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

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Running head: Spatiotemporal camouflage

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Abstract

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

Introduction

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

Almost all habitats vary spatially as well as temporally (i.e., between years and seasons) and animals that match the background in a given location might not be able to match it at 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 habitat (Merilaita et al., 2017). Some background types are relatively homogeneous, and can be characterized as a single surface texture. When the environment is homogeneous, backgrounds are similar, and therefore an animal's general resemblance to the background may suffice (Merilaita et al., 2017). In contrast, in heterogenous habitats that include two or more visually different microhabitats consisting of multiple heterogeneous patterns, animals can apply various tactics to optimize their survival (when physiological colour change is not possible). For instance, they could best match the colours of the most often utilised background, at the expense of other background types where their survival is lower: a specialist camouflage strategy (Cuthill, 2019). However, when the environment is heterogeneous, but the variation within local habitats is not high, a generalist strategy could outperform the specialist one (Merilaita, 2011). In such cases compromise camouflage, when animal colour best matches the average parameters of surrounding habitats, may maximize the survival rate (Michalis et al., 2017; Houston, Stevens & Cuthill, 2007; Hughes, Liggins & Stevens, 2019).

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

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

Materials and Methods

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 al., 2020; Boratyński et al., 2017).

Phenotype and immediate habitat colouration

To quantify phenotypes and their match to the immediate background, digital photographs of both animals and their habitat were collected during the expeditions. The photographs encompassed the entire dorsal view of animals and their respective immediate backgrounds (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-Rite ColorChecker; Fig. 1). Photographs were taken with a Canon EOS 400D digital camera, equipped with a Canon 18–55 mm kit lens and saved in RAW format. The images were standardized (equalized) with white and black standards presented in the frame in an ImageJ plugin, micaToolbox (Troscianko & Stevens, 2015). Each animal's dorsum (an area of at least 2 cm^2) and entire habitat colouration present on the image were used to calculate standard RGB values (0-255).

Spatial and temporal scales of environmental colouration

Remote sensing data were used to estimate environmental colouration of sample locations 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 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 scale habitat colouration we collected medians of the sample points (30 m, i.e., the spatial resolution of the visible bands of the Landsat satellite images) and of corresponding buffers around the sample points with diameters of 30 m, 100 m, 500 m, 1 000 m, 10 000 m, and 100 000 m. Thus, the spatial scale spanned from the micro (1-100 m) to macro scales (1-100 km), mirroring increments of increasing size, corresponding at one end to the resolution of the 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 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 data were always taken from the same season (within one month) of subject capture.

Phenotype-environment matching

We transformed both digital and satellite images from RGB (red, green, blue) to HSV (hue, saturation, brightness) space, because HSV better determines key parameters on how colour, 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 in a particular colour, while the brightness (V, or value) describes lightness-darkness of a particular colour, for the same level of hue (Kuehni, 2012; Schwarz, Cowan & Beatty, 1987). To quantify the level of camouflage, we calculated a matching (or similarity) index: the inverted absolute difference between the animal dorsum against the background colouration 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 inaccurate camouflage, and high similarity values indicating accurate camouflage (Tables 1 and 2).

Statistical analyses

To analyse camouflage patterns in the Sahara-Sahel rodent community we first combined data for all species and tested how spatial and temporal scales affected camouflage accuracy using a generalized linear mixed model test. We combined all collected data and constructed 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 as a factor (16 levels) and spatial and temporal scales (scaled) as continuous predictors. Then, 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 geographic structuring of the data and non-independence between records collected on the same individuals were accounted for by the random factors of country of origin and individual animal ID. Models with and without factorial interactions were evaluated using AIC statistics (Table 3).

Next, to determine species-specific camouflage responses to spatial and temporal scales, we 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* (58), *G. tarabuli* (37) and *G. amoenus* (32). The significance level of the analyses was interpreted after correction for multiple tests (Holm-Bonferroni correction, including 5 species and 3 mismatch analyses, $N = 15$, $\alpha = 0.0033$). In the species-specific analyses we included both linear and quadratic terms of spatial and temporal scale predictors, to account for nonlinearity in camouflage responses. The statistics for linear terms were estimated in 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).

Results

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 ($r = -0.02$, $df = 7357$, $t = -1.34$, $p = 0.91$).

Spatio-temporal variation of camouflage

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). 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: $\beta = -0.07$ (0.04), $z = -1.70$, $p = 0.089$; brightness: $\beta = 0.01$ (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).

Species-specific camouflage responses to spatial and temporal scales

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 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 regression terms indicated that they also had a good habitat match over a wide geographical scale (Fig. 4). Less consistent results were found for saturation and brightness. For saturation, both *Jaculus* species showed the best match at macro spatial scale (positive linear terms), while only one *Gerbillus* species (*G. tarabuli*) showed the best match at micro spatial scale (negative linear term; Fig. 4). For brightness, three species (*J. hirtipes*, *G. tarabuli* and *G. amoenus*) showed the best match at macro spatial scale (positive linear terms), while four (*J. hirtipes*, *J. jaculus*, *G. gerbillus*, *G. tarabuli*) had a good match at both micro and macro scales (positive quadratic terms; Fig. 4). For the temporal scale and hue (one species: *J. hirtipes*) and brightness (two species: *G. tarabuli, G. amoenus*) significant statistics indicated a better match to the most recent temporal scale (Fig. 4). In contrast, for one species (*G. amoenus*) significant statistics for temporal scale and hue showed a better match to older temporal scales. For saturation, two species (*G. tarabuli, G. amoenus*) best matched recent and two (*J. hirtipes, J. jaculus*) later years habitat colouration, while the quadratic terms indicating nonlinear relations were inconsistent (Fig. 4).

Discussion

Sixteen Sahara-Sahel rodent species (e.g.: Fig. 1) differed in the degree of their camouflage 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 matched the respective habitat parameters (Fig. 2) and all species showed the best hue camouflage to their local habitat (suggesting a habitat specialist strategy; Fig. 3). Three 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). 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 brightness, but the two *Jaculus* jerboas having the best saturation match to their older habitat (Fig. 4).

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 rodents (Nokelainen et al., 2020b). Following the general expectation for nocturnal prey (Penteriani et al., 2006), it was found that brightness of fur matched habitat relatively well (Fig. 4). At night, during dim light conditions, colour might be less detectable for predators. Nevertheless, our results indicated that hue and saturation of rodents' fur also matched their respective habitats well. We found that the spatial scale of the background matching may differ among colour parameters, even for the same species. For example, *Jaculus hirtipes* 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 specialist tactic in hue camouflage (Fig. 4, Fig. S1). In the same species other dorsal fur colour properties - saturation and brightness - best matched habitat at the broad geographical scale. This suggests effective generalist camouflage in saturation and brightness at a broad spatial scale, perhaps important during dispersal of this highly mobile species (Fig. 4, Fig. S1). The observations might be related to dynamic light conditions and the circadian activity patterns of the studied organisms, as some colour properties are more relevant during sunlight conditions (i.e., at dusk and dawn for this particular species) while others are more relevant at night (Johnsen et al., 2006). The analysed rodent species may differ in many characteristics. 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 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 determining camouflage in this rodent community.

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

Three species (*Jaculus hirtipes*, *Gerbillus tarabuli*, *G. amoenus*) showed good camouflage in their fur at the wide geographical scale in saturation and brightness (Fig. 4, Fig. S1). Camouflage theory states that when the background is homogeneous, a single optimal camouflage pattern for that animal to match the environment may exist (Merilaita et al., 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 therefore compromise camouflage to diversity of habitat could emerge. Saturation determines the intensity of colour: the higher the saturation the more vivid the colour (Ajmal et al., 2018). Interestingly, both *Jaculus* jerboa species showed good phenotype-habitat match for saturation at the broad geographical scale (Fig. 4), and jerboas are a widely distributed (Moutinho et al., 2020) and highly mobile species (Happold, 2013; Schröpfer, Klenner-Fringes & Naumer, 1985). It can be speculated that frequent crossing of a variety of background patches and heterogeneous environments would promote evolution of a generalist camouflage (Merilaita, 2011). Such differences between taxa and among colour parameters when determining the spatial scale of camouflage highlights the need for further studies on the life histories of specialist versus generalist camouflage species.

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

Conclusions

Sahara-Sahel rodents have developed habitat match at variable geographical scales and in different colour parameters. Depending on their predators' visual abilities and light conditions, selection on hue, saturation or brightness could prevail, with prey developing camouflage depending on the type and timing of the selection. Our results also show the importance of temporally dynamic habitats in determining camouflage. Prey life history 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 (Karmaoui, 2019; Wendling et al., 2019), prey response to such drastic shifts in habitat might compromise adaptations. If true, this poses a risk of extinction for locally maladapted populations, if the adaptive or plastic responses are too slow.

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Figure legends

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

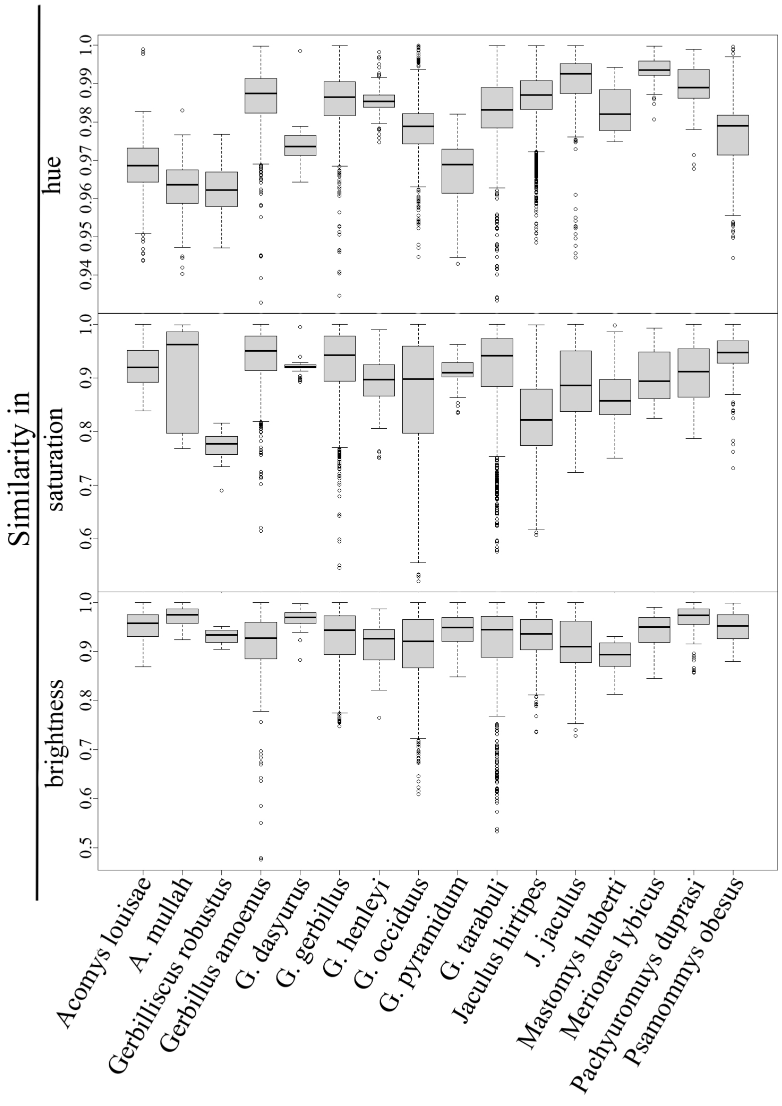

Figure 2. Variation in phenotype-habitat similarity in hue, saturation and brightness in sixteen studied Sahara-Sahel rodent species. Bold line in each box represents median, box represents interquartile range, whiskers represent data values between lower/upper quartiles and minimum/maximum values, dots (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).

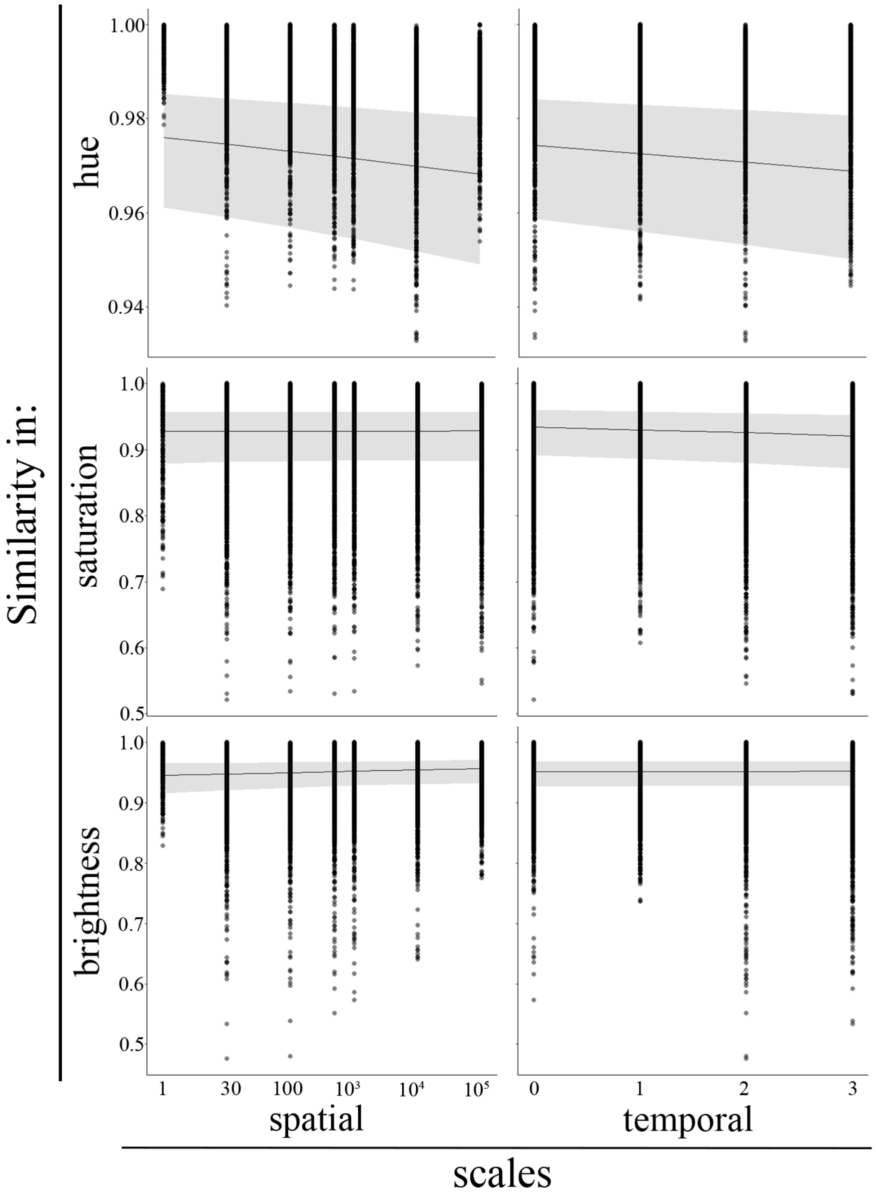

Figure 3. Results for three generalized linear mixed model analyses for sixteen Sahara-Sahel rodent species, with the phenotype-habitat similarity in hue, saturation or brightness as dependent variables, and spatial (meters around trapping location) and temporal (years before trapping) scales as predictors.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

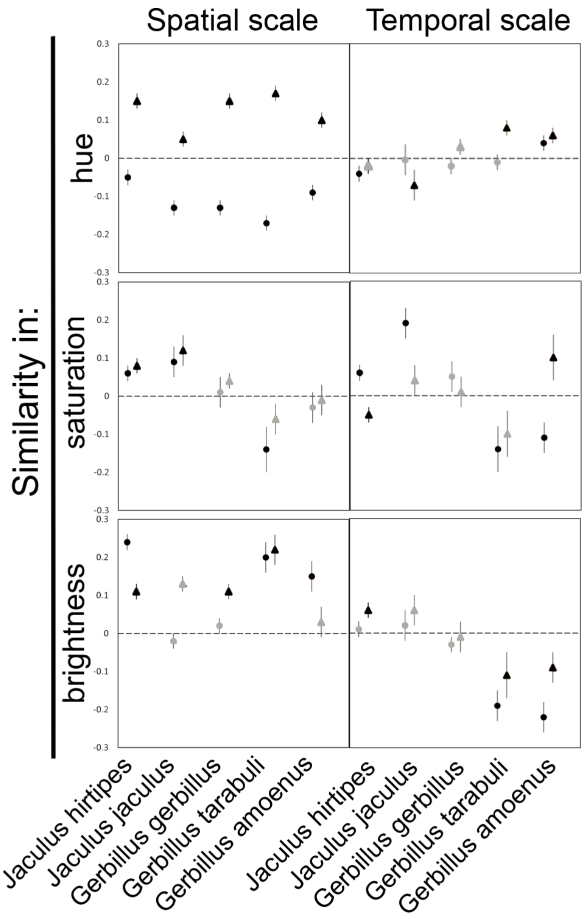

Figure 4. Effect sizes (circles - linear coefficients; triangles - quadratic coefficients) of the strength and direction of the relations between phenotype-habitat similarity and spatial (left panels) and temporal (right panels) scales. Coefficients (y-axis) were derived from generalized linear mixed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

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 dorsal fur and habitat in hue, saturation or brightness as dependent variables, species (16) as factor and spatial and temporal scales as predictors.

		hue		saturation		brightness	
	df	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	