

This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

Author(s): Macedo, Tiago; Campos, João Carlos; Nokelainen, Ossi; Scott-Samuel, Nicholas E; Boratyński, Zbyszek

Title: The effect of spatial and temporal scale on camouflage in North African rodents

Year: 2022

Version: Accepted version (Final draft)

Copyright: © The Author(s) 2022. Published by Oxford University Press on behalf of The Linnean Society of London

Rights: In Copyright

Rights url: <http://rightsstatements.org/page/InC/1.0/?language=en>

Please cite the original version:

Macedo, T., Campos, J. C., Nokelainen, O., Scott-Samuel, N. E., & Boratyński, Z. (2022). The effect of spatial and temporal scale on camouflage in North African rodents. *Biological Journal of the Linnean Society*, 137(3), 523-533. <https://doi.org/10.1093/biolinnean/blac107>

1 The effect of spatial and temporal scale on camouflage in North African rodents

2

3 Tiago Macedo ^{1*}, João Carlos Campos ², Ossi Nokelainen ³, Nicholas E. Scott-Samuel ⁴,

4 Zbyszek Boratyński ²

5 ¹ Department of Biology, Faculty of Science, University of Porto, 4099-002 Porto,

6 Portugal.

7 ² CIBIO-InBIO Associate Laboratory, Research Center in Biodiversity and Genetic

8 Resources, University of Porto; BIOPOLIS Program in Genomics, Biodiversity and Land

9 Planning, Campus Vairão, 4485-661 Vairão, Portugal

10 ³ Department of Biological and Environmental Science, University of Jyväskylä, P.O.

11 Box 35, 40014, Jyväskylä, Finland

12 ⁴ School of Psychological Science, University of Bristol, Bristol, UK

13

14 *Corresponding author: Tiago Macedo – macedo.tiago.a@gmail.com

15

16 Running head: Spatiotemporal camouflage

17

18 Keywords: adaptation, background matching, desert, generalist, rodents, Sahara-Sahel,

19 specialist

20 Abstract

21 Background matching, a common form of camouflage, is a widespread anti-predator
22 adaptation that hinders detection or recognition by increasing prey resemblance to its
23 environment. However, the natural environment is complex, and spatially and temporally
24 variable, which constrains effective background matching as an anti-predator strategy. Here,
25 using remote sensing data (publicly available satellite imagery), we investigated how
26 variation of habitat parameters predicts background matching in sixteen Sahara-Sahel rodent
27 species across spatial and temporal scales. All fur colour parameters (hue, saturation and
28 brightness) strongly matched species' respective habitats. Background matching in terms of
29 hue was best at the microscale, while results for saturation and brightness showed more
30 variation across spatial scales among species. Camouflage across the temporal scale (from
31 one to three years before capture) was variable among species for all colour parameters.
32 These complex interactions suggest that, in desert rodents, colour parameters are
33 differentially sensitive to the respective scale of the habitat, plausibly reflecting species'
34 behaviour, life history and the ecological properties determining their activity patterns.
35 Consequently, the division between habitat (camouflage) generalists and specialists may
36 become blurred in temporally changing and spatially variable environments.

37 **Introduction**

38 Camouflage, also known as visual crypsis, is a widespread anti-predator adaptation that
39 hinders detection or recognition by increasing prey resemblance to the natural environment or
40 the objects therein (Cuthill, 2019). Plausibly, the most common camouflage type is
41 background matching (Price et al., 2019). Camouflage acts to reduce the signal-to-noise ratio,
42 in which the signal is the object of interest (i.e., the prey), and the noise is anything that
43 interferes with processing of that signal (i.e., the background) in the visual environment
44 (Merilaita, Scott-Samuel & Cuthill, 2017). Both the noise and the signal are filtered through
45 the eyes of a predator, leading different visual receivers (i.e., predator species) to potentially
46 process the signal and the noise in a species-specific way (Cuthill, 2019; Endler, 1978). To
47 avoid being detected by visual predators (Endler, 1978; Nokelainen et al., 2020a), such as
48 aerial (e.g. owls; Kotler, Brown & Hasson, 1991) and terrestrial species (e.g. foxes and
49 wolves; Atickem et al., 2017), animals match the colour of their environment, reducing the
50 signal-to-noise ratio. In visually heterogeneous habitats, however, background matching is
51 not easy to achieve (Ramirez-Delgado & del Castillo, 2020).

52

53 Almost all habitats vary spatially as well as temporally (i.e., between years and seasons) and
54 animals that match the background in a given location might not be able to match it at
55 another location or time (Merilaita, 2011). Therefore, one of the critical requirements for
56 effective camouflage is accommodating for the spatial and temporal heterogeneity of the
57 habitat (Merilaita et al., 2017). Some background types are relatively homogeneous, and can
58 be characterized as a single surface texture. When the environment is homogeneous,
59 backgrounds are similar, and therefore an animal's general resemblance to the background
60 may suffice (Merilaita et al., 2017). In contrast, in heterogenous habitats that include two or

61 more visually different microhabitats consisting of multiple heterogeneous patterns, animals
62 can apply various tactics to optimize their survival (when physiological colour change is not
63 possible). For instance, they could best match the colours of the most often utilised
64 background, at the expense of other background types where their survival is lower: a
65 specialist camouflage strategy (Cuthill, 2019). However, when the environment is
66 heterogeneous, but the variation within local habitats is not high, a generalist strategy could
67 outperform the specialist one (Merilaita, 2011). In such cases compromise camouflage, when
68 animal colour best matches the average parameters of surrounding habitats, may maximize
69 the survival rate (Michalis et al., 2017; Houston, Stevens & Cuthill, 2007; Hughes, Liggins &
70 Stevens, 2019).

71

72 Camouflage in the Sahara-Sahel desert rodents represents a fine example of background
73 matching in a geographically widespread community (Fig. 1) (Boratyński et al., 2017;
74 Boratyński et al., 2014). The colours of Sahara-Sahel rodents are correlated with their
75 respective backgrounds and visual modelling has shown that their camouflage is effective
76 against their usual predators (owls, foxes and wolves; Kotler, Brown & Hasson, 1991;
77 Nokelainen et al., 2020a). However, colour parameters can influence spatial and temporal
78 scales of camouflage in different ways. For example, owls' visual systems are predicted to be
79 optimized for scotopic light levels, with high vision resolution and a clear retinal image
80 (Orlowski, Harmening & Wagner, 2012); therefore, camouflage in brightness can be
81 predicted in owls' main prey. The spatial scale of variable colour parameters of camouflage,
82 and how consistent they are across temporally changing environments, is under-explored in
83 the community of the Sahara-Sahel rodents.

84

85 In this work we investigated phenotype-environment matching across spatial and temporal
86 scales, in sixteen North African rodent species. First, we assessed whether colour phenotype
87 in some species is optimized at local spatial scales (<100 m), indicating behavioural
88 specialization of utilized habitats and a specialist camouflage strategy (Nokelainen et al.,
89 2020b). Alternatively, most broadly distributed species could have evolved camouflage to a
90 relatively wide geographical scale, indicating utilization of variable habitats and a generalist
91 camouflage strategy (Table 1). Variation in camouflage among species can relate to
92 differences in their studied life history characteristics (Table S1). Second, we assessed the
93 temporal scale of camouflage, indicative of delayed phenotypic responses following
94 environmental (e.g., climatic) changes. Following the suggestion that camouflage can evolve
95 rapidly (Boratyński et al. 2017), and because of the short generation time and supposedly
96 strong survival-selection in rodents, we expected good camouflage (high background-match)
97 to the most recent habitats utilized by the species (Table 2), giving them an advantage when
98 exposed to climate changes and habitat fluctuations in a changing environment.

99

100 **Materials and Methods**

101 **Specimens**

102 Data were collected across different seasons and years (2016-2020), during several
103 expeditions to the Sahara-Sahel, in Mauritania, Morocco, Algeria, Chad and Ethiopia (Table
104 S2) (Boratyński et al., 2013; Brito, 2011; Guerreiro et al., 2016; Moutinho et al., 2015; Bryja
105 et al., 2022). Rodent capture was performed with minimum invasive methods, using life-traps
106 (Sherman, Folding Aluminium Heavy Duty) and hand-held nets (when searching for active
107 animals at night). Data for 295 animals from 16 species were collected, with individuals
108 belonging to *Acomys louisae* (8 individuals), *Acomys mullah* (3), *Gerbilliscus robustus* (1),

109 *Gerbillus amoenus* (32), *G. dasyurus* (1), *G. gerbillus* (58), *G. henleyi* (5), *G. occiduus* (17),
110 *G. pyramidum* (5), *G. tarabuli* (37), *Jaculus hirtipes* (68), *J. jaculus* (40), *Mastomys huberti*
111 (1), *Meriones libycus* (3), *Pachyuromys duprasi* (8), *Psammomys obesus* (8). Cryptic species
112 were genetically barcoded to confirm their species affiliation (Bryja et al., 2022; Moutinho et
113 al., 2020; Boratyński et al., 2017).

114

115 Phenotype and immediate habitat colouration

116 To quantify phenotypes and their match to the immediate background, digital photographs of
117 both animals and their habitat were collected during the expeditions. The photographs
118 encompassed the entire dorsal view of animals and their respective immediate backgrounds
119 (within 1 m). Photographs were taken in bright but shaded daylight conditions. Photographs
120 were taken from similar height (c. 1 m) and included a colour and size reference scale (X-
121 Rite ColorChecker; Fig. 1). Photographs were taken with a Canon EOS 400D digital camera,
122 equipped with a Canon 18–55 mm kit lens and saved in RAW format. The images were
123 standardized (equalized) with white and black standards presented in the frame in an ImageJ
124 plugin, micaToolbox (Troscianko & Stevens, 2015). Each animal's dorsum (an area of at
125 least 2 cm²) and entire habitat colouration present on the image were used to calculate
126 standard RGB values (0-255).

127

128 Spatial and temporal scales of environmental colouration

129 Remote sensing data were used to estimate environmental colouration of sample locations
130 from available NASA Landsat satellite images, with Google Earth Engine's (GEE, Gorelick
131 et al., 2017). The dataset included the atmospherically corrected surface reflectance from
132 Landsat 8 OLI/TIRS sensors (Landsat 8 Surface Reflectance Tier 1 dataset). Data were

133 collected for the blue (B2), green (B3) and red (B4) bands. To calculate the gradient of spatial
134 scale habitat colouration we collected medians of the sample points (30 m, i.e., the spatial
135 resolution of the visible bands of the Landsat satellite images) and of corresponding buffers
136 around the sample points with diameters of 30 m, 100 m, 500 m, 1 000 m, 10 000 m, and 100
137 000 m. Thus, the spatial scale spanned from the micro (1-100 m) to macro scales (1-100 km),
138 mirroring increments of increasing size, corresponding at one end to the resolution of the
139 individual specimen's mobility (home ranges), and at the other end to the resolution of the
140 studied species geographic distributions (species ranges). To assess the temporal scale of
141 environmental colouration the medians were calculated for satellite data acquired for the year
142 of capture, as well as for three consecutive years before capturing animals. Remotely sensed
143 data were always taken from the same season (within one month) of subject capture.

144

145 Phenotype-environment matching

146 We transformed both digital and satellite images from RGB (red, green, blue) to HSV (hue,
147 saturation, brightness) space, because HSV better determines key parameters on how colour,
148 and consequently prey camouflage, is perceived (Ajmal et al., 2018). The hue (H) describes
149 the dominant wavelength (the actual colour), the saturation (S) describes the amount of grey
150 in a particular colour, while the brightness (V, or value) describes lightness-darkness of a
151 particular colour, for the same level of hue (Kuehni, 2012; Schwarz, Cowan & Beatty, 1987).
152 To quantify the level of camouflage, we calculated a matching (or similarity) index: the
153 inverted absolute difference between the animal dorsum against the background colouration
154 in which animals were found, at variable spatial and temporal scales. This HSV similarity
155 index was used as the dependent variable in further analyses: low similarity values indicating

156 inaccurate camouflage, and high similarity values indicating accurate camouflage (Tables 1
157 and 2).

158

159 Statistical analyses

160 To analyse camouflage patterns in the Sahara-Sahel rodent community we first combined
161 data for all species and tested how spatial and temporal scales affected camouflage accuracy
162 using a generalized linear mixed model test. We combined all collected data and constructed
163 three analyses, separately for hue, saturation and brightness, with the similarity index as
164 dependent variables, assuming beta distribution and logit link function. We included species
165 as a factor (16 levels) and spatial and temporal scales (scaled) as continuous predictors. Then,
166 we tested two-way factorial interactions between species, and spatial and temporal scales, to
167 test if Sahara-Sahel rodents responded differently to spatial and temporal scales. The
168 geographic structuring of the data and non-independence between records collected on the
169 same individuals were accounted for by the random factors of country of origin and
170 individual animal ID. Models with and without factorial interactions were evaluated using
171 AIC statistics (Table 3).

172

173 Next, to determine species-specific camouflage responses to spatial and temporal scales, we
174 constructed analyses similar to those above, but separately for five species with sufficient
175 records for conclusive analyses ($N > 30$): *Jaculus hirtipes* (70), *J. jaculus* (41), *G. gerbillus*
176 (58), *G. tarabuli* (37) and *G. amoenus* (32). The significance level of the analyses was
177 interpreted after correction for multiple tests (Holm-Bonferroni correction, including 5
178 species and 3 mismatch analyses, $N = 15$, $\alpha = 0.0033$). In the species-specific analyses we
179 included both linear and quadratic terms of spatial and temporal scale predictors, to account
180 for nonlinearity in camouflage responses. The statistics for linear terms were estimated in

181 simple models (without quadratic terms) while quadratic terms were estimated while
182 accounting also for linear terms. The positive linear terms indicate the best matching to wide
183 geographical scale and past habitat condition, while negative terms indicate the best matching
184 to narrow geographical scale and to the most recent habitats. The negative and positive
185 quadratic terms indicate bell and reverse bell-shaped relations. All statistical analyses and
186 visualizations were conducted in R software (packages: “rgb2hsv”, “glmmTMB2”,
187 “ggplot2”; “sjPlot”) (Team, 2021).

188

189 **Results**

190 Phenotype-environment correlations

191 We found that animal and habitat colour parameters, as well as similarities in hue, saturation
192 and brightness, varied significantly among species (different median values for each species,
193 Fig. 2). Simple Pearson's product-moment correlations between habitat and phenotype (not
194 accounting for variation among scales and species), that included all records for both spatial
195 and temporal scales and all species, was positive-moderate for brightness ($r = 0.48$, $df =$
196 7357 , $t = 46.55$, $p < 0.001$), positive-low for saturation ($r = 0.11$, $df = 7357$, $t = 9.76$, $p <$
197 0.001), and non-significant for hue ($r = -0.02$, $df = 7357$, $t = -1.34$, $p = 0.91$).

198

199 Spatio-temporal variation of camouflage

200 Results for mixed model analysis, including all species, showed that animal-to-habitat
201 similarity for hue related negatively with spatial [β (s.e.) = -0.08 (0.02), $z = -4.37$, $p < 0.001$]
202 and temporal scales [$\beta = -0.07$ (0.02), $z = -3.92$, $p < 0.001$]. In general, Sahara-Sahel rodents
203 better matched the hue of their habitat at micro spatial and recent temporal scales (Fig. 3).
204 The analyses for similarity in saturation and brightness showed no general pattern with
205 spatial [saturation: $\beta = 0.004$ (0.05), $z = 0.09$, $p = 0.931$, brightness: $\beta = 0.06$ (0.05), $z = 1.39$,

206 $p = 0.165$] and temporal scales [saturation: $\beta = -0.07$ (0.04), $z = -1.70$, $p = 0.089$; brightness:
207 $\beta = 0.01$ (0.04), $z = 0.14$, $p = 0.891$]. However, significant interactions between temporal and
208 spatial scales and species factor indicate that different rodents best match the saturation and
209 brightness parameters of their habitats at variable spatial and temporal scales (Table 3).

210

211 Species-specific camouflage responses to spatial and temporal scales

212 The results from mixed model analyses for the five best represented species (*J. hirtipes*, *J.*
213 *jaculus*, *G. gerbillus*, *G. tarabuli*, *G. amoenus*) showed a consistent relationship between
214 similarity in hue and spatial scale of camouflage (negative linear terms; Fig. 4). These species
215 best matched their habitat at the local scale, but the significant and positive quadratic
216 regression terms indicated that they also had a good habitat match over a wide geographical
217 scale (Fig. 4). Less consistent results were found for saturation and brightness. For saturation,
218 both *Jaculus* species showed the best match at macro spatial scale (positive linear terms),
219 while only one *Gerbillus* species (*G. tarabuli*) showed the best match at micro spatial scale
220 (negative linear term; Fig. 4). For brightness, three species (*J. hirtipes*, *G. tarabuli* and *G.*
221 *amoenus*) showed the best match at macro spatial scale (positive linear terms), while four (*J.*
222 *hirtipes*, *J. jaculus*, *G. gerbillus*, *G. tarabuli*) had a good match at both micro and macro
223 scales (positive quadratic terms; Fig. 4). For the temporal scale and hue (one species: *J.*
224 *hirtipes*) and brightness (two species: *G. tarabuli*, *G. amoenus*) significant statistics indicated
225 a better match to the most recent temporal scale (Fig. 4). In contrast, for one species (*G.*
226 *amoenus*) significant statistics for temporal scale and hue showed a better match to older
227 temporal scales. For saturation, two species (*G. tarabuli*, *G. amoenus*) best matched recent
228 and two (*J. hirtipes*, *J. jaculus*) later years habitat colouration, while the quadratic terms
229 indicating nonlinear relations were inconsistent (Fig. 4).

230

231 **Discussion**

232 Sixteen Sahara-Sahel rodent species (e.g.: Fig. 1) differed in the degree of their camouflage
233 across variable spatial and temporal scales (Tables 1-3). Despite the differences, there are
234 striking general patterns: all colour parameters (hue, saturation and brightness) strongly
235 matched the respective habitat parameters (Fig. 2) and all species showed the best hue
236 camouflage to their local habitat (suggesting a habitat specialist strategy; Fig. 3). Three
237 species had the best brightness matching, and *Jaculus* jerboas had the best saturation
238 matching, to the broad geographical scale (suggesting a habitat generalist strategy; Fig. 4).
239 The temporal changes in camouflage accuracy were less consistent among species, with two
240 *Gerbillus* gerbils showing the best camouflage against their recent habitat in saturation and
241 brightness, but the two *Jaculus* jerboas having the best saturation match to their older habitat
242 (Fig. 4).

243

244 Our results showed generally high phenotype-to-habitat similarities in all studied colour
245 parameters and species (Fig. 2), confirming good camouflage adaptation in Sahara-Sahel
246 rodents (Nokelainen et al., 2020b). Following the general expectation for nocturnal prey
247 (Penteriani et al., 2006), it was found that brightness of fur matched habitat relatively well
248 (Fig. 4). At night, during dim light conditions, colour might be less detectable for predators.
249 Nevertheless, our results indicated that hue and saturation of rodents' fur also matched their
250 respective habitats well. We found that the spatial scale of the background matching may
251 differ among colour parameters, even for the same species. For example, *Jaculus hirtipes*
252 expressed a high level of phenotype-to-habitat match in hue at the local spatial scale (1-
253 100m). This suggests an effective camouflage within individual home ranges and a habitat
254 specialist tactic in hue camouflage (Fig. 4, Fig. S1). In the same species other dorsal fur
255 colour properties - saturation and brightness - best matched habitat at the broad geographical

256 scale. This suggests effective generalist camouflage in saturation and brightness at a broad
257 spatial scale, perhaps important during dispersal of this highly mobile species (Fig. 4, Fig.
258 S1). The observations might be related to dynamic light conditions and the circadian activity
259 patterns of the studied organisms, as some colour properties are more relevant during sunlight
260 conditions (i.e., at dusk and dawn for this particular species) while others are more relevant at
261 night (Johnsen et al., 2006). The analysed rodent species may differ in many characteristics.
262 For some species camouflage might not be important, as for example savannah specialized
263 species (e.g.: *Mastomys* or *Gerbilliscus*) might apply different anti-predatory strategies, such
264 as: run and hide, run fast and manoeuvre sharply, or sit and wait (Nokelainen et al., 2020a).
265 More experimental work will be needed to resolve the importance of life histories on
266 determining camouflage in this rodent community.

267

268 Hue was the colour parameter most sensitive to the geographic scale of investigation: fur of
269 all studied species displayed a good match to the hue parameter of habitat at a local spatial
270 scale (Fig. 4). It can be speculated that this mirrors light conditions related to prey activity, as
271 well as the ability of predators to perceive colours. For instance, this apparent importance of
272 hue camouflage at the local geographical scale could reflect the ability of predators to detect
273 moving objects over contrasting surfaces (Fux & Eilam, 2009; Smart, Cuthill & Scott-
274 Samuel, 2020), promoting habitat specialization by prey. The resulting niche partitioning in
275 local geographical scale may reduce competition among sympatric species, promoting high
276 local diversity (Hector & Hooper, 2002; MacArthur, 1958, Simpson et al., 2021). The
277 relevant environmental and habitat variation found in the Sahara-Sahel, even with an
278 apparent lack of geographic barriers, could promote such local adaptation (Brito et al., 2014).
279 The micro-habitat specialization could be a mechanism behind the sympatric co-existence of
280 so many Sahara-Sahel rodents (Ndiaye et al., 2016; Shenbrot, Krasnov & Rogovin, 1999).

281

282 Three species (*Jaculus hirtipes*, *Gerbillus tarabuli*, *G. amoenus*) showed good camouflage in
283 their fur at the wide geographical scale in saturation and brightness (Fig. 4, Fig. S1).

284 Camouflage theory states that when the background is homogeneous, a single optimal
285 camouflage pattern for that animal to match the environment may exist (Merilaita et al.,
286 2017). Light and reflectance conditions are relatively homogeneous on the open desert
287 surface (Pinker & Karnieli, 1995), especially at nights when those rodents are active, and
288 therefore compromise camouflage to diversity of habitat could emerge. Saturation determines
289 the intensity of colour: the higher the saturation the more vivid the colour (Ajmal et al.,
290 2018). Interestingly, both *Jaculus* jerboa species showed good phenotype-habitat match for
291 saturation at the broad geographical scale (Fig. 4), and jerboas are a widely distributed
292 (Moutinho et al., 2020) and highly mobile species (Happold, 2013; Schröpfer, Klenner-
293 Fringes & Naumer, 1985). It can be speculated that frequent crossing of a variety of
294 background patches and heterogeneous environments would promote evolution of a
295 generalist camouflage (Merilaita, 2011). Such differences between taxa and among colour
296 parameters when determining the spatial scale of camouflage highlights the need for further
297 studies on the life histories of specialist versus generalist camouflage species.

298

299 The results of temporal camouflage scale were highly variable among species and colour
300 parameters (Fig. 4, Fig. S2). The fur of two *Gerbillus* species (*G. tarabuli*, *G. amoenus*)
301 matched the habitat brightness of the relatively recent time. This could correspond to 1-2
302 years delayed effect of population growth in *Gerbillus* rodents, responding to habitat
303 productivity after substantial rainfall in the Sahara-Sahel (Barros et al., 2018). Thus, the
304 selection and adaptation observed on individuals might be related to past rather than current

305 habitat structure (Morente-Lopez et al., 2020) and temporal scale can play a determinant role
306 in adaptation (Fox et al., 2019). With rapid ongoing environment changes (Chaparro-Pedraza,
307 2021), species may be exposed to increased risks of mismatching their optimal habitat and
308 might not be able to adapt quickly enough to survive such change (Otto, 2018).
309 Consequently, mismatching the most recent habitat structure, such as observed for *G.*
310 *amoenus* in hue and both *Jaculus* species in saturation (Fig. 4, Fig. S2), may reflect species'
311 sensitivity to sudden environment changes, potentially leading to population decreases and
312 increased extinction risks (Román-Palacios & Wiens, 2020).

313

314 **Conclusions**

315 Sahara-Sahel rodents have developed habitat match at variable geographical scales and in
316 different colour parameters. Depending on their predators' visual abilities and light
317 conditions, selection on hue, saturation or brightness could prevail, with prey developing
318 camouflage depending on the type and timing of the selection. Our results also show the
319 importance of temporally dynamic habitats in determining camouflage. Prey life history
320 strategies (e.g., fast-slow reproduction), spatial behaviours and mobility could all affect this
321 pattern and selection. But in ecosystems exposed to droughts, such as the Sahara-Sahel
322 (Karmaoui, 2019; Wendling et al., 2019), prey response to such drastic shifts in habitat might
323 compromise adaptations. If true, this poses a risk of extinction for locally maladapted
324 populations, if the adaptive or plastic responses are too slow.

325

326 **Funding**

327 ZB was supported by the Portuguese Foundation for Science and Technology (PTDC/BIA-
328 ECO/28158/2017) and National Geographic society (NGS-53336R-19). NESS was supported
329 by Biotechnology & Biological Sciences, UK, grant BB/S00873X/1.

330

331 **Acknowledgments**

332 We are grateful to two editors, three anonymous referees and Tim Caro for constructive
333 feedback on this manuscript.

334

335 **References**

336

337 **Ajmal A, Hollitt C, Freat M, Al-Sahaf H. 2018.** A comparison of RGB and HSV colour
338 spaces for visual attention models. 2018 International conference on image and vision
339 computing New Zealand (IVCNZ), 1-6.

340 **Barros MI, Brito JC, Campos JC, Mappes T, Qninba A, Sousa FV, Boratyński Z. 2018.**
341 The effect of rainfall on population dynamics in Sahara-Sahel rodents. *Mammal*
342 *Research* **63**: 485-492.

343 **Boratyński Z, Brito JC, Campos JC, Cunha JL, Granjon L, Mappes T, Ndiaye A,**
344 **Rzebik-Kowalska B, Serén N. 2017.** Repeated evolution of camouflage in speciose
345 desert rodents. *Scientific Reports* **7**: 3522.

346 **Boratyński Z, Brito JC, Campos JC, Karala M, Mappes T. 2014.** Large spatial scale of
347 the phenotype-environment color matching in two cryptic species of African desert
348 Jerboas (Dipodidae: *Jaculus*). *PLOS ONE* **9**: e94342.

349 **Boratynski Z CJ, Gonçalves DV, Granjon L, Martínez-Freiría F, Sow AS, Velo-Antón**
350 **G, Brito JC. 2013.** The Sudano-Sahelian Dalton's mouse, *Praomys daltoni*, in
351 Mauritania, Eastern Assaba mountains. *Go-South Bulletin* **10: 17-20.**

352 **Brito J, Campos, J., Gonçalves, D., Martínez-Freiría, F., & Sillero, N. 2011.** Status of
353 Nile crocodiles in the lower Senegal river basin. *Crocodile Specialist Group*
354 *Newsletter* **30: 7–10.**

355 **Brito JC, Godinho R, Martínez-Freiría F, Pleguezuelos JM, Rebelo H, Santos X, Vale**
356 **CG, Velo-Antón G, Boratyński Z, Carvalho SB, Ferreira S, Gonçalves DV, Silva**
357 **TL, Tarroso P, Campos JC, Leite JV, Nogueira J, Alvares F, Sillero N, Sow AS,**
358 **Fahd S, Crochet PA, Carranza S. 2014.** Unravelling biodiversity, evolution and
359 threats to conservation in the Sahara-Sahel. *Biol Rev Camb Philos Soc* **89: 215-231.**

360 **Bryja J, Meheretu Y, Boratyński Z, Zeynu A, Denys C, Muluaalem G, Welegerima K,**
361 **Bryjová A, Kasso M, Kostin DS, Martynov AA, Lavrenchenko LA. 2022.** Rodents
362 of the Afar Triangle (Ethiopia): geographical isolation causes high level of endemism.
363 *Biodiversity and Conservation.*

364 **Chaparro-Pedraza PC. 2021.** Fast environmental change and eco-evolutionary feedbacks
365 can drive regime shifts in ecosystems before tipping points are crossed. *Proceedings*
366 *of the Royal Society B: Biological Sciences* **288: 20211192.**

367 **Cuthill IC. 2019.** Camouflage. *Journal of Zoology* **308: 75-92.**

368 **Endler JA. 1978.** A predator's view of animal color patterns. In: Hecht MK, Steere WC and
369 Wallace B, eds. *Evolutionary Biology.* Boston, MA: Springer US. 319-364.

370 **Fox RJ, Donelson JM, Schunter C, Ravasi T, Gaitán-Espitia JD. 2019.** Beyond buying
371 time: the role of plasticity in phenotypic adaptation to rapid environmental change.
372 *Philosophical Transactions of the Royal Society B: Biological Sciences* **374:**
373 **20180174.**

374 **Fux M, Eilam D. 2009.** How barn owls (*tyto alba*) visually follow moving voles (*microtus*
375 *socialis*) before attacking them. *Physiology & Behavior* **98**: 359-366.

376 **Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R. 2017.** Google
377 Earth Engine: planetary-scale geospatial analysis for everyone. *Remote Sensing of*
378 *Environment*.

379 **Guerreiro R, Boratyński, Z., Cunha, J., Maaloum, H., Mappes, T., El, Agbani MA, &**
380 **Qninba, A. 2016.** Diversity of mammals in the Lower Drâa valley. A preliminary
381 survey. *Go-South Bulletin* **13**: 68–71.

382 **Happold DCD. 2013.** Mammals of Africa volume III rodents, hares and rabbits. In: Happold
383 DCD, ed. *Mammals of Africa : Rodents, Hares and Rabbits*. 1 ed. London:
384 Bloomsbury Publishing. 137-138.

385 **Hector A, Hooper R. 2002.** Darwin and the first ecological experiment. *Science* **295**: 639-
386 640.

387 **Smart IE, Cuthill IC, Scott-Samuel NE. 2020.** In the corner of the eye: Camouflaging
388 motion in the peripheral visual field. *Proceedings. Biological sciences* **287**:
389 20192537-20192537.

390 **Houston AI, Stevens M, Cuthill IC. 2007.** Animal camouflage: compromise or specialize in
391 a 2 patch-type environment? *Behavioral Ecology* **18**: 769-775.

392 **Hughes A, Liggins E, Stevens M. 2019.** Imperfect camouflage: how to hide in a variable
393 world? *Proceedings of the Royal Society B: Biological Sciences* **286**: 20190646.

394 **Johnsen Sn, Kelber A, Warrant E, Sweeney AM, Widder EA, Lee RL, Jr, Hernández-**
395 **Andrés J. 2006.** Crepuscular and nocturnal illumination and its effects on color
396 perception by the nocturnal hawkmoth *Deilephila elpenor*. *Journal of Experimental*
397 *Biology* **209**: 789-800.

398 **Karmaoui A. 2019.** Drought and desertification in Moroccan Pre-Sahara, Draa valleys:
399 exploring from the perspective of young people. *Geoenvironmental Disasters* **6**: 2.

400 **Kotler BP, Brown JS, Hasson O. 1991.** Factors affecting gerbil foraging behavior and rates
401 of owl predation. *Ecology* **72**: 2249-2260.

402 **Kuehni RG. 2012.** Color an introduction to practice and principles color : An introduction to
403 practice and principles. Wiley: Hoboken, NJ Hoboken, N.J.

404 **MacArthur RH. 1958.** Population ecology of some warblers of northeastern coniferous
405 forests. *Ecology* **39**: 599-619.

406 **Merilaita S, Lyytinen A, Mappes J. 2001.** Selection for cryptic coloration in a visually
407 heterogeneous habitat. *Proceedings of the Royal Society of London. Series B:*
408 *Biological Sciences* **268**: 1925-1929.

409 **Merilaita, Scott-Samuel, Cuthill. 2017.** How camouflage works. *Philosophical*
410 *Transactions of the Royal Society B-Biological Sciences* **372**.

411 **Merilaita S. 2011.** Animal camouflage: mechanisms and function. *Cambridge University*
412 *Press: Cambridge*.

413 **Michalis C, Scott-Samuel NE, Gibson DP, Cuthill IC. 2017.** Optimal background
414 matching camouflage. *Proceedings of the Royal Society B: Biological Sciences* **284**:
415 20170709.

416 **Morente-Lopez J, Scheepens JF, Lara-Romero C, Ruiz-Checa R, Tabares P, Iriundo**
417 **JM. 2020.** Past selection shaped phenological differentiation among populations at
418 contrasting elevations in a Mediterranean alpine plant. *Environmental and*
419 *Experimental Botany* **170**.

420 **Moussa H, Karim S, Salaheddine D. 2015.** Diversity and richness of rodent communities in
421 various landscapes of Touggourt Area (Southeast Algeria).

422 **Moutinho AF, Qninba, A., Harrington, A., Forbes, K., Sérén, N., Mappes, T.**
423 **Boratyński, Z. 2015.** Winter breeding of the Lesser Egyptian Jerboa *Jaculus jaculus*
424 (Linnaeus, 1758) in Southern Morocco. *Go-South Bulletin* **12**: 24-27.

425 **Moutinho AF, Serén N, Paupério J, Silva TL, Martínez-Freiria F, Sotelo G, Faria R,**
426 **Mappes T, Alves PC, Brito JC, Boratyński Z. 2020.** Evolutionary history of two
427 cryptic species of northern african jerboas. *BMC Evolutionary Biology* **20**: 26.

428 **Ndiaye A, Chevret P, Dobigny G, Granjon L. 2016.** Evolutionary systematics and
429 biogeography of the arid habitat-adapted rodent genus *Gerbillus* (Rodentia, Muridae):
430 a mostly Plio-Pleistocene African history. *Journal of Zoological Systematics and*
431 *Evolutionary Research* **54**: 299-317.

432 **Nokelainen O, Sreelatha LB, Brito JC, Campos JC, Scott-Samuel NE, Valkonen JK,**
433 **Boratyński Z. 2020a.** Camouflage in arid environments: the case of Sahara-Sahel
434 desert rodents. *Journal of Vertebrate Biology* **69**: 1-12, 12.

435 **Nokelainen O, Brito JC, Scott-Samuel NE, Valkonen JK, Boratyński Z. 2020b.**
436 Camouflage accuracy in Sahara–Sahel desert rodents. *Journal of Animal Ecology* **89**:
437 1658-1669.

438 **Orlowski J, Harmening W, Wagner H. 2012.** Night vision in barn owls: Visual acuity and
439 contrast sensitivity under dark adaptation. *Journal of Vision* **12**: 4-4.

440 **Otto SP. 2018.** Adaptation, speciation and extinction in the Anthropocene. *Proceedings of*
441 *the Royal Society B: Biological Sciences* **285**: 20182047.

442 **Penteriani V, del Mar Delgado M, Alonso-Alvarez C, Sergio F. 2006.** The importance of
443 visual cues for nocturnal species: eagle owls signal by badge brightness. *Behavioral*
444 *Ecology* **18**: 143-147

445 **Pinker RT, Karnieli A. 1995.** Characteristic spectral reflectance of a semi-arid environment.
446 *International Journal of Remote Sensing* **16**: 1341-1363.

447 **Price N, Green S, Troscianko J, Tregenza T, Stevens M. 2019.** Background matching and
448 disruptive coloration as habitat-specific strategies for camouflage. *Scientific Reports*
449 **9**.

450 **Ramirez-Delgado VH, del Castillo RC. 2020.** Background matching, disruptive coloration,
451 and differential use of microhabitats in two neotropical grasshoppers with sexual
452 dichromatism. *Ecology and Evolution* **10**: 1401-1412.

453 **Román-Palacios C, Wiens JJ. 2020.** Recent responses to climate change reveal the drivers
454 of species extinction and survival. *Proceedings of the National Academy of Sciences*
455 **117**: 4211.

456 **Schröpfer R, Klenner-Fringes B, Naumer E. 1985.** Locomotion pattern and habitat
457 utilisation of the two jerboas *Jaculus jaculus* and *Jaculus orientalis* (Rodentia,
458 Dipodidae). **49**: 445-454.

459 **Schwarz MW, Cowan WB, Beatty JC. 1987.** An experimental comparison of RGB, YIQ,
460 LAB, HSV, and opponent color models. *ACM Trans. Graph.* **6**: 123-158.

461 **Shenbrot GI, Krasnov BR, Rogovin KA. 1999.** Composition of the rodent faunas of
462 different desert regions *Spatial Ecology of Desert Rodent Communities*. Berlin,
463 Heidelberg: Springer Berlin Heidelberg. 25-61.

464 **Simpson RK, Wilson DR, Mistakidis AF, Mennill DJ, Doucet SM. 2021.** Sympatry drives
465 colour and song evolution in wood-warblers (Parulidae). *Proceedings of the Royal*
466 *Society B: Biological Sciences* **288**: 20202804.

467 **Team RC. 2021.** R: A language and environment for statistical computing. *R Foundation for*
468 *Statistical Computing*.

469 **Troscianko J, Stevens M. 2015.** Image calibration and analysis toolbox – a free software
470 suite for objectively measuring reflectance, colour and pattern. *Methods in Ecology*
471 *and Evolution* **6**: 1320-1331.

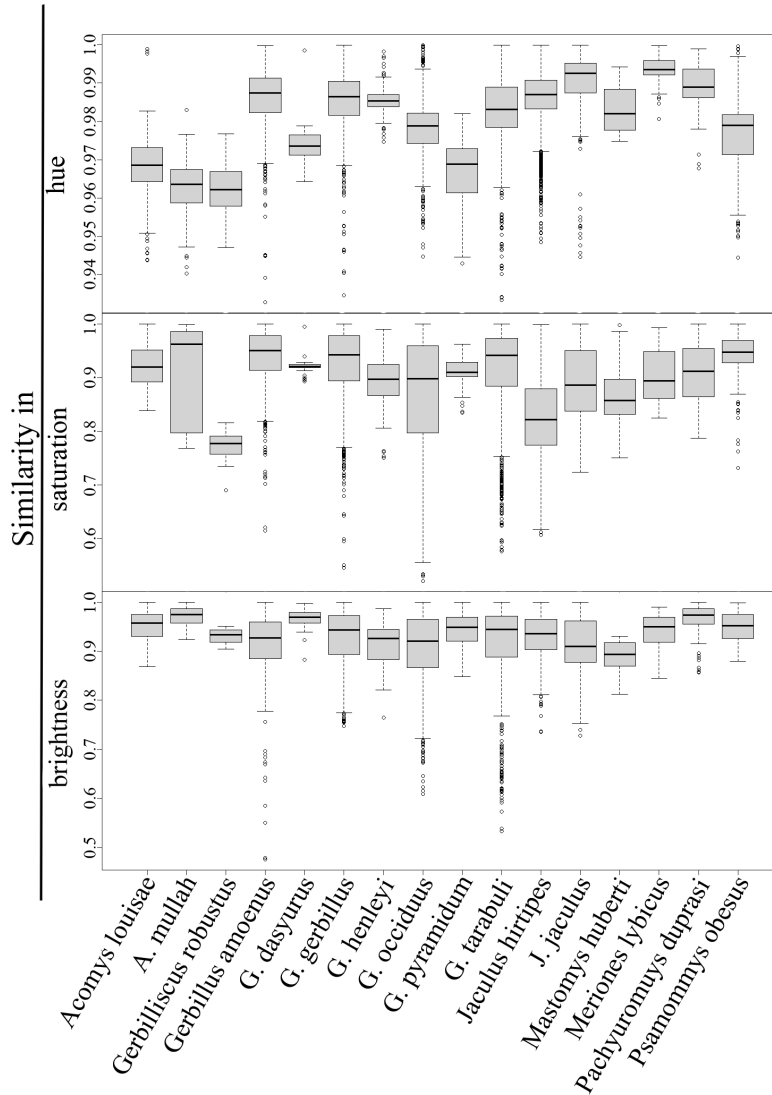
472

473 **Wending V, Peugeot C, Mayor AG, Hiernaux P, Mougin E, Grippa M, Kergoat L,**
474 **Walcker R, Galle S, Lebel T. 2019.** Drought-induced regime shift and resilience of a
475 Sahelian ecohydrosystem. *Environmental Research Letters* **14**: 105005.

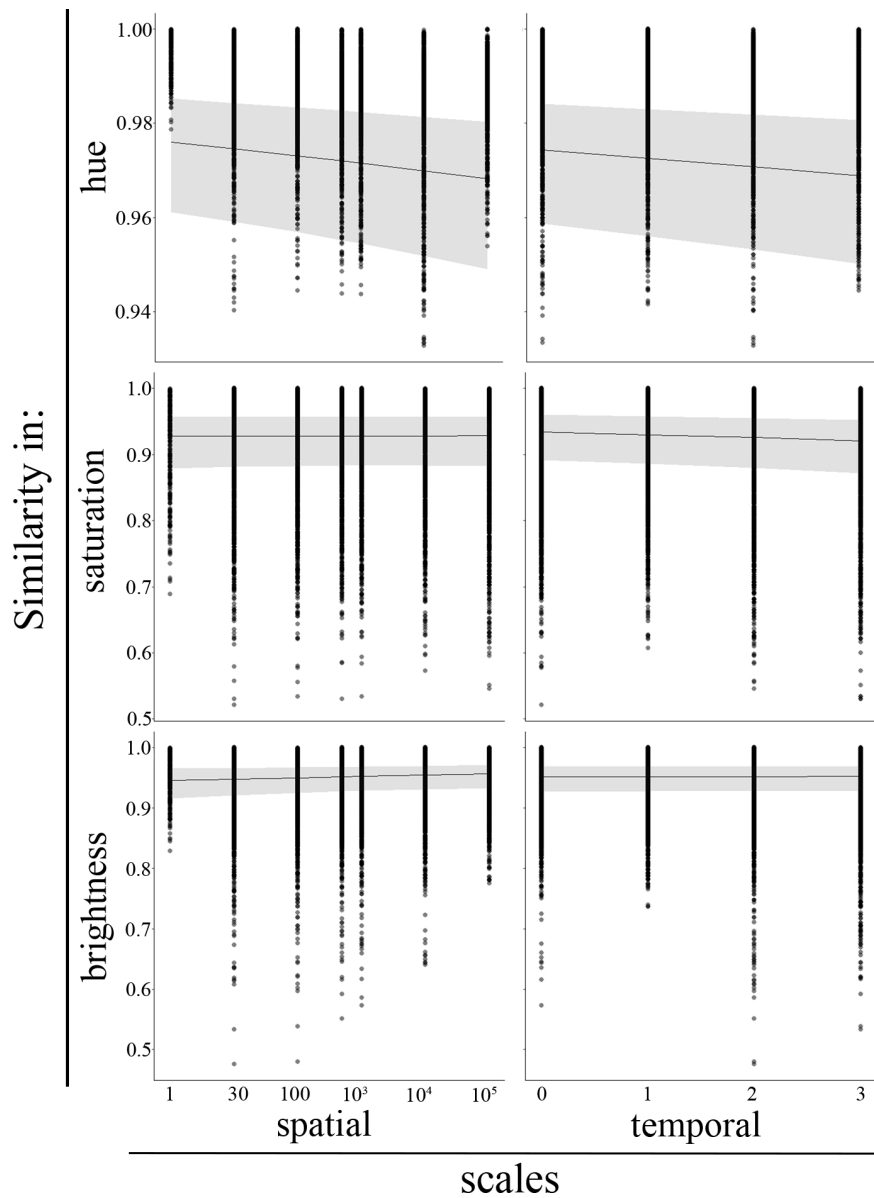
476 Figure legends



477 Figure 1. Examples of Sahara-Sahel desert rodents on their natural background. Top left:
478 *Jaculus hirtipes*, Assa-Zag, Morocco; top right: *Gerbillus amoenus*, Adrar, Mauritania
479 (including colour and size reference); bottom left: *Pachyuromys duprasi*, Assa-Zag,
480 Morocco; bottom right: *Gerbillus gerbillus*, Ounianga lakes, Chad.

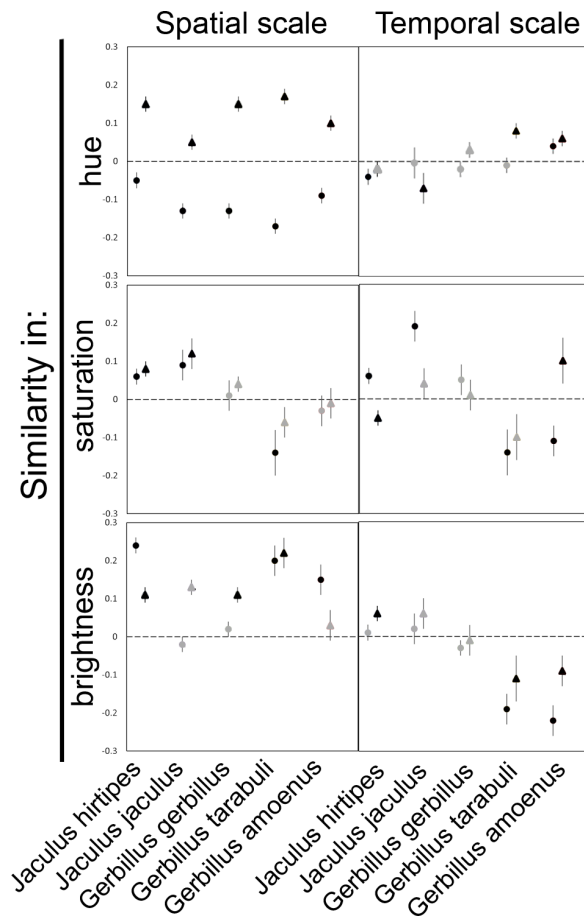


482 Figure 2. Variation in phenotype-habitat similarity in hue, saturation and brightness in sixteen
 483 studied Sahara-Sahel rodent species. Bold line in each box represents median, box represents
 484 interquartile range, whiskers represent data values between lower/upper quartiles and
 485 minimum/maximum values, dots (above and below whiskers) represents outliers (1.5 outside
 486 the interquartile range). For each specimen the similarity was calculated repeatedly, for all
 487 spatial (1-100 000 m) and temporal scales (1-4 years before capture).



488 Figure 3. Results for three generalized linear mixed model analyses for sixteen Sahara-Sahel
 489 rodent species, with the phenotype-habitat similarity in hue, saturation or brightness as
 490 dependent variables, and spatial (meters around trapping location) and temporal (years before
 491 trapping) scales as predictors. Data points are represented as dots (vertical lines are a
 492 concentration of data points) and shaded areas represent standard deviations.

493



494 Figure 4. Effect sizes (circles - linear coefficients; triangles - quadratic coefficients) of the
 495 strength and direction of the relations between phenotype-habitat similarity and spatial (left
 496 panels) and temporal (right panels) scales. Coefficients (y-axis) were derived from
 497 generalized linear mixed models for five Sahara-Sahel rodent species (x-axis), where
 498 phenotype to habitat similarity in hue, saturation and brightness were included as dependent
 499 variables and spatial and temporal scales as predictors. Positive linear terms indicate better
 500 camouflage in wider geographical, and older temporal scales, whereas negative linear terms
 501 indicate better camouflage in narrower geographical and recent temporal scales. Positive and
 502 negative quadratic terms represent reverse-bell and bell shaped relations, respectively. The
 503 significance of multiple test corrections (Holm-Bonferroni) for α 0.0033 is indicated by black
 504 (significant) and grey (non-significant) data points.

505 Table 1. Hypothetical relationships between phenotype-habitat colour similarities and
506 geographical (spatial) scale. Putative camouflage specialist species express the best match at
507 narrow (micro) spatial scale and the worst at wide (macro) spatial scale. Generalist species
508 express the worst match at micro spatial scale and the best at macro spatial scale.

| Habitat: | Spatial scale | |
|------------|---------------|------------|
| | Micro | Macro |
| specialist | good match | poor match |
| generalist | poor match | good match |

509

510 Table 2. Hypothetical relationships between phenotype-habitat colour similarities and
511 temporal scale. Sensitive to habitat change, slowly adapting to environmental shifts, species
512 would express the best camouflage to older habitat and the worst to recent habitat along the
513 temporal scale. Fast adapting species would express the best camouflage to recent habitat and
514 the worst to older habitat along the temporal scale.

| Habitat change | Temporal scale | |
|----------------|----------------|------------|
| | Recent | Older |
| sensitive | bad match | good match |
| insensitive | good match | bad match |

515 Table 3. Anova results from three mixed model analyses with similarity between animal
 516 dorsal fur and habitat in hue, saturation or brightness as dependent variables, species (16) as
 517 factor and spatial and temporal scales as predictors.

| | df | hue | | saturation | | brightness | |
|-----------------|----|-------------------------------|--------|-------------------------------|--------|-------------------------------|--------|
| | | Ch ² | p | Ch ² | p | Ch ² | p |
| Species | 15 | 108.63 | <0.001 | 188.38 | 0.11 | 31.81 | <0.001 |
| Spatial scale | 1 | 517.05 | <0.001 | 2.61 | <0.001 | 238.56 | <0.01 |
| Temporal scale | 1 | 137.60 | <0.001 | 0.02 | 0.89 | 229.78 | <0.001 |
| Spatial*species | 15 | 221.55 | <0.001 | 172.80 | <0.001 | 273.86 | <0.001 |
| Temp.*species | 15 | 76.11 | <0.001 | 413.06 | <0.001 | 422.68 | <0.001 |
| | | AIC = -55988, BIC = -55636 | | AIC = -24045, BIC = -23693 | | AIC = -29119, BIC = -28767 | |

518