

Nest covering in plovers: how modifying the visual environment influences egg camouflage

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Summary

1. Camouflage is one of the most widespread anti-predator defences, and its mechanistic basis has attracted considerable interest in recent years. The effectiveness of camouflage depends on the interaction between an animal's appearance and its background. Concealment can therefore be improved by changes to an animal's own appearance, by behaviourally selecting an optimal background, or by modifying the background to better match the animal's own appearance. Research to date has largely focussed on the first of these mechanisms, whereas there has been little work on the second and almost none on the third. Even though a number of animal species may potentially modify their environment to improve individual-specific camouflage, this has rarely if ever been quantitatively investigated, or its adaptive value tested.
2. Kittlitz's plovers (*Charadrius pecuarius*) use material (stones and vegetation) to cover their nests when predators approach, providing concealment that is independent of the inflexible appearance of the adult or eggs, and that can be adjusted to suit the local surrounding background. We used digital imaging and predator vision modelling to investigate the camouflage properties of covered nests, and whether their camouflage affected their survival.
3. The plovers' nest covering materials were consistent with a trade-off between selecting materials that matched the colour of the eggs, while resulting in poorer nest pattern and contrast matching to the nest surroundings. Alternatively, the systematic use of materials with high contrasts and small pattern grain sizes could reflect a deliberate disruptive

21 coloration strategy, whereby high contrast material breaks up the tell-tale outline of the
22 clutch. No camouflage variables predicted nest survival.

- 23 4. Our study highlights the potential for camouflage to be enhanced by background
24 modification. This provides a flexible system for modifying an animal's conspicuousness, to
25 which the main limitation may be the available materials rather than the animal's
26 appearance.

27 **Running Head**

29 Camouflage by Nest Covering in Kittlitz Plovers

30 **Key Words**

31 Adaptive camouflage, animal vision, background matching, background modification, crypsis,
32 disruptive coloration, predator vision, shorebird ecology, visual ecology.

34 **Introduction**

35 Camouflage is a key mechanism for evading predators, and offers striking and intuitive examples of
36 natural selection (Wallace 1867). Considerable research over recent years has focussed on the
37 mechanistic basis of camouflage, typically using artificially made or manipulated stimuli (Cuthill *et al.*
38 2005; Schaefer & Stobbe 2006; Webster *et al.* 2013), or laboratory experiments (Chiao *et al.*
39 2009; Skelhorn *et al.* 2010; Lovell *et al.* 2013; Kang *et al.* 2014b; Merilaita & Dimitrova 2014).
40 However, comparatively few studies have investigated camouflage in natural systems, especially
41 while accounting for predator vision, and even fewer have investigated the ability of animals to
42 select or modify backgrounds to complement their camouflage (e.g. Marshall, Philpot & Stevens
43 2016). The effectiveness of any individual's camouflage depends on the interaction between an
44 animal's appearance and its background (Endler 1978; Troscianko *et al.* 2016). As such,
45 behavioural choice of suitable microhabitats or modification of the visual environment, as opposed
46 to adaptation of the animal's own phenotypic appearance, are additional routes to effective
47 camouflage. Animals that modify their surroundings provide interestingly flexible systems for
48 investigating camouflage in natural systems.

49 Background selection to enhance an animal's camouflage was a strategy noted by Wallace
50 (Wallace 1867), who reported that *Kallima* butterflies would only settle on twigs and branches that
51 facilitated the butterfly's concealment. Similar effects have been noted more recently in other
52 species such as coral reef flounders *Bothus lunatus* (Tyrie *et al.* 2015), while moths have been

53 shown to use multisensory cues (including vision) when selecting resting positions (Kang *et al.*
54 2013, 2014a), and laboratory experiments on Japanese quail *Coturnix japonica* demonstrated that
55 females with darker eggs chose to nest on darker backgrounds (Lovell *et al.* 2013). One recent field
56 study of microhabitat choice in reptiles showed that individual Aegean wall lizards (*Podarcis*
57 *erhardii*) were more likely to be found resting on backgrounds that improved their own individual
58 camouflage to predator vision than on backgrounds that did not (Marshall, Philpot & Stevens 2016).
59 Furthermore, this tendency was more pronounced in females living in habitats with higher predation
60 risks, suggesting concealment by habitat selection is dependent on predation pressure. However,
61 beyond the above examples, few studies have tested microhabitat selection for camouflage,
62 especially in the field and with respect to predator vision.

63 Modification of backgrounds in order to enhance camouflage is a distinct strategy from
64 background selection and a further potential route to concealment. Numerous species decorate their
65 own bodies with elements of the background to conceal themselves (Ruxton & Stevens 2015), such
66 as blue-footed boobys *Sula nebouxii* that cake their eggs with mud (Mayani-Parás *et al.* 2015),
67 caddisfly and bagworm moth larvae that construct cases around their bodies, and crustacea that
68 attach sediment (Lee *et al.* 2014) or seaweed to their carapaces (Hultgren & Stachowicz 2009), thus
69 changing their own appearance. However, background modification refers instead to cases where
70 animals change the appearance of their surroundings. Such an approach is widely reported to be
71 used by some bird species to conceal their nests and eggs (Hansell 1996; Bailey *et al.* 2014), and
72 also by invertebrates, such as wasps that use lichen and other materials to conceal their nests
73 (Strassmann, Hughes & Queller 1990). The structures created by these species often have numerous
74 functions that can be difficult to disentangle from camouflage alone, particularly in nests that hold
75 the eggs off the ground and therefore also serve a structural function. Kittlitz's plovers *Charadrius*
76 *pecuarius* provide an ideal study system for investigating the camouflage strategies used to conceal
77 nests because the raw materials providing colour and pattern matching are not limited by the adults'
78 or the eggs' phenotypic appearance. Furthermore, their nests provide little or no structural or
79 mechanical protection to the eggs, which simply lie within a shallow scrape in the ground, although
80 covering may confer some thermal protection (see below). When leaving their nests, Kittlitz's
81 plovers cover their clutch with plant or inorganic material in a so called "leaving-scuffle" (Hall
82 1958, 1960), standing with their legs either side of the nest and kicking material in from the sides,
83 often rotating on the spot to cover the eggs from all sides (see accompanying video). Nest covering
84 is a concealment strategy found in numerous other bird species, including other Charadriiformes
85 (Hall 1960; Maclean 1974; Summers & Hockey 1981; Amat, Monsa & Masero 2012) as well as the
86 Anatidae (Opermanis 2004; Kreisinger & Albrecht 2008, Fast *et al.* 2010) and Podicipedidae

87 (*Tachybaptus*; Prokop & Trnka 2010).

88 In addition to camouflage, nest materials also affect the thermal properties and humidity of
89 the nest (Hilton *et al.* 2004; Prokop & Trnka 2010), and some Charadriiform species may select nest
90 materials that reflect light to protect them from overheating (Mayer *et al.* 2009), or covering
91 materials that reduce heat loss (Reid *et al.* 2002). Leaving the nest covered by material from the
92 environment could be advantageous for adult birds, freeing them from incubation so that they can
93 forage, while potentially providing better camouflage than provided by their own bodies. For the
94 Kentish plover *Charadrius alexandrinus*, covering appears to perform a dual function, providing
95 both concealment and thermoregulation (Amat *et al.* 2012). Amat *et al.* (2012) found that Kentish
96 plovers left their nests covered most frequently around mid-morning, a time of day that also created
97 the optimal temperatures for egg development (embryogenesis) in covered nests. Temperatures in
98 our study area (the Western Cape Province of South Africa) during the Kittlitz's plover breeding
99 season are unlikely to overheat the eggs (the August to October time-frame average high
100 temperatures at the nearby Langebaanweg weather station are 17–18 degrees, with average low
101 temperatures of 10–11 degrees, data from 2000 to 2012; World Weather Online 2016). However,
102 covering could help to insulate the eggs from the less damaging lower temperatures caused by
103 strong winds and sometimes heavy rain, which at worst would slow down embryonic development.
104 Nevertheless, concealment has been assumed to be the primary factor driving nest covering in
105 Kittlitz's plovers (Maclean 1974), and recent data from our study system at the same site
106 demonstrate that uncovered artificial nests designed to mimic Kittlitz's plover nests were more
107 likely to be depredated than covered nests (Ferguson 2016).

108 We aimed to determine how the nest covering behaviour of Kittlitz's plovers affected the
109 appearance of their nests, using measures of camouflage that take into account their main predators'
110 visual systems. If Kittlitz's plovers cover their nests in order to achieve perfect background
111 matching, then we should find no consistent difference between the colours, patterns and other
112 appearance attributes of the nests and those of their local surroundings. We tested this by measuring
113 the appearance of the nests at a number of distances, creating concentric zones to take into account
114 the gradually changing boundaries of their nests. However, nests are not always fully covered, so
115 we might instead expect the plovers to select materials that complement the eggs themselves. If so,
116 then we would expect the nest material to be a better match to the colour or patterns of the eggs than
117 the nest's surroundings, or represent a compromise between the two (i.e. a poor match to both that
118 is an intermediate between them). However, limitations in the available materials could force
119 plovers to select materials that match one appearance attribute over another, resulting in a good
120 colour or pattern match to the eggs or surrounds, while simultaneously worsening the nests' colour

121 or pattern match in other respects. Alternatively, any observed deviations from perfect background-
122 matching or egg-matching could indicate the use of specific camouflage strategies, such as
123 disruptive coloration whereby high contrast nesting material could break up the edges of the clutch
124 (Cuthill *et al.* 2005).

125 Here, we investigate the visual characteristics of Kittlitz's plover nests to determine which of
126 these scenarios best describes their nest camouflage strategies. Recently, in a similar system we
127 found that pattern and contrast matching were most important in the survival of Zambian ground-
128 nesting birds (Troscianko *et al.* 2016). Therefore, we might expect the Kittlitz's plovers to focus on
129 matching the pattern of the eggs or backgrounds to reduce the likelihood of predation, although
130 previous studies (that did not take predator vision into account) suggest colour could also be
131 valuable for survival (Solis & De Lope 1995), and as could matching the size of other objects in the
132 local environment (Castilla *et al.* 2007; Colwell *et al.* 2011). Finally, we tested whether egg
133 appearance and nest modifications predicted the likelihood of nest predation.

134 **Methods**

135 **Study Site and Natural History**

136 Kittlitz' plover nests were located in the Western Cape Province of South Africa, around
137 commercial salt pans on the Berg River estuary (Kliphhoek Farm, centred on -32.794907, 18.159825,
138 and Cerebos Saltpans, centred on -32.824639, 18.200353), and on the coast at a site between
139 Laingville and the mouth of the Berg River, centred on -32.778601, 18.087064). All sites were on
140 private land and permission was granted from the land owners and CapeNature. The nature of the
141 salt pan embankments and coastal habitat restricted nest sites to bands of land between the water
142 and either road, tracks or agricultural land. Nests were located by walking slowly along the
143 potential nesting habitats with binoculars, searching for plovers fleeing their nests and/or
144 performing the leaving-scuffle behaviour, or by exhaustive visual searching during slow systematic
145 patrols. We suspect that the Kittlitz's plovers covered their nests whenever they left them
146 irrespective of the presence of potential threats because we rarely found uncovered nests, even
147 when observing and approaching vacant nests from distances beyond their normal fleeing distances.
148 However, in these cases we cannot rule out nest covering as a response to prior threats that we did
149 not see. Nests were photographed and their GPS positions logged. Each nest was checked on every
150 second day for evidence of hatching or predation. Motion-triggered video cameras were placed at a
151 subset of nests to record any predation events.

152 Camera traps used at our study recorded nest predation by pied crows *Corvus albus* on three
153 occasions, and one additional nest was lost shortly after a pied crow was caught on camera being

154 mobbed by Hartlaub's gulls. One nest disappeared shortly after an African sacred ibis *Threskiornis*
155 *aethiopicus* was caught on camera, suggesting this could have been the predator if it took the eggs
156 before the motion triggered camera could restart filming. Blacksmith plovers nesting near the
157 Kittlitz's plover nests were recorded piercing the eggs of Kittlitz's plovers on two separate
158 occasions; blacksmith plovers pierced one egg at a time, and each pierced egg was later removed by
159 the Kittlitz's plovers. Although the blacksmith plovers were likely not preying upon the nests as
160 food, the survival of Kittlitz's plover nests partially depended on being undetected by blacksmith
161 plovers. Two additional nests that were not monitored by cameras lost one egg, followed by the
162 second a short time later. This pattern is consistent with blacksmith plovers piercing the eggs, as all
163 of the predators we recorded took the entire clutch. Two additional clutches were taken at night by
164 mongooses (presumed to be water mongoose *Atilax paludinosus*), where non-visual sensory cues
165 are likely to play more of a role in detection. The videos also revealed one nest being washed away
166 by high water. One additional nest not videoed was presumed to have been depredated by a
167 mongoose, based on the presence of tracks. Monitoring of other plover species at the same field site
168 with motion-sensitive cameras revealed a similar pattern, with high rates of predation from pied
169 crows (taking one chestnut-banded plover nest *Charadrius pallidus*, and two blacksmith plover
170 nests) and one instance of predation by a predatory mammal (possibly a black-backed jackal *Canis*
171 *mesomelas mesomelas*) of a crowned plover nest *Vanellus coronatus* on nearby farmland.

172

173 **Photography**

174 Our photography methods followed Troscianko et al. (2016) and Wilson-Aggarwal et al. (2016).
175 Prior to photography, nests were approached at a slow walking pace to allow the Kittlitz' plovers to
176 cover their clutches with nesting materials. Nests were photographed with two Nikon D7000
177 cameras that had been converted to full-spectrum sensitivity, fitted with Micro Nikkor AF-S VR
178 105 mm lenses that transmit ultraviolet (UV) light. Photographs were taken through Baader Venus-
179 U filters (transmitting UV wavelengths from ~320 to 380 nm) and Baader UV/IR cut filters
180 (transmitting human-visible wavelengths from ~400 to 700 nm). For further details and spectral
181 sensitivities of this camera setup, see Troscianko and Stevens (2015). Photographs were taken from
182 a height of 1.25 m directly above the nest with the nest material in place. Without moving the
183 camera, further images were taken after we pushed the covering nest material to the side of the nest
184 (for details on finding the centre of the nest, see below). Two further control photographs were
185 taken approximately 5 m either side of the nest (see Fig. 1). This distance was chosen as being
186 representative of the nesting habitat of the plovers, but sufficiently far from the nest to not risk

187 having had its visual appearance substantially altered by the plovers' nest-covering behaviour.
188 Lighting conditions were controlled for and reflectance measured by normalising the images against
189 40% reflectance Spectralon (Labsphere) grey standards (Stevens et al. 2007), placed flat on the
190 ground adjacent to the nest, or in the centre of control photographs. A sequential normalisation
191 procedure was used, whereby photographs of the grey standards were taken immediately after the
192 nest and control photos while ensuring there were no changes in lighting conditions or camera
193 settings (Stevens, Stoddard & Higham 2009; Troscianko & Stevens 2015). All photographs were
194 taken in direct sunlight conditions and not within one hour of sunrise or sunset, to ensure that
195 lighting conditions were as diffuse and as consistent as possible between images (for example, to
196 remove the light spill or shadows of nearby objects). Eggs were removed from the nests and
197 photographed in diffuse, shade conditions (approximating D65 standard illumination) against a
198 white background, and with a grey standard and ball bearing (for use as a scale bar) in the same
199 photograph.

200

201 **Image Analysis**

202 Images were calibrated and analysed using the multispectral image calibration and analysis toolbox
203 (Troscianko & Stevens 2015; Troscianko *et al.* 2016). Camera traps demonstrated that the principal
204 diurnal threats to nest survival were from birds with violet-sensitive (VS) visual systems (as
205 opposed to UV systems (Ödeen & Håstad 2013); see Results. Images were therefore converted to
206 the cone-catch values of the peafowl (*Pavo cristatus*); this is a model visual system often used for
207 VS bird species (Hart 2002). The centre of the nest was manually located in each image from
208 photographs showing the uncovered nest (see Fig. 2), and then four concentric rings at radius
209 intervals of 650 pixels (px) were generated around this centre, creating five zones in the nest image,
210 labelled from "a" at the centre to "e" at the edge of the image (Fig. 1). Any egg visible through the
211 nest material was removed from the analysis. The central zone ("a") always unambiguously
212 comprised nest material or partially visible eggs; however, the degree of nest material manipulation
213 is expected to reduce with distance from the centre, resulting in the nests' observed gradual edges
214 (see Fig. 2 and Supplementary Video). The use of concentric rings and 5 m control images in the
215 analysis reflects this spatial shift from unambiguous nest material to unmodified background.
216 Image statistics were generated independently in each ring, and using the entirety of the 5 m control
217 images.

218 Peafowl double cone responses scaled down uniformly to 10 px/mm were used to generate
219 luminance data, which included mean luminance, contrast (luminance standard deviation divided by

220 mean luminance), and pairwise luminance difference measurements (based on comparing the
221 luminance histograms of the egg and background sample using 100 bins; Troscianko & Stevens
222 2015). Pattern processing is thought largely to rely on luminance information (Osorio & Vorobyev
223 2005), so was also processed from double cone responses with bandpass analysis at 15 levels, from
224 2 to 256 px in multiples of $\sqrt{2}$. Pattern metrics included the dominant pattern size (the spatial
225 frequency with the highest energy), the maximum energy (the energy at the maximum frequency),
226 summed energy (the energy summed across all scales), proportion energy (the maximum energy
227 divided by the summed energy, which describes the diversity of pattern sizes), mean energy, and
228 energy standard deviation (Chiao *et al.* 2009; Stoddard & Stevens 2011). In addition, pairwise
229 pattern difference measures were calculated between the clutch and background regions, and zone
230 “a” and all other background regions, describing the level of dissimilarity between any two patterns
231 (Troscianko & Stevens 2015).

232 Nesting habitats often contained background objects that had different colours, such as
233 vegetation, rocks, or mud (see figures 1–2). Taking the mean colour measurement across these
234 discrete objects would not generate representative colour information, and might even produce
235 intermediate colours that do not exist in the scene. We therefore used a custom-written
236 ‘agglomerative hierarchical clustering algorithm’ to separate out these different colours based on
237 peafowl colour discrimination, as follows. For colour analysis, images were scaled to a uniform 5
238 px/mm. The code first clustered each pixel with its nearest neighbour based on discrimination units
239 of “just noticeable differences” (JNDs; Vorobyev & Osorio 1998), calculating new colour averages
240 for each clustered group on each pass. Neighbours were joined from larger receptive fields in
241 consecutive passes, starting with a 1 px radius, and doubling the radius with each pass. Analysis
242 was performed after 7 passes, which on average split each clutch into 1.86 discrete colours, each
243 concentric background ring into 9.34 colours, and the control images into 42.19 colours. Each of the
244 colours identified in each clutch were then compared to all of the colours in each background zone
245 based on JNDs, and a weighted average JND was created that took into account the percentage area
246 coverage of each colour. Therefore discrete colours that were rare in a scene contributed less to the
247 weighted JND than did more abundant background colours. The same pairwise colour differences
248 were also created to compare the colours in zone “a” to all other background zones.

249 The materials available to Kittlitz’ plovers for lining and covering their nests varied between
250 locations, from almost entirely inorganic material (small stones) to almost entirely dried vegetation
251 (dried sticks and leaves). We scored each nest visually for the nest material composition, from 0 (>
252 90% inorganic material), to 1 (a mixture of materials), to 2 (> 90% organic material); Fig. 2 shows
253 examples of all three scores.

255 **Statistics**

256 Statistics were performed in R version 3.2.2. All pattern metrics and JND values were log-
257 transformed to produce a normal error distribution. Spearman covariance matrices of camouflage
258 metrics revealed high autocorrelation between numerous pattern variables (values > 0.5 or < -0.5 ;
259 (Zuur *et al.* 2009)). Therefore, only dominant pattern size and maximum energy were used as
260 pattern descriptive statistics as these were uncorrelated with one another. Survival was modelled in
261 mixed-effects Cox models (coxme package, version 2.2-5). Survival time was measured in days.
262 Nests for which the outcome was uncertain, nests which were still intact at the end of the fieldwork,
263 and nests which had hatched were all censored from the survival model at their last recorded time
264 (censoring in survival models allows all survival data to be included until the point of censoring,
265 even if the outcome of any given nest is uncertain). Survival was modelled against camouflage
266 variables, with zone and nest material scores included as ordinal variables, and nest as a random
267 factor because multiple background zones were measured in each nest. Nest appearance as a
268 function of increasing distance from the eggs was tested with cumulative link mixed models
269 (ordinal package, version 2015.6-28), modelling zone as an ordinal dependent variable against
270 camouflage variables and nest material score, with nest as a random effect. Likelihood ratio tests
271 were used to simplify a full model containing all two-way interactions, resulting in a final model.
272 Significance levels were generated by dropping single terms from the model while maintaining
273 marginality and using Chi-square tests between models.

274

275 **Results**

276 **Nest covering**

277 A total of 35 Kittlitz's plover nests was photographed and monitored from 2 August–14 September
278 2013. Observations from motion-triggered video cameras and direct observations on foot and from
279 cars revealed Kittlitz's plovers covering their nests on approach of humans, pied crows, and
280 blacksmith plovers (see Supplementary Video). Large flocks of Hartlaub's gulls *Chroicocephalus*
281 *hartlaubii* frequently congregated within 20 m of some Kittlitz's plover nests; however, we
282 observed neither nest covering in response to their presence, nor predation by the gulls. This nest-
283 covering behaviour only in the presence of potential threats suggests that one of the roles of nest
284 covering is indeed concealment (Maclean 1974).

285 Perfect background matching would predict that there should be no differences in

286 appearance at different distances (zones) from the centre of the nest, implying no variables in our
287 model would be significant. Any camouflage variables that do vary consistently between zone
288 suggest that background matching is imperfect; additional interactions with nesting material and the
289 match to the colours and patterns of the eggs themselves test for limitations and trade-offs in nest
290 appearance. Cumulative link mixed models revealed a number of camouflage variables that varied
291 significantly with distance from the centre of the Kittlitz's plover nests, implying that nest covering
292 does not provide perfect background matching. The final model demonstrated an interaction with
293 nesting material score and dominant pattern size (likelihood ratio test (LRT) = 8.72, $p = 0.013$); this
294 arose because the centres of nests composed of dried vegetation had smaller dominant pattern sizes
295 than nests composed of inorganic materials, and were a worse match to the surrounding dominant
296 pattern sizes. Nests covered with inorganic materials were more consistent in their pattern sizes
297 across the zones (i.e. there was a less strong correlation between pattern size and distance from the
298 centre of the nest for inorganic material than organic), suggesting they achieved a better background
299 pattern match (Fig. 3a). There was also a significant interaction between dominant pattern size and
300 maximum energy (LRT = 13.60, $p < 0.001$); maximum energy values decreased with distance from
301 the nest, meaning the background patterns were smaller and the dominant patterns had lower
302 contrast further from the nest (Fig. 3c). Colour difference between the eggs and their backgrounds
303 increased significantly with distance (LRT = 86.28, $p < 0.001$), indicating the nesting material was a
304 better colour match to the eggs than the surrounding background (Fig. 3b). Contrast decreased
305 significantly with distance (LRT = 102.11, $p < 0.001$), meaning the centre of the nests had higher
306 contrast than their surrounds (Fig. 3d).

307

308 **Nest Survival**

309 Just three nests were known to survive to hatching. Eighteen were depredated (video footage
310 confirmed four of these events), while others were presumed to have been depredated because the
311 eggs disappeared before sufficient incubation time, and with no evidence of hatching (methods for
312 determining clutch fate followed Troscianko *et al.* 2016). Eight nests were still present at the end of
313 our fieldwork, four disappeared without a clear cause, one nest was destroyed by high water, and
314 one was deserted by the parents.

315 Survival analyses did not reveal any correlations between nest camouflage and likelihood of
316 predation (no models were better than the null). These models included pairwise comparisons
317 between zone “a” and all other background zones, pairwise comparisons between the clutch and all
318 background zones, and overall descriptive statistics across all the background zones.

320 **Discussion**

321 Kittlitz's plovers conceal their nests by covering them with material that they accumulate in
322 advance, allowing us to determine what visual cues (if any) they use when selecting covering
323 material, and how this affected their survival in a natural system. The nests of Kittlitz's plovers
324 rarely have clear boundaries, such that the arranged material looks continuous with the background.
325 We found that the appearance of the nests – as modelled through the visual system of their main
326 predator – changed with distance from the nest centre, indicating that nests are not a perfect match
327 to their backgrounds. Moreover, this systematic change in appearance differed between camouflage
328 variables: while the selected materials were a near-perfect match to the colour of the eggs,
329 consistent with Mayer et al. (2009), they created higher contrast and pattern differences with their
330 backgrounds. Such a mismatch might arise from a trade-off between different aspects of
331 camouflage created by material constraints or thermal considerations, from an intentional
332 camouflage strategy, or from a combination of the two.

333 The plovers' eggs were a poor match to their overall surrounds, meaning that they would be
334 visible to predators against their backgrounds without nesting materials to cover them (Fig. 3b). The
335 plovers could therefore either select covering material that matches the background, thus creating
336 no colour cues for predators; or, they could select material that matches the colour of the eggs, such
337 that any eggs visible through the material do not create a strong colour contrast. Alternatively, the
338 plovers might not be selective in their choice of material, in which case we would expect the nest
339 material to be closer in colour to the surrounding environment than to the eggs. We found that the
340 nesting material was a near-perfect colour match to the eggs, irrespective of whether they were
341 composed of dried vegetation or stones (median = 1.9 JNDs, see Fig. 3b; Siddiqi *et al.* 2004).
342 However, these materials were a poor colour match to their surrounds, suggesting that in covering
343 their nests, the plovers used material that matched their egg colour better than the nest's background
344 colour, thereby making the entire nest a worse colour match to its surrounds. The gradual decrease
345 in nesting material with distance observed in the Kittlitz's nests could mitigate for the imperfect
346 colour of the nest. Such a strategy of gradual colour shifts could enhance camouflage by confusing
347 the local colour constancy mechanisms of the receiver (Hurlbert 1999), a potential camouflage
348 mechanism that has received almost no attention to date.

349 In addition to the colour-based trade-offs above, the Kittlitz's nests also varied from their
350 backgrounds in pattern and contrast. Nests had higher contrast and higher maximum pattern energy
351 (the contrast of the dominant pattern scale) than their surroundings. Nests covered with entirely

352 organic material also had smaller pattern details than the average surroundings, demonstrating that
353 organic and inorganic materials do differ substantially in appearance even though the plovers
354 managed to match the colours of their eggs perfectly irrespective of material. Such systematic
355 changes from a background-matching strategy could result from two mechanisms that are not
356 mutually exclusive: limitations in material availability, and an adaptive camouflage strategy. The
357 material limitation hypothesis makes the assumption that the available nesting materials are unable
358 to match all of the desired appearance characteristics simultaneously; for example, if the plovers
359 were selecting materials for a perfect colour match with their eggs, these same materials may be
360 unable to match the egg or background appearance characteristics closely. If this is the case, our
361 findings suggest that the plovers value colour matching above other camouflage variables, contrary
362 to our predictions that pattern and contrast should be most important (Troscianko *et al.* 2016;
363 Wilson-Aggarwal *et al.* 2016). Alternatively, the adaptive strategy hypothesis would suggest that
364 the nests' deviation from perfect background matching reflects a shift in camouflage strategy from
365 background-matching to some other (presumably more effective) strategy. The most well-
366 documented alternative to background matching is disruptive coloration, where the prey's edges are
367 broken up by high contrasting patches (Thayer 1909; Cott 1940; Cuthill *et al.* 2005). The higher
368 luminance contrasts and higher pattern contrasts of the plover nests compared to the background are
369 consistent with such a disruptive coloration strategy (Troscianko *et al.* 2013). Although the Kittlitz's
370 plover nests generally have no clear boundaries or fixed shapes, a recent study has demonstrated the
371 effectiveness of disruptive camouflage in prey with graduated boundaries (Webster, Godin &
372 Sherratt 2015), suggesting that the higher contrast of the nests could help to disrupt the predator's
373 perception of a nest-shape.

374 We found no evidence that camouflage affected the likelihood of clutches surviving to
375 hatching in this study. This could be due to a modest sample size of 35 nests, which is
376 comparatively small for survival analysis, although predation rates were extremely high in this
377 system. Predation of poorly-camouflaged nests could also have been so high that the frequency with
378 which we monitored nests was insufficient to detect any effect of camouflage metrics.
379 Alternatively, the lack of any detected effect of camouflage on survival could indicate that the
380 primary purpose of nest covering is something other than concealment, such as thermal insulation,
381 or it could indicate that the predators are utilising some other cue to find nests, such olfactory cues
382 or watching the adult plovers for their covering scuffle. However, we suggest that the primary
383 function of nest covering at our field site is likely to be visual concealment, for the following
384 reasons. First, nest-covering behaviour was specifically associated with the presence of potential
385 threats, but not the presence of animals that did not pose a threat. Second, a number of other plover

386 species nest in the same habitat at the same time and lay similarly-sized eggs without requiring
387 further nest insulation (e.g. chestnut banded-plovers, three-banded plovers *C. tricoloris*, and white-
388 fronted plovers *C. marginatus*). Third, artificial Kittlitz's plover nests at our field site in a
389 subsequent breeding season were more likely to be detected by predators than were uncovered nests
390 (Ferguson 2016). However, given the large geographical distribution of Kittlitz's plovers
391 throughout much of Africa, there are likely to be sites where thermal factors are more important,
392 and this may have influenced the evolution of the behaviour in the species as a whole.

393 Our study highlighted the importance of the pied crow as a nest predator, not just for the
394 Kittlitz's plover, but also for other plover species monitored at this field site. Pied Crows have
395 greatly increased in numbers in our study region over the last two decades (Cunningham et al.
396 2016). We were unable to determine how many individual pied crows were responsible for the
397 predation events in this study, but they were most often observed in pairs, although we occasionally
398 observed larger flocks at one of the study sites that was adjacent to a farm. It is therefore possible
399 that the majority of Kittlitz's plover predation events were caused by a single individual or pair at
400 each site. If so, then these intelligent, visually-guided predators would be afforded substantial
401 learning opportunities, allowing them to specialise in finding the concealed Kittlitz's plover nests
402 using a search image (Bond & Kamil 1999). The use of high-contrast nest-covering material we
403 observed could also be a salient factor that enhances learning rates, as experiments on humans show
404 that while high contrast prey benefit from increased disruptive camouflage, people also learnt to
405 find higher contrast prey faster over successive prey encounters (Troscianko *et al.* 2013).

406 The appearance of most camouflaged animals represents a compromise between the
407 different traits that best protect them from detection in range of habitat types and visual
408 backgrounds where they are vulnerable to predation (Endler 1978), and can also be constrained by
409 their thermal properties (Grant 1982, Mayer et al. 2009, Amat et al. 2012, Gómez *et al.* 2015;
410 Wilson-Aggarwal *et al.* 2016). The nest-covering behaviour of Kittlitz's plovers therefore provides
411 a useful study system for investigating camouflage that is not subject to the same visual constraints
412 as the adults and eggs, in that it can be plastically modified within and between breeding attempts.
413 Surprisingly, our data suggest that Kittlitz's plovers did not select nest material to match their
414 specific nest background, but rather to match the colour of their eggs. However, the selection
415 criteria used by the plovers when collecting nesting material – and how exactly the colour match is
416 achieved – remains unknown. Future work should investigate whether our findings reflect a trade-
417 off between selecting materials that matched egg colour at the expense of rendering the covered
418 nest a poor pattern and contrast match to the background, or whether the systematic use of materials
419 with high contrast and small pattern grain size was adaptive, reflecting a switch from a background-

420 matching strategy to a disruptive coloration strategy. Our study also suggests that increasing pied
421 crow numbers (Cunningham et al. 2016) could pose a threat if high-contrast nests offer a salient
422 learning cue to these predators. If so, then changes in predator communities and abundance may
423 have significant effects on the adaptive value of anti-predator strategies such as camouflage.

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433 **Data Accessibility**

434 Data are available in the Open Research Exeter repository.

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570 Figures

571 **Figure 1;** Kittlitz's plovers rarely have clearly-defined nest edges; instead, the amount of loose
572 material they move decreases with distance from the nest. We therefore measured the nest visual
573 appearance in concentric rings centred on the nest (white rings, “a” to “e”). Zone “a” was always
574 composed of entirely modified material, while zone “e” was typically minimally modified or
575 unmodified. Any egg visible through the nest covering material was excluded from analysis (red).
576 We also took a pair of control photographs 5 m either side of each nest as random background
577 samples that are highly unlikely to have been substantially modified by the plovers (bottom left and
578 right).

579

580 **Figure 2;** Three sample nest images. Images in the left column show LW, MW and SW peafowl
581 cone-catch quanta, the central column shows false colour MW, SW and VS cone-catch, and the
582 right column shows the uncovered nest. Cone-catch values were square-root transformed for this
583 figure to optimise viewing. The rows show examples of the different nest materials, with organic
584 material (primarily sticks and dried leaves, top row), a mixture (central row), and inorganic material
585 (primarily small stones and sand).
586

587 **Figure 3;** Boxplots showing the camouflage metrics found to vary significantly with distance from
588 the nest. Regression lines also show standard error (shaded region). Zones “a” to “e” are concentric
589 rings increasing in distance from the centre of the nest, the final zones (“5 m”) are control images
590 taken 5 m from each nest.

591

592

593 **Figure 4 (Cover Image);** Kittlitz's plover sitting on its nest. When the plover sees a threat
594 approaching it will perform a 'leaving scuffle' over the nest to conceal its eggs. The plovers
595 carefully select materials for covering theirs nests in advance that are a near-perfect match to the
596 colour of their eggs when viewed by predators.

597

598

599 **Supplementary Video:** <https://youtu.be/Q11zjdQnjIU> This video shows footage from hides and
600 from motion-sensitive cameras monitoring the Kittlitz's plover nests. Pied crows were the main
601 daytime threat to nest survival. Other causes of nest destruction were egg-piercing blacksmith
602 plovers, and high water. The video also shows examples of the "leaving-scuffle" used to cover the
603 clutch with material, and the selection of nest covering material, which once selected in the nearby
604 region, is thrown back towards the nest.