
203 block, 90 targets were placed (10 replicates of each of the nine treatments). Overall, 27
204 blocks were completed, totalling 2,430 targets.

205 (c) Analysis

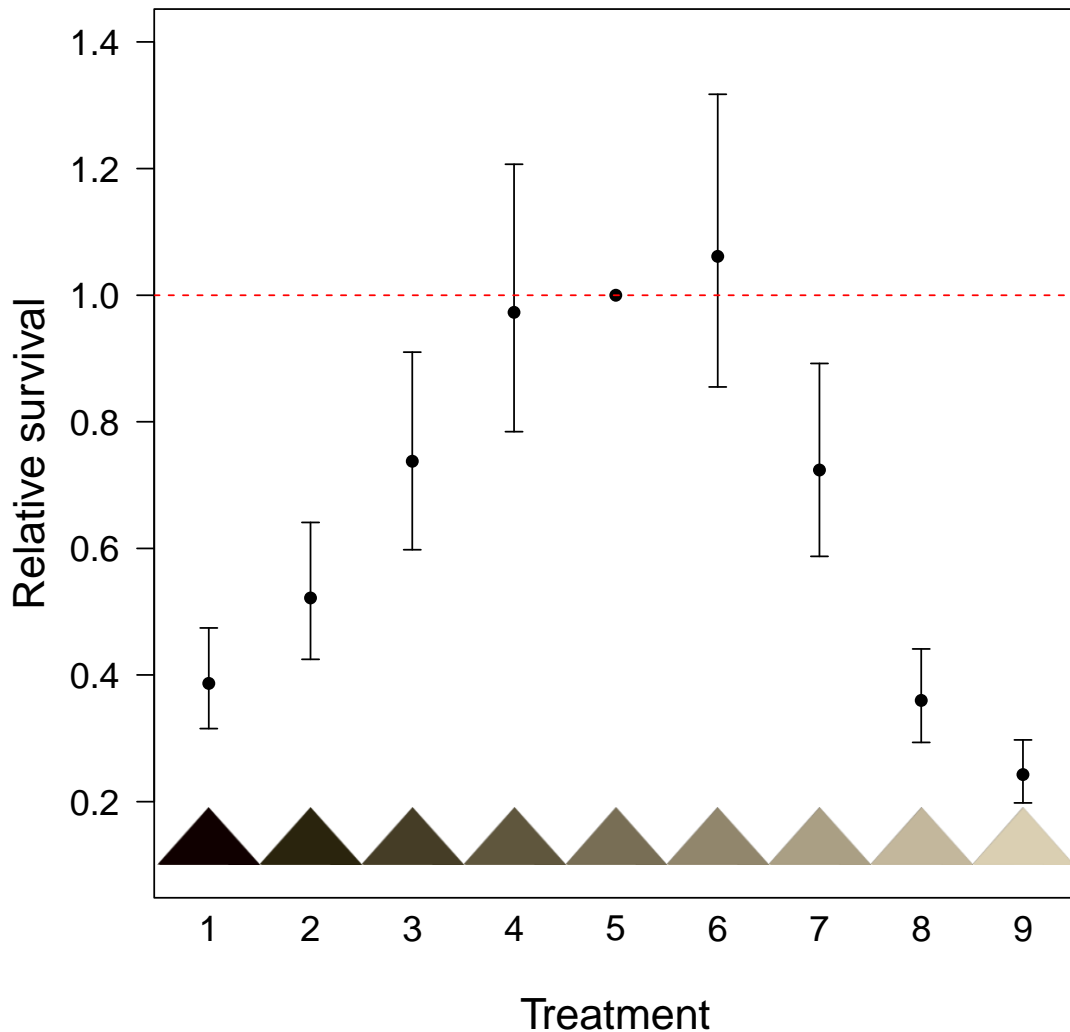
206 Mixed-effects Cox regression was applied using the 'coxme' function from the 'coxme' R
207 package (Therneau, 2020; R Core Team, 2020). Block was fitted as a random effect,

208 treatment and the three metrics of feature congestion of the background were treated as
209 fixed effects. The significance of effects were tested using an analysis of deviance comparing
210 the unexplained variation of models with and without the factor in question, tested against
211 a χ^2 distribution. Starting with a maximal model including interactions between treatment
212 and each of the feature congestion metrics, models were step-wise simplified based on non-
213 significance of terms. Effect sizes are presented as odds ratios with 95% confidence
214 intervals. Treatment 5 was chosen as the baseline for comparison with other treatment
215 levels, as this lay close to the mean of the whole distribution (0.48; see also Figure S1 in the
216 Supplementary Material) and was also close to the luminance of the single treatment used
217 in Xiao & Cuthill [10].

218 **3. Results**

219 Overall, 27% of targets were censored (8.6% eaten by spiders, 6.6% by slugs, 3.3% lost, and
220 8.7% remained uneaten after 96 h). The main effect of treatment, ignoring background
221 complexity, affects target mortality in a pattern that loosely mirrors the frequency of each
222 luminance in the background ($\chi^2 = 376.41$, d.f. = 8, $p < 0.001$; compare Figure 2 with Figure
223 1). Targets which have a more common background shade (treatment 2 to 7) have a lower
224 relative mortality than rarer shades.

225

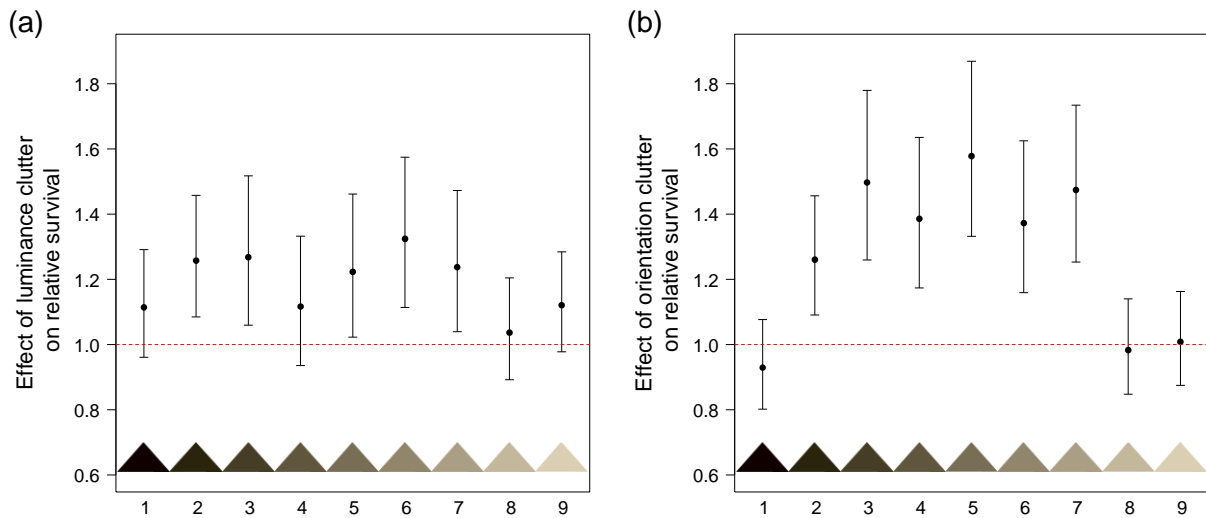


226

227 **Figure 2-** More common background shades have enhanced survival. Odds ratio plot for the
 228 relative survival of each treatment compared to treatment 5, which lies near to the mean of
 229 the whole distribution. Treatments with 95% confidence intervals not overlapping the red
 230 dashed line have a lower relative survival (< 1) than treatment 5. Odds ratios and 95%
 231 confidence intervals (bars) were estimated using a mixed-effects Cox regression.

232 We then examined how the metrics of background complexity altered the survival of the
 233 targets; all steps in the statistical modelling can be found in the Supplementary Material.
 234 There was no significant interaction between treatment and colour clutter ($\chi^2 = 5.09$, d.f. =
 235 8, $p = 0.748$), treatment and luminance clutter ($\chi^2 = 10.05$, d.f. = 8, $p = 0.262$), or a main
 236 effect of colour clutter ($\chi^2 = 0.00$, d.f. = 8, $p = 0.979$). However, the interaction between
 237 treatment and orientation clutter and the main effect of luminance clutter remained in the
 238 minimal adequate model ($\chi^2 = 57.04$, d.f. = 8, $p < 0.001$ and $\chi^2 = 22.89$, d.f. = 1, $p < 0.001$,
 239 respectively). Survival was higher with greater luminance clutter (odds ratio 0.866, 95% c.i.
 240 0.818 to 0.918). The effect of orientation clutter was also found to boost survival, but only

241 for those treatments with commoner background shades (treatments 2 to 7), with no
 242 significant effect for the treatments representing very rare shades, both dark (1) and light
 243 (8, 9); see Figures (3a,b).



244
 245 **Figure 3-** Odds ratios of the effect of (a) luminance clutter and (b) orientation clutter on the
 246 relative survival of the treatments. Background complexity only enhances survival for
 247 targets that match the background to some degree (treatment 5 is close to the average
 248 background luminance, with treatment 1 much darker, and treatments 8 and 9 much
 249 lighter, than any background colours). The red dotted line signifies no effect (= 1); data
 250 above the line has a higher relative survival on more complex bark (> 1). Odds ratios and
 251 95% confidence intervals were estimated using a mixed-effects Cox regression.

252 4. Discussion

253 Our results support Merilaita's [6] conclusion, based on neural network modelling, that
 254 background complexity has an important influence on detectability, and that higher
 255 background complexity enhances the benefits of background-matching camouflage. When
 256 examining the three visual characteristics of feature congestion (luminance, colour, and
 257 orientation of edges), we found that two of them had a significant effect on predation rates.
 258 A higher background orientation clutter reduced the detectability of all but the rarest
 259 background-matching camouflaged treatments (treatment 1, 8 and 9) (Figure 3b). With
 260 regards to a higher background luminance clutter, there was also a pattern of lower
 261 mortality (Figure 3a). This effect was similar to, but weaker than, that seen with orientation
 262 clutter, but with no detectable treatment-by-background interaction. Therefore, unlike
 263 orientation clutter, we cannot confidently conclude that the concealment benefits of high
 264 background luminance contrast disappear for rarer background matching samples. The
 265 effect of orientation clutter has been previously found in experiments involving humans and
 266 wild birds [10]. Although luminance clutter was not significant in that study, we note that
 267 our sample size was an order of magnitude greater, so capable of detecting smaller effects.
 268 We make no claims that orientation clutter will be the most important factor in all
 269 situations; oak bark is characterised by deep linear ridges, and our targets have linear edges,
 270 so an effect on the signal-to-noise ratio in the domain of edge detection is expected. Oak

271 bark also has low chromatic variation (mainly different shades of brown), so it will be
272 interesting to carry out analogous experiments with backgrounds, and targets, with
273 different chromatic and structural characteristics.

274 A corollary of background complexity aiding concealment is that background complexity
275 mitigates less-than-perfect camouflage [6]. Targets which are matched to at least some of
276 the background are less detectable on visually complex backgrounds than those on
277 backgrounds of lower complexity. These findings have implications for habitat selection and
278 thus animal distributions. If an animal benefits from concealment, all things being equal, it
279 should choose a complex background [9]. Conversely, those benefiting from
280 conspicuousness (e.g. to convey a visual signal) should choose to be seen against a less
281 complex background to maximise their saliency [28]. Habitat choice with respect to habitat
282 complexity could be an effective means of changing the balance between salience and
283 crypsis [29], with different costs and benefits from changing appearance per se. We also
284 found that the rarest background shades were little affected by the complexity of the
285 background. Background complexity does not mitigate a very poor match to the
286 background.

287 Moving beyond the effect of background complexity, on average the treatments with more
288 common background shades survived better than rarer shades (Figure 2). This is expected
289 as, all things being equal, the best camouflage strategy is expected to be the most probable
290 background sample [19]. Settling at random (as in our experiment), a common sample has a
291 higher chance of being against a background that is a similar colour to itself, reducing
292 detectability. In our data, survival generally matched the peaks in background luminance
293 (Figures 1 and 2), although there was no detectable dip in survival in treatment 5 compared
294 to 4 and 6, as might be expected from the bimodal luminance distribution (Figure 1). This
295 could be a lack of statistical power (although our sample size was large, the benefits of a
296 precise match to the background may be small), or an example of where there is an
297 advantage to a 'compromise' strategy intermediate between the two modal background
298 shades [14, 15, 17, 30].

299 In summary, the experiments of Murali *et al.* [13], for humans searching on artificial
300 backgrounds, and our findings – using natural backgrounds – suggest that background
301 complexity alters the detectability of background-matched targets. This is true even for
302 those targets which have relatively poor, but not the poorest, background matching. This
303 suggests that visual complexity can play a role in the evolution of camouflage in
304 heterogenous environments [6] and can mitigate the costs of a poorer match. One caveat is
305 that none of our targets were maximally cryptic (all lacked patterning) and tree bark is
306 relatively homogeneous in comparison with other natural substrates (e.g. leaf litter); it
307 would be of interest to see if similar trends obtain for such environments. Animals could
308 also make habitat choices based on visual clutter, selecting habitats of higher complexity for
309 concealment and lower complexity for signalling. This prediction deserves to be tested.
310 Beyond biology, the results are also relevant to understanding human visual search in
311 natural environments, and extending approaches familiar to those in applied psychology
312 and ergonomics (e.g. with regard to visual displays) to more naturalistic tasks.

313

314 **Ethics**

315 The experiment was approved by the University of Bristol Animal Welfare and Ethical
316 Review Body.

317

318 **Competing interests**

319 The authors declare no competing interests.

320

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324

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327 manuscript.

328

329 **Data accessibility**

330 All data are available from Dryad:

331 https://datadryad.org/stash/share/X880Q6n6MS_CXdwoj-QNK2I60mwqHb4QGEQTM92mk5E

332

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399

400

401 **Supplementary Material for Rowe et al. “Background complexity can mitigate poor**
402 **camouflage”.**

403

404 **Zeke W. Rowe^{1*}, Daniel J. D. Austin¹, Nicol Chippington¹, William Flynn¹, Finn**
405 **Starkey¹, Edward J. Wightman¹, Nicholas E. Scott-Samuel² and Innes C. Cuthill¹**

406

407 **¹ School of Biological Sciences, University of Bristol, Life Sciences Building, 24**
408 **Tyndall Avenue, Bristol BS8 1TQ, United Kingdom**

409 **² School of Psychological Science, University of Bristol, 12A Priory Avenue, Bristol**
410 **BS8 1TU, United Kingdom**

411 *** Corresponding author: zr17137@bristol.ac.uk**

412

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414 **10.1098/rspb.2021-2029.**

415

416 **Supplementary Methods**

417

418 Where indicated with quotation marks, much of the information that follows is taken, with
419 permission, from [1]. The presence of ellipses (“...”) indicates deletion of irrelevant material
420 (e.g. reference to a figure which is numbered differently from the current paper) and italic font
421 indicates insertion of new text that was not present in [1] but are necessary to make
422 grammatical sense in the current context.

423

424 “The targets, being of fixed and known dimensions, were used to resize all images to a
425 common scale (all images were downsized such that the analysed area... was 256 x 256
426 pixels; thus image-processing time was not a limiting factor in analysis). Because digital
427 cameras often show a non-linear relationship between the pixel value recorded and changes
428 in light intensity, the images were first calibrated to linearize the RGB pixel values’ relationship
429 with light intensity [2]. A Gretag-Macbeth Mini-Colorchecker chart (X-Rite, Grand Rapids,
430 Michigan, USA) was used as a colour standard in the images, allowing us to covert the
431 camera’s RGB values to linearized and device-independent sRGB. For human vision, the
432 standardised sRGB values *would be* converted to L*a*b* colour space (CIELAB 1976;
433 Commission Internationale de l'Eclairage; <http://cie.co.at>). CIELAB colour space represents

434 colour in triplet coordinates of, first, lightness and, second, two of hue that approximate the
435 red-green and yellow-blue opponent channels of humans [3]. It has the advantage that
436 Euclidean distances in the colour space approximate perceived colour differences. This colour
437 space is the result of decades of psychophysical experiments, modelling and arguments (it is
438 still an approximation that does not hold under some conditions), so it is no surprise that there
439 is no avian CIELAB. However, we constructed an equivalent colour space for a generalized
440 passerine bird (these being the main avian predators of our targets), following the method of
441 Stevens & Cuthill [4]. sRGB data were converted to photon catches of blue tit UV, S, M and L
442 single cones, and double cones [5] using a standard D65 daylight illuminant [3]. D65 was used,
443 rather than for example woodland shade [6] because, at the time and place of carrying out the
444 experiment (winter), most targets were illuminated by a mixture of skylight and direct sun
445 rather than being in shade. The double cone photon catch was used as a surrogate for
446 luminance (the L in $L^*a^*b^*$); the ratio of $(L - M)$ to $(M + L)$ photon catch as a red-green opponent
447 channel; the ratio of $(M + L - 2*S)$ to $(S + M + L)$ photon catch as a yellow-blue opponent
448 channel. Each channel/dimension was scaled to lie between 0 and 1 (for L, black = 0 and 1 =
449 white; for a, 0 = green, 1 = red; for b, 0 = blue, 1 = yellow). Luminance contrast was calculated
450 as the distance in the L, or surrogate L dimension; chromatic contrast was calculated as the
451 Euclidean distance in the 2D $L^*a^*b^*$, or surrogate $L^*a^*b^*$, chromatic space.”

452

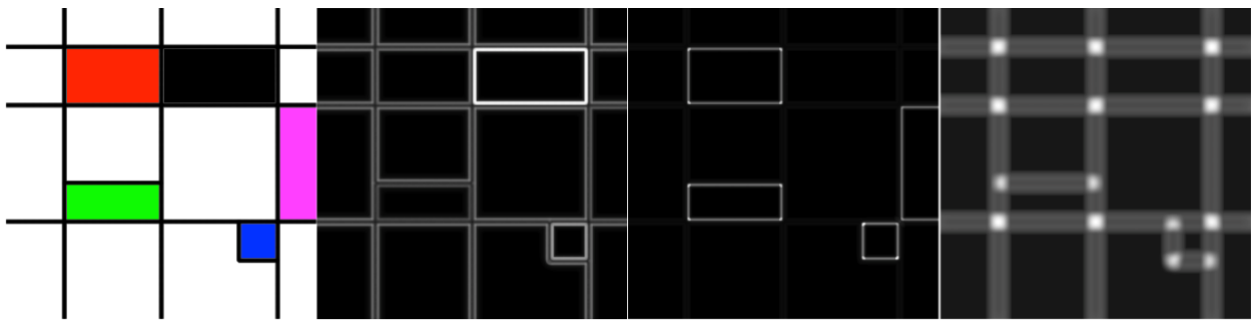
453 “Complexity of the tree bark was calculated using ... feature congestion *metrics* [7, 8]. The
454 logic behind feature congestion is that cluttered scenes are ones in which there are many
455 features similar to features in the target. The difficulty of detecting a target increases as
456 background features that are similar to the target’s features increase in number. This parallels
457 the effect of distractors on performance in visual search tasks where the field of view contains
458 only discrete objects rather than a texture. In order to extract relevant information from its
459 surrounding, an animal needs information about rapid changes from one part of the visual
460 scene to another (which will relate to object boundaries, or that specify the structure of
461 objects). The scale of intensity change is determined by the range of variation in the features
462 processed in early vision. Thus, the main measure of feature congestion is rapid change in
463 luminance, chroma and orientation of lines or “blobs” (an edge detector responds to points as
464 “short lines” of no particular orientation, often called blobs in the computational vision
465 literature). In non-technical terms, feature congestion estimates the amount of luminance and
466 chromatic variation around the target, and orientation congestion the variation in the
467 orientation of edges in the bark surrounding a target. Targets near rapid changes in luminance,
468 chroma and edge-orientation are predicted to be harder to detect than targets further from
469 such ‘clutter’. ... An intuitive illustration of what the feature congestion metrics measure is

470 provided in figure S1; the application to experimental images is shown in figure S2). The
471 Rosenholtz et al. [7, 8] functions operate on a transformation of a calibrated RGB photograph
472 to L*a*b* colour space. Luminance and orientation clutter calculations are based on the L
473 dimension; chromatic clutter is based on the a and b dimensions. Our equivalent for a bird
474 instead passes image data in our avian surrogate L*a*b* colour space, as described above,
475 to the Rosenholtz et al. [7, 8] functions.”

476

477 “All computations used the Image Processing Toolbox in Matlab [9] plus Rosenholtz et al.’s
478 functions (available at <http://hdl.handle.net/1721.1/37593>). The latter also provide a weighted
479 composite metric of feature congestion based on a weighted sum of luminance, chroma and
480 orientation clutter. Because the weights are unknown for birds, we analysed the potential
481 influence of the three feature congestion metrics separately...”

482

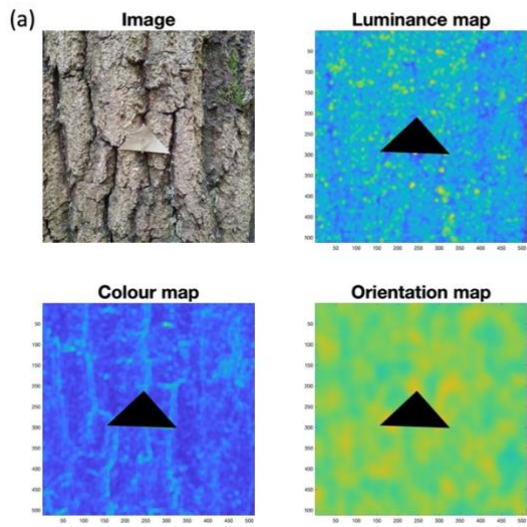


483

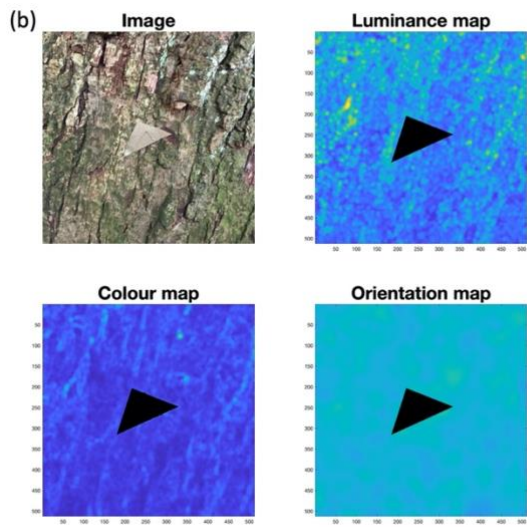
484 **Figure S1** Intuitive illustration of the feature congestion metrics applied to a ‘Mondrian’ image.
485 Left to right: (i) original ‘Mondrian’, (ii) the map of rapidly changing luminance, (iii) the map of
486 rapidly changing colour, and (iv) the map of rapidly changing edge orientations.

487

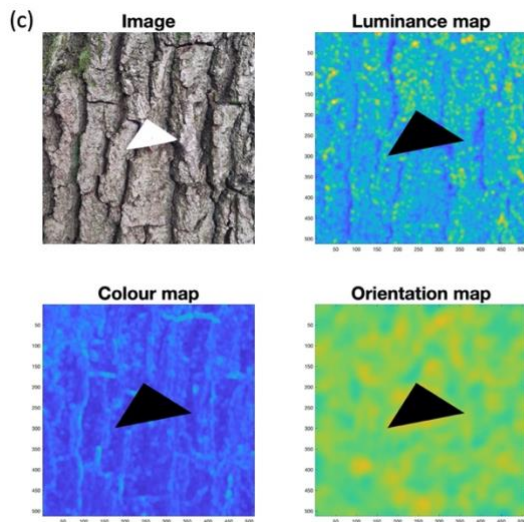
488



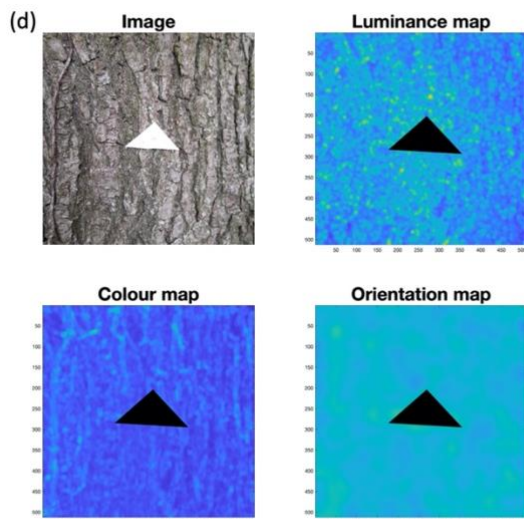
489



490



491



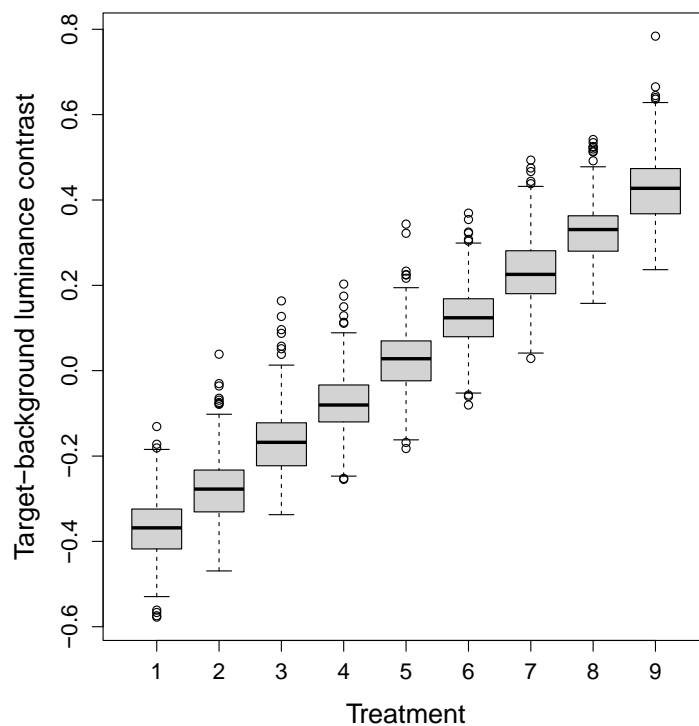
492

493 **Figure S2** Examples of different treatments and different bark complexities. (a) Average
 494 bark colour (treatment 5), complex bark; (b) Average bark colour (treatment 5), simpler bark;
 495 (c) Lightest colour (treatment 9), complex bark; (c) Lightest colour (treatment 9), simpler
 496 bark. In each panel, clockwise from top left, are: the original image; the map of rapidly
 497 changing luminance; the map of rapidly changing colour; the map of rapidly changing edge
 498 orientations. A mask (black triangle), slightly larger than the target, indicates that the areas
 499 of the maps corresponding to the target were not included in the calculation of each of the
 500 three clutter metrics (luminance, colour and edge orientation). The three clutter maps were
 501 plotted using Matlab's 'imagesc' function, which uses a heatmap to indicates a increasing
 502 value of the metric at each pixel, from blue ('cool') through green, yellow, to white ('hottest').

503 **Validation of intended effect of Treatment**

504 The different shades of lightness (avian luminance equivalent) of the targets were based on
505 the analysis of the bark of 1000 oak trees in the year before the experiment. However, as
506 photographs were taken of all targets in situ, we could validate that the manipulation had the
507 intended effect. Figure S1 shows that it did.

508



509

510

511 **Figure S1.** Boxplot of the contrast between each target and the bark of the tree on which it
512 was attached, expressed as the double cone catch for the target minus the double cone
513 catch for the background (so a negative value means that the target is darker than the
514 background). The double cone catch is standardised to lie between 0 (0% reflectance, or
515 black) and 1 (100% reflectance, or white). Thick horizontal lines represent medians, boxes
516 span the inter-quartile range, and 'whiskers' run to the first point within 1.5 inter-quartile
517 ranges from the box. Circles are potential outliers.

518

519 We can also check that there was no unexpected confound between target-background
520 luminance contrast (as manipulated by our experiment) and the orientation clutter metric of
521 background complexity. There was no correlation ($r = 0.03$, 95% c.i. -0.01 to 0.07, d.f. =
522 2245, $p = 0.118$), nor for luminance clutter ($r = 0.03$, 95% c.i. -0.07 to 0.01, d.f. = 2245, $p =$
523 0.197).

524

525 Tables S1 to S4, which follow, comprise different components of the same, stepwise, mixed
526 effects Cox regression of mortality rates with respect to Treatment and the three clutter
527 metrics (luminance, colour and orientation).

528

529 **Table S1. Analysis of mortality rates using mixed effects Cox regression 1.**

530 Stepwise simplification process starting with a model including the fixed effects Treatment (9
531 levels), the three covariates luminance clutter (lum.clutt), colour clutter (col.clutt), orientation
532 clutter (ori.clutt), and the interaction between Treatment and the three covariates. All three
533 covariates have been converted to z-scores (mean of 0 and standard deviation of 1), using
534 R's 'scale' function, to remove collinearity between covariates and their interactions. We use
535 the R notation for model terms, such that ":" indicates an interaction. All models include the
536 random effect of Block, but only fixed effects are listed for simplicity. The sequence of term
537 removal was: interaction terms first and, for interactions of the same order (i.e. all two-way),
538 the *a priori* expectation of their (lack of) effect, based on the results of Xiao & Cuthill [1],
539 namely colour clutter then luminance clutter then orientation clutter. The component main
540 effects of significant interact terms were always retained.

541

Step	Model	Term removed	Chi	df	p
1	Treatment + scale(lum.clutt) + scale(col.clutt) + scale(ori.clutt) + Treatment:scale(lum.clutt) + Treatment:scale(col.clutt) + Treatment:scale(ori.clutt)	Treatment:scale(col.clutt)	5.092	8	0.748
2	Treatment + scale(lum.clutt) + scale(col.clutt) + scale(ori.clutt) + Treatment:scale(lum.clutt) + Treatment:scale(ori.clutt)	Treatment:scale(lum.clutt)	10.045	8	0.262
3	Treatment + scale(lum.clutt) + scale(col.clutt) + scale(ori.clutt) + Treatment:scale(ori.clutt)	Treatment:scale(ori.clutt)	57.042	8	<0.001
4	Treatment + scale(lum.clutt) + scale(col.clutt) + scale(ori.clutt) + Treatment:scale(ori.clutt)	scale(col.clutt)	0.000	1	0.979

5	Treatment + scale(lum.clutt) scale(ori.clutt) + Treatment:scale(ori.clutt)	scale(lum.clutt)	22.886	1	<0.001
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542

543

544 **Table S2. Analysis of mortality rates using mixed effects Cox regression 2.**

545 Final model (step 5 of Table S1), retaining only significant terms and the main effects
546 associated with the interaction between orientation clutter and Treatment. Values are the
547 estimates of the coefficients of each term (Coef) and the associated standard error
548 (SE(Coef)), the exponential function or odds ratio of the coefficient (exp(Coef)), the z-test for
549 the difference between the estimated coefficient and zero, and associated p-value. The odds
550 ratio of 0.866 for the main effect of (standardised) luminance clutter on mortality means that
551 for every increase in luminance clutter of one standard deviation, mortality is reduced by
552 13.4% (1 – 0.866). The intercept of the whole model is the mortality rate for treatment 5 (a
553 luminance close to the mean of all backgrounds) and the contrasts for the main effects of
554 Treatment therefore are the differences between the mean mortality rate of each level of
555 Treatment compared to the mean mortality rate of treatment 5. So, for example, the odds
556 ratio (exp(Coef)) for the main effect contrast of treatment1 indicates that mortality of
557 treatment 1 (the darkest targets) is, on average, 2.278 times that of treatment 5 (average
558 bark luminance targets). Analogously, the contrasts for the Treatment by orientation clutter
559 interaction are the slopes of the effect of orientation clutter within each treatment level,
560 compared to the slope of the effect of orientation clutter for treatment 5. For example, the
561 statistically significant odds ratio of 1.789 for the comparison of the slope of orientation
562 clutter in treatment 1 with that in treatment 5 means that the slope is 78.9% steeper in
563 treatment 1 than 5. However, this is not because there is a stronger effect in treatment 1
564 than 5; the opposite in fact, as the slope is close to 1 (not significant) and significantly
565 negative in treatment 5 (i.e. orientation clutter reduces mortality in treatment 5, but not
566 treatment 1). This becomes evident in the separate analyses for each level of treatment (see

567 Tables S3 and S4 below). We use the R notation for model terms, such that “:” indicates the
 568 interaction term.

569

570

Fixed effects	Coef	exp(Coef)	SE(Coef)	z	p
Treatment1	0.823	2.278	0.106	7.79	<0.001
Treatment2	0.651	1.917	0.106	6.16	<0.001
Treatment3	0.264	1.302	0.108	2.44	0.015
Treatment4	0.048	1.049	0.111	0.43	0.670
Treatment6	-0.007	0.993	0.111	-0.06	0.950
Treatment7	0.338	1.403	0.107	3.17	0.002
Treatment8	0.979	2.662	0.105	9.35	<0.001
Treatment9	1.316	3.727	0.106	12.4	<0.001
scale(lum.clutt)	-0.143	0.866	0.029	-4.88	<0.001
scale(ori.clutt)	-0.409	0.665	0.083	-4.92	<0.001
Treatment1:scale(ori.clutt)	0.582	1.789	0.110	5.29	<0.001
Treatment2:scale(ori.clutt)	0.177	1.194	0.109	1.63	0.100
Treatment3:scale(ori.clutt)	0.048	1.049	0.117	0.41	0.680
Treatment4:scale(ori.clutt)	0.139	1.149	0.112	1.24	0.210
Treatment6:scale(ori.clutt)	0.101	1.106	0.114	0.89	0.380
Treatment7:scale(ori.clutt)	0.041	1.042	0.111	0.37	0.710
Treatment8:scale(ori.clutt)	0.395	1.485	0.111	3.56	<0.001
Treatment9:scale(ori.clutt)	0.394	1.483	0.109	3.63	<0.001
Random effect	StDev				
Block intercept	0.301				

571

572 **Table S3. Analysis of mortality rates using mixed effects Cox regression 3.**

573 Separate mixed model Cox regressions for the effect of orientation clutter within each level
 574 of Treatment. Values are the estimates of the coefficients of each term (Coef) and the
 575 associated standard error (SE(Coef)), the exponential function or odds ratio of the coefficient

576 (exp(Coef)), the z-test for the difference between the estimated coefficient and zero, and
 577 associated p-value. The odds ratio of 1.076 for the main effect of (standardised) orientation
 578 clutter on mortality means that for every increase in orientation clutter of one standard
 579 deviation, mortality is increased by 7.6% (1.076 – 1), although this is not significantly
 580 different from an odds ratio of 1; in other words, no effect (on the odds of mortality). All
 581 models include the random effect of Block, but only fixed effects are listed for simplicity.

582

Fixed effects	Coef	exp(Coef)	SE(Coef)	z	p
Orientation clutter in Treatment1	0.074	1.076	0.075	0.98	0.328
Orientation clutter in Treatment2	-0.231	0.794	0.074	-3.14	0.002
Orientation clutter in Treatment3	-0.403	0.668	0.088	-4.57	<0.001
Orientation clutter in Treatment4	-0.326	0.722	0.085	-3.85	<0.001
Orientation clutter in Treatment5	-0.456	0.634	0.086	-5.27	<0.001
Orientation clutter in Treatment6	-0.316	0.729	0.086	-3.67	<0.001
Orientation clutter in Treatment7	-0.388	0.678	0.083	-4.68	<0.001
Orientation clutter in Treatment8	0.017	1.017	0.076	0.23	0.820
Orientation clutter in Treatment9	-0.008	0.992	0.073	-0.11	0.909

583

584 **Table S4. Analysis of mortality rates using mixed effects Cox regression 4.**

585 Separate mixed model Cox regressions for the effect of luminance clutter within each level of
 586 Treatment. Following the analysis in (a), the final model in (b) does not include the
 587 Treatment by luminance clutter interaction, so there is no justification for treating any of
 588 these slopes as different from the average odds ratio (main effect) in (b) of 0.866. These
 589 separate analyses were carried out purely for the purpose of producing figure 3(b), which
 590 illustrates the effects of contrast clutter as compared with the treatment-dependent effects of
 591 orientation clutter. Values are the estimates of the coefficients of each term (Coef) and the
 592 associated standard error (SE(Coef)), the exponential function or odds ratio of the coefficient
 593 (exp(Coef)), the z-test for the difference between the estimated coefficient and zero, and

594 associated p-value. All models include the random effect of Block, but only fixed effects are
 595 listed for simplicity.

596

Fixed effects	Coef	exp(Coef)	SE(Coef)	z	p
Luminance clutter in Treatment1	-0.108	0.898	0.075	-1.43	0.152
Luminance clutter in Treatment2	-0.229	0.795	0.075	-3.04	0.002
Luminance clutter in Treatment3	-0.237	0.789	0.092	-2.59	0.010
Luminance clutter in Treatment4	-0.110	0.896	0.090	-1.22	0.222
Luminance clutter in Treatment5	-0.201	0.818	0.091	-2.21	0.027
Luminance clutter in Treatment6	-0.281	0.755	0.088	-3.18	0.001
Luminance clutter in Treatment7	-0.213	0.808	0.089	-2.40	0.017
Luminance clutter in Treatment8	-0.036	0.965	0.077	-0.47	0.640
Luminance clutter in Treatment9	-0.114	0.893	0.070	-1.63	0.102

597

598

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