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15

16 Running head: Spatiotemporal camouflage

17

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19 specialist

20 Abstract

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

37 Introduction

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

52

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

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

71

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

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

99

100 Materials and Methods

101 Specimens

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

Gerbillus amoenus (32), G. dasyurus (1), G. gerbillus (58), G. henleyi (5), G. occiduus (17),
G. pyramidum (5), G. tarabuli (37), Jaculus hirtipes (68), J. jaculus (40), Mastomys huberti
(1), Meriones libycus (3), Pachyuromys duprasi (8), Psammomys obesus (8). Cryptic species
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

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

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

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

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

144

145 Phenotype-environment matching

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

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

158

159 Statistical analyses

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

172

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

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

188

189 **Results**

190 Phenotype-environment correlations

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

199 Spatio-temporal variation of camouflage

200 Results for mixed model analysis, including all species, showed that animal-to-habitat

similarity for hue related negatively with spatial [β (s.e.) = -0.08 (0.02), z = -4.37, p < 0.001]

and temporal scales [$\beta = -0.07 (0.02)$, z = -3.92, p < 0.001]. In general, Sahara-Sahel rodents

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

spatial [saturation: $\beta = 0.004 (0.05)$, z = 0.09, p = 0.931, brightness: $\beta = 0.06 (0.05)$, z = 1.39,

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

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

231 Discussion

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

243

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

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

267

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

Three species (Jaculus hirtipes, Gerbillus tarabuli, G. amoenus) showed good camouflage in 282 their fur at the wide geographical scale in saturation and brightness (Fig. 4, Fig. S1). 283 Camouflage theory states that when the background is homogeneous, a single optimal 284 camouflage pattern for that animal to match the environment may exist (Merilaita et al., 285 286 2017). Light and reflectance conditions are relatively homogeneous on the open desert surface (Pinker & Karnieli, 1995), especially at nights when those rodents are active, and 287 therefore compromise camouflage to diversity of habitat could emerge. Saturation determines 288 the intensity of colour: the higher the saturation the more vivid the colour (Ajmal et al., 289 2018). Interestingly, both Jaculus jerboa species showed good phenotype-habitat match for 290 saturation at the broad geographical scale (Fig. 4), and jerboas are a widely distributed 291 (Moutinho et al., 2020) and highly mobile species (Happold, 2013; Schröpfer, Klenner-292 Fringes & Naumer, 1985). It can be speculated that frequent crossing of a variety of 293 294 background patches and heterogeneous environments would promote evolution of a generalist camouflage (Merilaita, 2011). Such differences between taxa and among colour 295 parameters when determining the spatial scale of camouflage highlights the need for further 296

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

studies on the life histories of specialist versus generalist camouflage species.

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

313

314 Conclusions

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

325

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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.



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



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



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

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

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

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

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

- 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.

		hue		saturation		brightness	
	df –	Ch ²	р	Ch ²	р	Ch ²	р
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,		AIC = -24045,		AIC = -29119,	
		BIC = -55636		BIC = -23693		BIC = -28767	