Specialist vs generalist: a study on North African rodent's camouflage through different spatial and temporal scales.

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Mestrado em Ecologia e ambiente
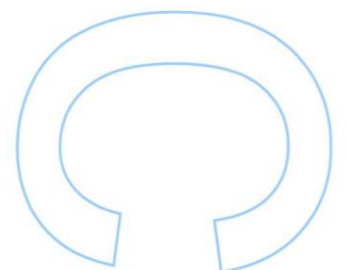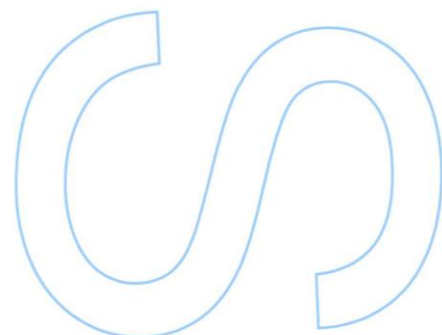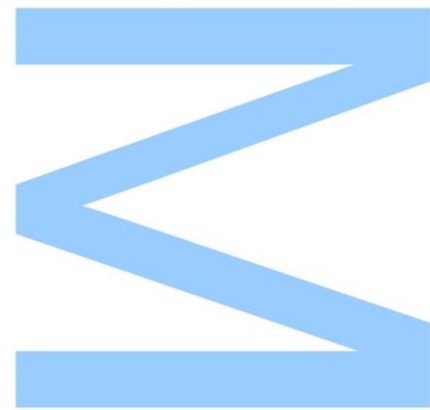
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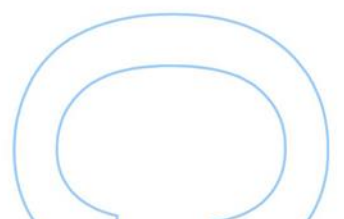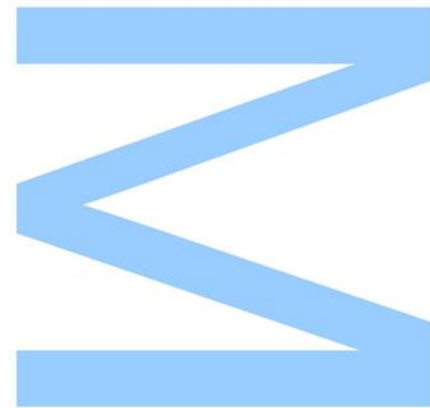UNIVERSIDADE DO PORTO

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pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

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Resumo

As mudanças climáticas antropogénicas estão a aumentar a probabilidade de condições climatéricas extremas que excederão as tolerâncias biológicas atuais, sendo por isso uma grave ameaça à biodiversidade, assim como provocarão mudanças permanentes na paisagem e no meio ambiente. Embora a plasticidade possa ajudar os indivíduos a manter o desempenho, há limites para a sua capacidade, deste modo os animais serão forçados a adaptar-se às mudanças em curso ou acabarão extintos. Os desertos são uma das regiões biogeográficas mais propensas a sofrer com as mudanças climáticas. Estas alteram a estrutura geográfica e a dinâmica temporal dos habitats de diversas comunidades de animais. Neste trabalho, investigamos uma das adaptações clássicas ao habitat, a camuflagem, numa comunidade de roedores do Norte da África. Especificamente, testamos a resolução espacial da camuflagem para distinguir entre estratégias de camuflagem generalista e especialista, tendo investigado também a consistência temporal de tais estratégias. No estudo, foram obtidas imagens digitais e de satélite de animais e habitats. As imagens de habitats foram obtidas e analisadas desde a pequena escala espacial (1m) até a ampla escala espacial (100km). Estas imagens foram também obtidas com uma resolução temporal de 3 anos, para se desenvolver uma escala de tempo. Apresentamos assim, os resultados das análises de camuflagem em dezasseis espécies de roedores do Sahara-Sahel, conduzidas num total de 295 indivíduos. Mostramos que as espécies diferem na sua resolução espacial e temporal na adaptação da camuflagem. Também descobrimos que diferentes características de cor (matiz, saturação e brilho) têm importância variável entre as espécies estudadas, talvez refletindo os padrões de atividade das espécies, estratégias de história de vida e outras propriedades ecológicas. Concluímos que a divisão entre estratégias de camuflagem generalistas e especialista pode não ser tão direta quanto pensávamos anteriormente. Ficou evidente que os animais desenvolveram diferentes estratégias de camuflagem dependendo das propriedades de cor estudadas (matiz, saturação e brilho). O nosso estudo também permitiu descobrir que a resolução no tempo é algo importante a se ter em consideração para a adaptação, sugerindo que a seleção pode ser mais forte dependendo do tempo e da frequência de reprodução entre as espécies estudadas.

Abstract

Anthropogenic climate change is increasing the likelihood of extreme weather conditions that exceed current biological tolerances, posing severe threats to biodiversity, as well as permanent changes to landscape and environment. While plasticity can help individuals to maintain performance, there are limits to their capacity, because of this, animals are forced to adapt to the ongoing changes or face extinction. Deserts are one of the biogeographical regions most prone to suffer from the climate change, that alter geographical structure and temporal dynamic of habitats perceived by diverse community of animals. In this work we have investigated one of the classical adaptations to habitat, camouflage, in a community of North African rodent. Specifically, we tested the spatial resolution of camouflage to distinguish between the generalist and specialist camouflage strategy and investigated the temporal consistency of such strategies. In the study, digital and satellite images were obtained for animals and habitats. Habitat images were obtained and analysed from small spatial (1m) to broad spatial scale (100km). Images were collected for 3 years' time resolution, to develop a time scale. Here we have presented results from analyses on camouflage in sixteen Sahara-Sahel rodent species, conducted on in total 295 individuals. We have showed that species differed in their spatial and temporal resolution of the camouflage adaptation. We also discovered that different colour characteristics (hue, saturation and brightness) have variable importance among studied species, perhaps reflecting species activity patterns, life history strategies and other ecological properties. We concluded that the division between generalist vs specialist camouflage strategies might not be as straightforward as we previously thought. It became evident that animals developed different camouflage strategies depending on the colour properties studied (hue, saturation, and brightness). Our research also allowed that time resolution is something important to consider for adaptation, suggesting that selection might be strongest in depending on the timing and frequency of reproduction among studied species.

Keywords

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General Introduction

This thesis and research were made with article submission in mind. The article is in its finishing stages, so it was decided to put the article manuscript in its entirety. Even so, it was decided that a general introduction needed to be done, before the manuscript, to further explain and mention important topics that usual article manuscript constraints don't allow for, therefore taking full advantage of the liberties that a thesis dissertation allows me to have. Consequently, some parts of general introduction are likely echoed in the article introduction, as one is the extension of the other. Following this general introduction is the article manuscript in its entirety.

Climate Change

The history of life on Earth is closely associated with environmental changes on multiple spatial and temporal scales (Davis & Shaw, 2001). Observed and projected climatic changes for the 21st century, most notably, global warming, are comparable in magnitude to the largest global changes in the past 65 million years (Diffenbaugh & Field, 2013). The effect of this global crisis is already noticeable and resulting in a planet-wide biological response. Marine and terrestrial organisms are already altering their distributions to stay within their ideal environmental conditions. At the cooler extremes of their distributions, species are moving poleward, whereas range limits are contracting at the warmer range edge, where temperatures are no longer tolerable. On land, species are also moving to cooler, higher elevations; in the ocean, they are moving to colder waters at greater depths (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011). Furthermore, species are doing this at an unprecedented rate (Lenoir & Svenning, 2015). Because different species respond at different rates and to varying degrees, key interactions among species are often disrupted, and new interactions develop. These idiosyncrasies can result in novel biotic communities and rapid changes in ecosystem functioning, with pervasive and sometimes unexpected consequences that propagate through and affect both biological and human communities (Pecl et al., 2017). While plasticity can help individuals maintain performance, there are limits to their capacity. Climate change together with the increasing anthropogenic barriers for migration will force populations to adapt to a new set of conditions or face extinction (Peterson, Doak, & Morris, 2019). Although no region of the world will be entirely spared, the negative impacts are likely to fall most heavily on poor nations around the tropical region. The generalized lack of knowledge and preparation, together with their historical climate and biogeography, makes these regions one of the worst prepared to face the climate change consequences (Akpodiogaga-a & Odjugo, 2010). As such, deserts and arid regions are especially exposed to the consequences of climate change (Mahmoud & Gan, 2018), with some changes already being noticed: desert encroachment,

coastal inundations, drying up of surface waters and shifts in crops cultivated over time was also noticed (Akpodiogaga-a & Odjugo, 2010). Additionally, measurements of warming of deserts were estimated at 0.25 C per decade from 2002 to 2015 but the reanalysis of models estimated a trend varying from −0.14 to 0.1 C per decade (Zhou & Wang, 2016). Therefore, there's a need to further scientific knowledge in order to be better prepared for the challenges of the upcoming years.

Deserts

Deserts are known to be among the harshest environments on Earth. These regions are characterized by extreme diurnal temperatures, intense solar radiation, low relative humidity, drying winds, and sparse rainfall (Hadley, 1972). Because of this, deserts have long been seen as natural laboratories for learning how individuals are challenged by different aspects of the environment, and how organisms have adapted to these challenges, providing a unique opportunity to study adaptation at different scales (Behera, Matin, & Roy, 2014; Giannoni, Dacar, Taraborelli, & Borghi, 2001; Mulroy & Rundel, 1977). Deserts and arid regions represent about 18% of the world's landmass (José C. Brito et al., 2016) and are generally perceived as homogeneous and species-poor. However, they harbour about 25% of continental vertebrate species, including some of the most endangered species in the world (Durant et al., 2012), and their communities are largely made up of highly adapted, specialized species that are found nowhere else. The species present in these regions are normally patchily distributed, as their range limits are under strong climatic control, and have a relatively high rate of endemism due to the adaptive processes of organisms to extreme environments (Davies et al., 2012; Murphy, Breed, Guzik, Cooper, & Austin, 2012).

Sahara-Sahel region

This thesis will have the Sahara Desert and the neighbouring arid Sahel as the region of interest, as the studied communities' habit situates itself in this biogeographic region. The Sahara is the largest warm desert in the world and, together with the neighbouring arid Sahel, covers 11,230,000 km^2 and crosses over 17 different countries (Olson et al., 2001) (Fig.1).
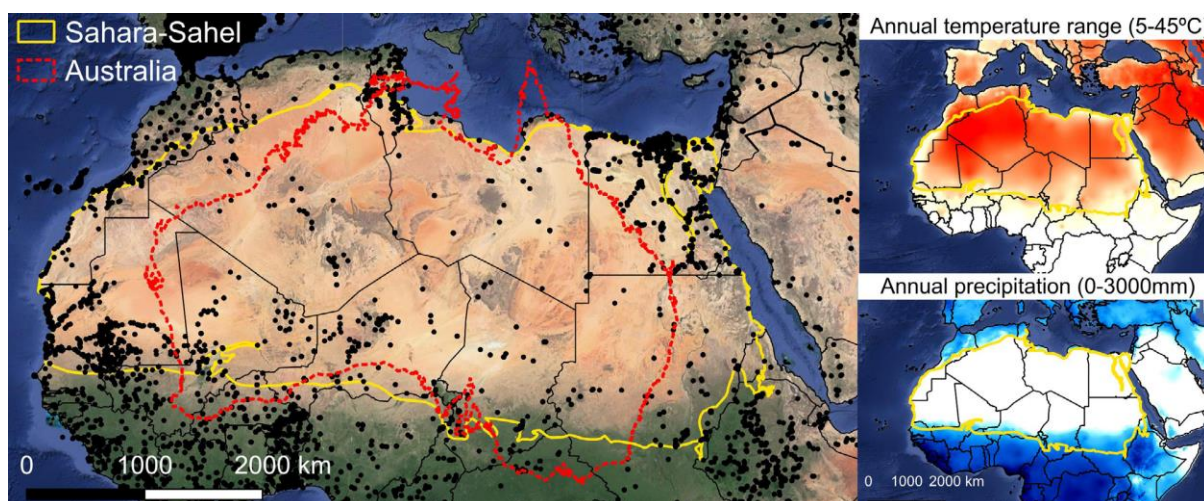
Figure 1. Aerial vision of Sahara-Sahel biogeographic region. Black lines represent country borders. In red, Australia continent, was overlapped to compare the dimensions. The figure also chows annual temperature range and precipitation. Image taken from:(Nokelainen, Sreelatha, et al., 2020).

Therefore, the vibrant Sahara-Sahel region is highly appealing for biodiversity, evolutionary and ecological research, but its large size, its difficulty of access, as well as long-term political instability led to a generalised lack of research and knowledge during most of the 20th century. The relatively peaceful period experienced in the decade 2001–2010 has translated into an impressive increase in the number of studies devoted to the region, for all taxonomic groups examined. These research efforts coupled molecular and geomatic (Global Navigation Satellite Systems and Geographical Information Systems) tools together with a broad sampling of taxa. Such studies are starting to unravel micro-hotspots of biodiversity and cryptic diversity, showing that the Sahara-Sahel region isn't the barren landscape we once thought. These studies are also expanding tremendously our knowledge on biodiversity distribution and evolution, but also revealing gaps on these topics which are in urgent need of research effort for efficient planning of biodiversity conservation (J. C. Brito et al., 2014). Therefore, the Sahara-Sahel region can be seen as the perfect natural laboratory to study adaptation at different scales.

North African rodent communities

Rodentia is the largest order of Mammalia, encompassing 2,277 of 5,422 living mammal species, or approximately 42% of worldwide mammalian biodiversity. Rodents are indigenous all around the globe and even inhabit most small to large oceanic islands (Wilson & Reeder, 2005). In Africa, the level of species endemism is very high, nearly 95%, although this remains an underestimate. The number of rodent species considered to be valid has continued to increase in the last quarter-century (Figure 2). Rodentia in Africa is a remarkable model to study. This is proven true by the remarkable species richness, coupled with enormous

morphological diversity. Also, in the African rodents taxa, it's possible to find every ecological, behavioural, trophic and locomotory adaptations that have evolved within the order (Happold, 2013).
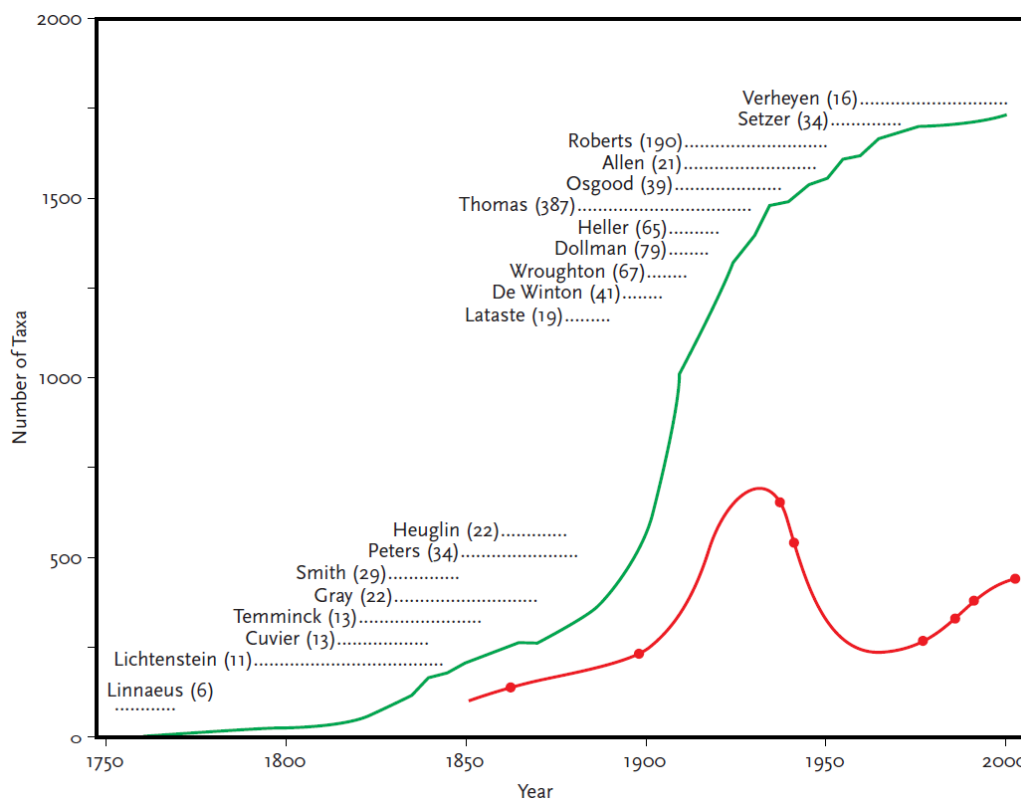
Figure 2. Number of taxa of African rodents through the years. Green line represents the cumulative number of species-group taxa (species and subspecies)(total = 1729). Red line represents the number of species considered scientifically valid. [Image taken from: (Happold, 2013)]

Most African rodents are typical 'mouse-like but there are many that are very different (Figure 3) (Renaud et al., 2005); for example, jerboas (*Allactaga*, *Jaculus*) and springhare (*Pedetes*) have extremely long hindlimbs and jump like kangaroos; anomalures (*Anomalurus*, *Idiurus*) have large winglike membranes so they can glide from tree to tree; and mole-rats (*Bathyergus*, *Georhychus*, *Heliophobius*) have blunt muzzles, cylindrical bodies, rudimentary (or non-existent) eyes, and huge incisor teeth (for excavating burrows) (Happold, 2013). Because of the large number of species representing families of distant evolutionary origins, there are some interesting examples of ecological and morphological convergence: species of *Dipodidae* and *Pedetidae* are bipedal and saltatorial; species of *Bathyergidae* and *Spalacidae* are permanently subterranean; and species of *Dipodidae* and *Gerbillinae* can produce very concentrated urine and hence can live in very dry habitats devoid of free water (Mares, 1993).

Figure 3. Four images demonstrating different species from African rodents' taxa, and their different but similar morphology. A) Gerbillus campestris; B and C) Jaculus hirtipes; D) Gerbillus gerbillus. Photo credits: Zbyszek Boratyński

African rodents show a wide range of reproductive methods and reproductive strategies. The strategy of any particular species is determined partly by its phylogeny, but also by the environment and location, Pregnancy and lactation is adaptively time to ensure a high survival rate for the young. Because small rodents have relatively short gestations (ca. 25-40 days), they can be very responsive to changes in the climate. Hence, the end of 'winter' initiates the reproductive process, and the young are born while the favourable conditions last. Within this reproductive period, many species show a 'peak' of reproductive activity (as measured by the percentage of adult females that are pregnant) (Barros et al., 2018). Because of this short gestation, a female may have several litters when conditions are favourable for reproduction. A strategy that includes short gestation, the rapid growth of young to independence and postpartum oestrus (the female can conceive again immediately after parturition) is especially important to species where favourable conditions are short-lived or unpredictable. A corollary of small size is a short lifespan and hence it is necessary for small rodents to attain sexual maturity rapidly, to have large litters, and to produce several litters in quick succession to maximize their lifetime reproductive success (Happold, 2013).

The behaviour of African rodents has not been studied as extensively as that of the larger mammals. Their small size, nocturnal activity and lack of visibility make it very difficult to pursue behavioural studies on rodents (Rosenzweig & Winakur, 1969). Therefore, additional

studies (which provide information on sociality, agonistic behaviour, nesting behaviour and maternal behaviour) have been made on several species in captivity. Although most species tend to be asocial and/or solitary except for times during reproductive activity, some species form loose aggregations and social groups. All species of rodents that have been studied show many forms of intra- and inter-specific communication; these include vocal (e.g., call, squeaks, whistles), visual (e.g., amicable, or aggressive displays, postures, tail-flicking, etc.), non-vocal auditory (foot-drumming, tooth-chattering) and olfactory (scent-marking) signals (Happold, 2013).

Rodents play an important role in ecological processes in Africa due to the many species present, their collectively widespread distributions and the, sometimes, large populations numbers within particular habitats. Because the vast majority of species are herbivores and granivores, they assume a major role in recycling nutrients, increasing seed dispersal and changing their surrounding environment (a process known as 'ecological engineering'). Although the influence of one individual rodent may seem trivial (compared with that of a mega-herbivore), the very large numbers of rodents in many ecosystems mean that their total influence is not inconsiderable. Rodents also play an important role in the food web, as they are important prey for many small and medium-sized carnivores (Sillero-Zubiri & Gottelli, 1995).

Camouflage adaptation

Natural selection can shape phenotypic variation through the process of animal adaptation. In this way, adaptation can be defined as the inheritable phenotypic change (whether on a molecular, e.g. hormonal, or morphological, e.g. tooth shape, level) resulting in increased fitness of individuals caring such change in a particular matching environment (Boomsma, 2016). As previously stated, the adaptation of rodents to desert environments involves more than mere tolerance or avoidance of extreme conditions. They include specific behavioural, morphological, and physiological modifications, which usually are not unique to desert organisms but often are more highly developed and efficiently utilized than in their mesic counterparts (Hadley, 1972; Ott & Rogers, 2010; Williams & Tieleman, 2005). In this way, adaptation is an outcome of natural selection, which shapes heritable components of prey anti-predatory adaptations, such as phenotype environment convergence for visual crypsis (Tim Caro, 2005).

Visual crypsis, also known as camouflage, can be described as a widespread anti-predator adaptation that hinders detection or recognition by increasing prey resemblance to the natural environment or objects they are in (Cuthill, 2019; Cuthill et al., 2005). Camouflage colouration can be used to reduce the prominence of the primitive features, edges, parts of the body and

even the whole animal impeding predators accurate sensory processing. There are two indispensable principles in understanding camouflage. Firstly, whichever mechanism is employed, it will act to reduce the signal-to-noise ratio, in which the signal is the object of interest, the prey, and the noise is anything else that surrounds and belongs to the habitat of the prey (S. Merilaita, N. E. Scott-Samuel, & I. C. Cuthill, 2017). Secondly, both the noise and the signal are filtered through the eyes of a predator, leading to each different predator species filtering the signal and the noise in a species-specific way (Cuthill, 2019; Endler, 1978). Because of this, we can find white species or species that become white in the winter, in artic and tundra biomes, such as the snowshoe hare Lepus americanus (Di Bernardi et al., 2021); pale species in the desert and open environments, such as the lesser Egyptian gerbil *Gerbillus gerbillus* (Nokelainen, Brito, et al., 2020), and red and grey species in rocky habitats, such as the rocky mountain sheep *Ovis Canadensis* (Tankus & Yeshurun, 2001); as well as many more cases of background matching in the wild (T. Caro & Mallarino, 2020). Camouflage is a very diverse adaptation and includes background matching, disruptive colouration, self-shadow concealment, obliterative shading, flicker-fusion camouflage, distractive markings, transparency, silvering, masquerade, motion dazzle and motion camouflage (Merilaita, 2011).

The most common camouflage type is background matching. It can be defined as the adaptation of an animal's body colouration to reduce the signal-to-noise ratio to visual dependent predators (Endler, 1978; Sami Merilaita, Nicholas E. Scott-Samuel, & Innes C. Cuthill, 2017). Through matching the hue, saturation, brightness and pattern of the immediate background, the animal looks like and if successful, is indistinguishable from a sample of the background (Merilaita, 2011). In visually heterogeneous habitats, background matching is not easy to achieve (Ramirez-Delgado & del Castillo, 2020). Almost all habitats vary spatially and temporally, and animals that match the background in a given location might not be able to match the background in another location or time (Merilaita, 2011). Some background types are relatively homogeneous and can be described as a single surface, but many may include multiple surfaces. Therefore, one of the critical factors for camouflage is the spatial and temporal heterogeneity of the habitat (Sami Merilaita et al., 2017). When the environment is homogeneous at the spatial scale of the animal, then all samples of habitat that form that background are the same, homogenous, and therefore there is a single optimal camouflage pattern for the animal (Sami Merilaita et al., 2017). But when the animals occur in very different habitats, and the physiologic colour change is not possible, the animal should match one of the backgrounds well at the expense of the others. Such tactic is called a specialist strategy (Cuthill, 2019). In contrast, when the environment background is heterogeneous, but the variation within local habitats isn't high, a generalist strategy could outperform the specialist tactic (Merilaita, 2011). In a generalist strategy, compromise camouflage is used where the

animal averages the colour and/or textures of surrounding habitats, obtaining the best fitness benefits (Michalis, Scott-Samuel, Gibson, & Cuthill, 2017). On one hand, a prey that has a colouration matching a rare background sample will be more likely to mismatch its local background than a prey bearing coloration equivalent to an average sample (Michalis et al., 2017). On the other hand, a prey that can recognize mismatch to their immediate background can move to a more suitable substrate (Kang, Moon, Lee, & Jablonski, 2013). It is also important to note that prey that as the colours of a more common background will have fewer biological costs of finding suitable resting places.

Figure 4. Photographs of four different habitats found in the Sahara-Sahel biogeographic region. Underlining the unexpected diversity found here. Photo credits: Zbyszek Boratyński

Article manuscript

Introduction

Anthropogenic climate change is increasing the likelihood of extreme weather conditions that exceed current biological tolerances, posing severe threats to biodiversity, as well as permanent changes to landscape and environment (Bontrager et al., 2020). While plasticity can help individuals to maintain performance, there are limits to their capacity, because of this, animals are forced to adapt to the ongoing changes. The increasing anthropogenic barriers for migration will force populations to adapt to a new set of conditions or face extinction (Peterson et al., 2019). Arid regions are especially exposed to ongoing climate change (Mahmoud & Gan, 2018). Deserts are known to be among the harshest environments on Earth, characterized by extreme diurnal temperatures, intense solar radiation, low relative humidity, drying winds, and sparse rainfall (Hadley, 1972). Deserts have long been seen as natural laboratories for learning how individuals are challenged by different aspects of the environment, and how organisms have adapted to these challenges (Behera et al., 2014; Giannoni et al., 2001; Mulroy & Rundel, 1977). The Sahara-Sahel arid region spans over a large and heterogenous biogeographic zone, providing a unique opportunity to study adaptation at different geographical scales (Nokelainen, Brito, Scott-Samuel, Valkonen, & Boratyński, 2020).

Adaptation can be defined as the inheritable phenotypic change (whether on a molecular, e.g. hormonal, or morphological, e.g. tooth shape, level) resulting in increased fitness of individuals caring such change in a particular matching environment (Boomsma, 2016). The adaptation of individuals to desert environments involves more than mere tolerance or avoidance of extreme conditions. They include specific behavioural, morphological, and physiological modifications, which usually are not unique to desert organisms but often are more highly developed and efficiently utilized than in their mesic counterparts (Hadley, 1972; Ott & Rogers, 2010; Williams & Tieleman, 2005). As an example, small mammals, like rodents, with a high ratio of surface to body volume became primarily active at night to avoid overheating during the hot days (Haim & Izhaki, 1995). Adaptation is an outcome of natural selection, which shapes heritable components of phenotypic variation. Therefore, predator-induced selection can drive the evolution of prey anti-predatory adaptations, such as phenotype environment convergence for visual crypsis (Tim Caro, 2005).

Visual crypsis, also known as camouflage, can be described as a widespread anti-predator adaptation that hinders detection or recognition by increasing prey resemblance to the natural

environment or objects they are in (Cuthill, 2019; Cuthill et al., 2005). Camouflage comprises an array of mechanisms that impede predators accurate sensory processing. There are two indispensable principles in understanding camouflage. Firstly, whichever mechanism is employed, it will act to reduce the signal-to-noise ratio, in which the signal is the object of interest, the prey, and the noise is anything else that surrounds and belongs to the habitat of the prey (S. Merilaita, N. E. Scott-Samuel, & I. C. Cuthill, 2017). Secondly, both the noise and the signal are filtered through the eyes of a predator, leading to each different predator species filtering the signal and the noise in a species-specific way (Cuthill, 2019; Endler, 1978). Because of this, we can find white species or species that become white in the winter, in artic and tundra biomes, such as the snowshoe hare *Lepus americanus* (Di Bernardi et al., 2021); pale species in the desert and open environments, such as the lesser Egyptian gerbil *Gerbillus gerbillus* (Nokelainen, Brito, et al., 2020), and red and grey species in rocky habitats, such as the rocky mountain sheep *Ovis Canadensis* (Tankus & Yeshurun, 2001); as well as many more cases of background matching in the wild (T. Caro & Mallarino, 2020). Camouflage is a very diverse adaptation and includes background matching, disruptive colouration, self-shadow concealment, obliterative shading, flicker-fusion camouflage, distractive markings, transparency, silvering, masquerade, motion dazzle and motion camouflage (Merilaita, 2011). The most common camouflage strategy is background matching (Price, Green, Troscianko, Tregenza, & Stevens, 2019). It is an adaptation of an animal's body colouration to reduce the signal-to-noise ratio to predators who rely on their visual capacities (Endler, 1978). The animal accomplishes this by matching the hue, saturation, brightness, and pattern of the habitat as perceived by the predator (Nokelainen, Brito, et al., 2020). Hence the animal will look like and, if successful, will be indistinguishable from a sample of the habitat background (Sami Merilaita et al., 2017).

In visually heterogeneous habitats, background matching is not easy to achieve (Ramirez-Delgado & del Castillo, 2020). Almost all habitats vary spatially and temporally, and animals that match the background in a given location might not be able to match the background in another location or time (Merilaita, 2011). Some background types are relatively homogeneous and can be described as a single surface, but many may include multiple surfaces. Therefore, one of the critical factors for camouflage is the spatial and temporal heterogeneity of the habitat (Sami Merilaita et al., 2017). When the environment is homogeneous at the spatial scale of the animal, then all samples of habitat that form that background are the same and therefore there is a single optimal camouflage pattern for the animal (Sami Merilaita et al., 2017). But when the animals occur in very different habitats, and physiologic colour change is not possible, the animal should match one of the backgrounds well at the expense of the others. Such tactic is called a specialist strategy (Cuthill, 2019). In

contrast, when the environment background is heterogeneous, but the variation within local habitats isn't high, a generalist strategy could outperform the specialist tactic (Merilaita, 2011). In a generalist strategy, compromise camouflage is used where the animal averages the colour and/or textures of surrounding habitats, obtaining the best fitness benefits (Michalis et al., 2017). Natural environments vary continuously in colour and texture. Therefore, a prey that has a colouration that matches a rare background will be more likely to mismatch its habitat than a prey bearing colouration equivalent to an average of habitats. Naturally, a prey that can recognize a mismatch to their immediate background can move to a more suitable substrate, but it is also important to note that prey that has the colours of a more common background will have fewer costs in finding suitable resting places (Kang et al., 2013; Michalis et al., 2017). Camouflage in the Sahara-Sahel desert rodent community presents a fine-tuned example of background matching in geographically widespread taxa (Boratyński et al., 2017; Boratyński, Brito, Campos, Karala, & Mappes, 2014). Both the colour and the pattern of the animals are correlated with their respective backgrounds and vision modelling has shown that their camouflage is effective against both mammalian and avian vision models (Nokelainen, Brito, et al., 2020). Animal-to-background differences are generally low in Sahara-Sahel rodents at large spatial scales, supporting the hypothesis of a generalist camouflage strategy, but some species (e.g. *Jaculus hirtipes*) may also match their local habitat very well (Nokelainen, Brito, et al., 2020). However, the frequency of occurrence of alternative specialist and generalist strategies, and their temporal consistency in changing environments, is not known in the community of the Sahara-Sahel rodents, or elsewhere in the world.

In this work, we investigated camouflage in several North African rodent species. Specifically, we tested the spatial resolution of camouflage to distinguish between the generalist and specialist strategies and investigated the temporal consistency of such strategies. We expected that most of the rodent species would have evolved a generalist strategy matching the average background of habitats that they experience. However, we expected that some species would specialize to utilize selectively microhabitats and, therefore, have evolved a specialist camouflage. Because of the short generation time of most rodents and supposedly strong selection experienced, we expected that the strongest camouflage match would be within the shortest time resolution. Moreover, because studied species are mostly nocturnal it was also expected that camouflage will be most evident for colouration parameters better detected at night (i.e., hue).

Materials and methods

Data collection

Animal data were collected in several expeditions that were organized to the Sahara-Sahel parts of Mauritania and Morocco, as well as Algeria, Chad, and Ethiopia (Boratynski Z, 2013; J. Brito, Campos, J., Gonçalves, D., Martínez-Freiría, F., & Sillero, N., 2011; Guerreiro & Agbani, 2016; Moutinho & T., 2015). Specimen 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). Altogether, 295 animals were obtained for analysis, with individuals belonging to *Acomys louisae* (8 individuals), *Acomys mullah* (3), *Gerbilliscus robustus* (1), *Gerbillus amoenus* (32), *Gerbillus dasyurus* (1), *Gerbillus gerbillus* (58), *Gerbillus henleyi* (5), *Gerbillus occiduus* (17), *Gerbillus pyramidum* (6), *Gerbillus tarabuli* (37), *Jaculus hirtipes* (68), *Jaculus jaculus* (40), *Mastomys huberti* (1), *Meriones libycus* (3), *Pachyuromys duprasi* (8), *Psammomys obesus* (8).

Animal 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 animal dorsal view and their respective immediate backgrounds (within 1m). Photographs were taken from similar heights (c. 1 m) and included a colour and size reference scale (X-Rite ColorChecker target) (Figure 4). Photographs were taken with a Canon EOS 400D digital camera 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 by using an ImageJ plugin, micaToolbox (Troscianko & Stevens, 2015). The entire animals' dorsum and entire habitat colouration present on the image were used to calculate standard RGB values (0-255). Ultra-violet radiation was not included in the analysis, however, as the analysed species are crepuscular or nocturnal the UV reflectance was expected to be unimportant. On the other hand, as many of these animals are active during dusk and dawn there may be differences in ambient light conditions.
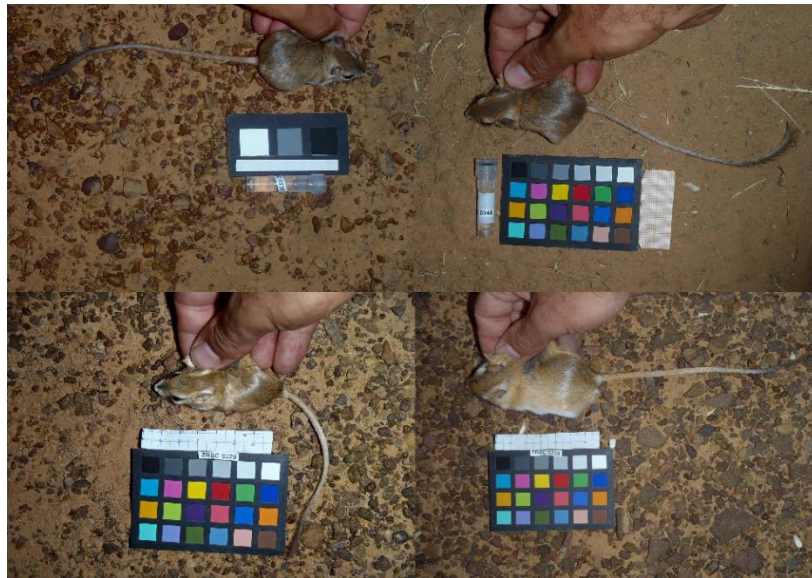
Figure 5. Examples of photographs used to analyse colour parameters, including a colour and size reference scale. Photo credits: Zbyszek Boratyński

The spatial and temporal scale of environmental colouration

Remote sensing techniques were applied to estimate environmental colouration of sample locations from available NASA Landsat satellite images, obtained from Google Earth Engine's (GEE, USGS Landsat 8 Surface Reflectance Tier 1 dataset). This dataset includes the atmospherically corrected surface reflectance from Landsat 8 OLI/TIRS sensors. From GEE data we collected information that included B2 (blue), B3 (green) and B4 (red) bands, i.e., satellite data is provided as RGB values. To calculate the gradient of spatial scale habitat colouration we collected medians of buffers with diameters of 10 m, 100 m, 500 m, 1.000 m, 10.000 m, and 100.000 m, with animals' capture points at their centres. Such medians were calculated for satellite data acquired for the year of the capturing, as well as for three consecutive years before capturing animals (i.e., temporal scale of the data).
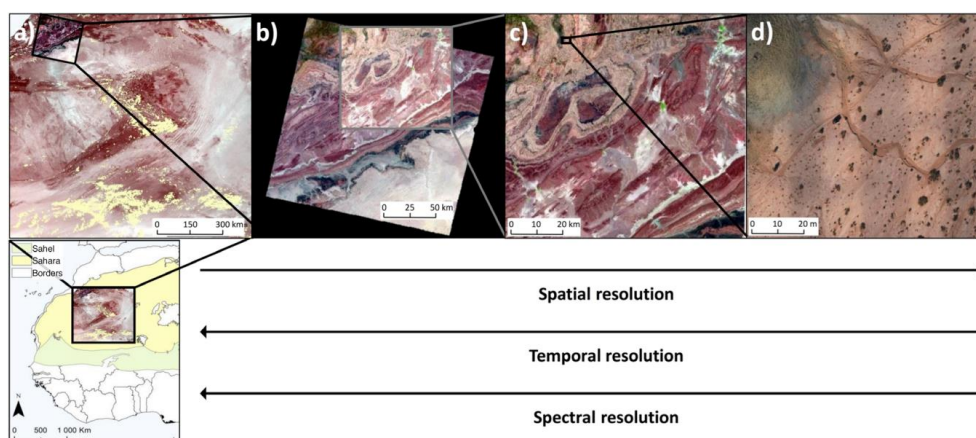
Figure 6. Visual representation of several scales of satellite imagery. From several hundred kilometres (a) to a few meters (d). The figure is taken from: (Nokelainen, Sreelatha, et al., 2020).

Statistical analyses

Because hue, saturation, and value (HSV) are a colour space that is closer to how colour, and consequently prey camouflage, is really perceived (Ajmal, Hollitt, Frean, & Al-Sahaf, 2018), we transformed both digital and satellite images from RGB to HSV colour space (in "rgb2hsv" R package). The hue (H) describes the dominant wavelength, the saturation (S) describes the amount of grey in a particular colour, while the value (V, or brightness) determines the amount of light in the colour. We calculated mismatches as the difference between the values of the animal dorsum against the background in which they were found, at the different spatial and temporal scales. Such HSV mismatches were used as dependent variables in further analyses.

First, we tested how spatial and temporal scales affected camouflage accuracy using a generalized linear mixed model test (with "glmmTMB2" R package). We combined all collected data and constructed three separate analyses for hue, saturation, and brightness, with mismatches 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. We tested two-way factorial interactions between species and spatial and temporal scales to test for the differences among species in camouflage. The geographic structuring of the data and non-independence between records collected on the same individuals were accounted for by random factors of the country of origin and individual animal ID. Models with and without factorial interactions were evaluated using AIC statistics.

Second, to determine species-specific camouflage responses to spatial and temporal scales we constructed similar to the above analyses but separately for five species which consisted of enough records for conclusive statistical investigation (N>30). Those species included: *Gerbillus amoenus* (32), *Gerbillus gerbillus* (58), *Gerbillus tarabuli* (37), *Jaculus hirtipes* (70) and *Jaculus jaculus* (41). In species-specific analyses we included both linear and quadratic terms of spatial and temporal scales predictors, to account for nonlinearity in camouflage responses. The statistics for linear terms were estimated in simple models while quadratic terms were estimated while accounting also for linear terms. Analyses were interpreted by accounting for multiple tests (Bonferroni correction, including 5 species and 3 mismatch analyses). All statistical analyses and visualizations were conducted in R project software (packages: "rgb2hsv", "glmmTMB2", "ggplot2"; "sjPlot") (Team, 2021)

Results

In general, we found that both animal and habitat colour parameters varied substantially in our data (Fig. 6) Likewise, mismatches in hue, saturation and brightness showed variability in the data (Fig. 5). When including all records to test correlations between animal and habitat coloration (combining all spatial and time scales) we found strong and significant correlation for brightness (Pearson's product-moment correlation: $r = 0.48$, df = 7357, $t = 46.55$, $p < 0.001$), the correlation for saturation was low but significant ($r = 0.11$, df = 7357, $t = 9.76$, $p < 0.001$), but insignificant for hue ($r = -0.02$, df = 7357, $t = -1.34$, $p = 0.91$).
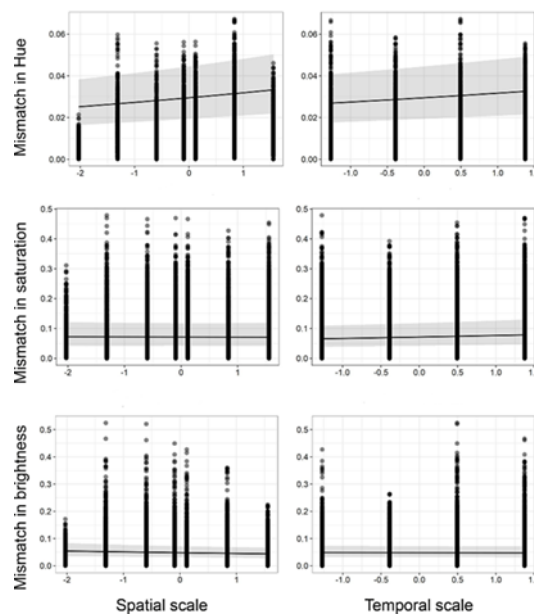
Figure 7. The overall relations, including species mismatches of animal habitat colouration in hue, saturation and brightness and spatial and temporal scales of camouflage.

Results from three mixed model analyses, for mismatches between phenotype and habitat in hue, saturation or brightness as dependent variables, that included all records and species, showed that the animal to habitat mismatch for hue correlated positively with spatial [β (s.e.) = 0.08 (0.02), z = 4.37, p < 0.001] and temporal scales [β = 0.07 (0.02), z = 3.92, p < 0.001] of camouflage adaptation (Table 1). The analysis for mismatch in saturation showed no relation with spatial [β = -0.003 (0.05), z = -0.09, p = 0.93] nor temporal scales [β = 0.07 (0.04), z = 1.70, p = 0.09] . The analysis for mismatch in brightness also showed no correlation with spatial [β = -0.06 (0.05), z = -1,39, p = 0.17] and temporal scales [β = -0.01 (0.04), z = -0.14, p = 0.89] . Those overall results were complicated by strong interactions between temporal and spatial scales and species factors in predicting mismatches in hue, saturation and brightness, indicating that different species express different spatial and temporal camouflage strategies (Table 1). Therefore, further analyses were conducted separate for species which

consisted of more than 30 records and they significance levels were interpreted after correction for multiple tests (N = 15, α = 0.0033).
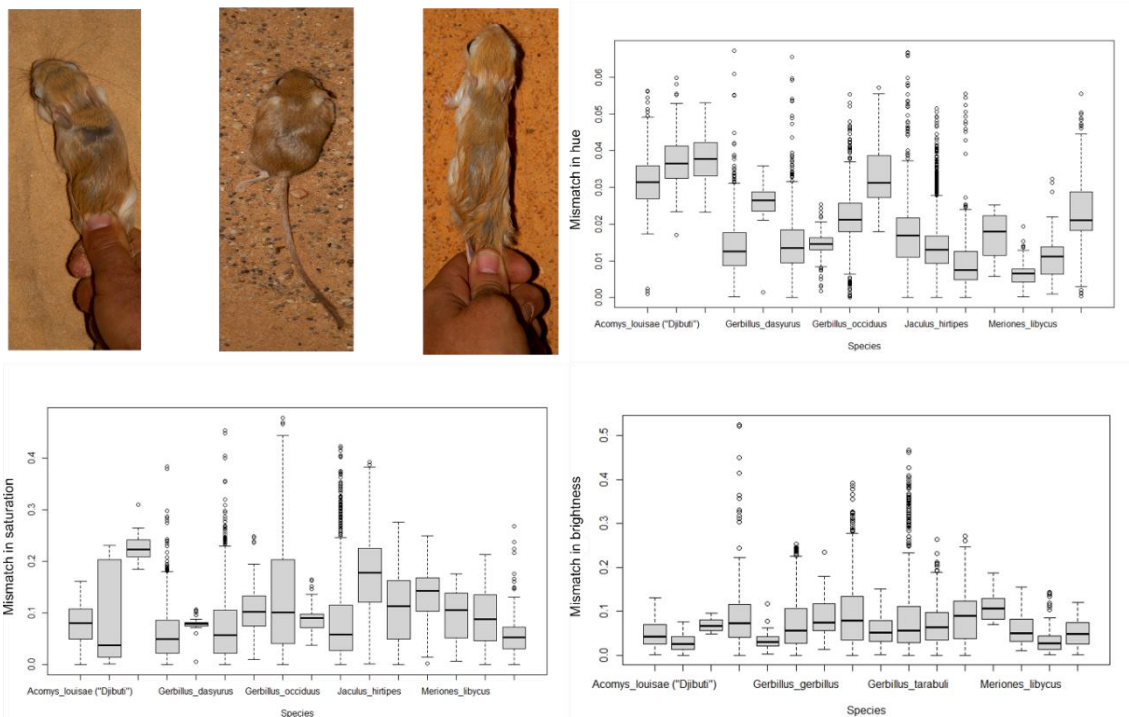
Figure 8. Mismatch in hue (top right), saturation (bottom left) and brightness (bottom right) grouped by species. Together with photographs of captured and studied specimens. Photo credits: Zbyszek Boratyński

The results, from a mixed model analysis for *Jaculus hirtipes* species (N = 70) for mismatches in hue showed that both quadratic and linear terms were significant for spatial scale; linear term was positive [β (s.e.) = 0.04 (0.01)] and quadratic was negative [β = -0.14 (0.01), Table 2, Figure 3]. For temporal scale, linear term was significant and positive [β = 0.07 (0.01)] but quadratic term was not significant [β = 0.02 (0.01), Figure 4]. The results for analysis for mismatch in saturation showed significant linear [β = -0.19 (0.01)] but negative quadratic terms [β = -0.08 (0.01)] for spatial scale. For temporal scale, it showed significant negative linear [β = -0.04 (0.01)] but positive quadratic terms [β = 0.05 (0.01)]. The results for analysis for mismatch in brightness, showed both significant negative linear [β = -0.19 (0.01)] and quadratic terms [β = -0.11 (0.01)] for spatial scale. For temporal scale, it showed insignificant linear [β = -0.01 (0.01)] but significant negative quadratic terms [β = -0.06 (0.01)].

Table 1. Anova results from three mixed model analyses with mismatches between mismatch in hue, saturation or brightness as dependent variables, species (16) as a factor and spatial and temporal scales as continuous predictors.

	df	Mismatch in 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	517.02	<0.001	2.61	<0.001	238.56	<0.01
Temporal scale	1	137.59	<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	76.10	<0.001	413.06	<0.001	422.68	<0.001

The results, from a mixed model analysis for *Gerbillus gerbillus* species (N=58) for mismatches in hue showed that both quadratic and linear terms were significant for spatial scale; linear was positive [β = 0.13 (0.01)] and quadratic was negative [β = -0.15 (0.01)]. For temporal scale, linear term was significant [β = 0.05 (0.01)] but quadratic was negative [β = -0.03 (0.01)]. The results for analysis for mismatch in saturation showed insignificant linear [β = -0.01 (0.02)] and quadratic terms [β = -0.04 (0.01)] for spatial scale. For temporal scale, it showed insignificant linear [β = -0.04 (0.02)] and quadratic [β = -0.01 (0.02)] terms. The results for analysis for mismatch in brightness, showed insignificant linear [β = -0.004 (0.01)] but significant negative quadratic [β = -0.10 (0.02)] terms for spatial scale. For temporal scale it showed significative linear [β = 0.03 (0.01)] but insignificant quadratic terms [β = -0.01 (0.02)].

The results, from a mixed model analysis for *Jaculus jaculus* (N = 40) species for mismatches in hue showed that both linear and quadratic terms were significant for spatial scale, linear was positive [β = 0.11 (0.01)] and quadratic was negative [β = -0.05 (0.01)]. For temporal scale linear term was insignificant [β = 0.02 (0.02)] but quadratic was significant and positive [β = 0.07 (0.02), Table 2]. The results for analysis for mismatch in saturation showed significant negative linear [β = -0.08 (0.02)] and quadratic terms [β = -0.11 (0.02)] for spatial scale. For temporal scale, it showed negative linear [β = -0.16 (0.02)] but insignificant quadratic terms [β = -0.04 (0.02)]. The results for analysis for mismatch in brightness, showed insignificant linear [β = 0.04 (0.01)] but negative significant quadratic terms [β = -0.13 (0.01)] for spatial scale. For temporal scale, it showed insignificant linear [β = -0.0007 (0.02)] but significant negative quadratic terms [β = -0.06 (0.02)].

Table 2. Results for 5 rodent species from three mixed model analyses with hue, saturation or brightness as dependent variables, and spatial and temporal scales as continuous predictors.

	Hue			Saturation			Brightness		
	β(S.E.)	Z	P	β(S.E.)	Z	P	β(S.E.)	Z	P
Jaculus hirtipes (N = 70)									
Intercept	-4.14 (0.25)	-16.9	<0.001	-1.7 (0.15)	-11.7	<0.001	-2.91 (0.20)	-14.532	<0.001
Spatial scale	0.04 (0.01)	6.17	<0.001	-0.19 (0.01)	-6.53	<0.001	-0.20 (0.01)	-17.05	<0.001
Temporal scale	0.07 (0.01)	9.27	<0.001	-0.04 (0.01)	-4.48	<0.001	-0.01 (0.01)	-0.60	0.55
Spatial2	-0.14 (0.01)	-22.27	<0.001	-0.08 (0.01)	-9.73	<0.001	-0.11 (0.01)	-10.39	<0.001
Temp.2	0.02 (0.01)	2.42	0.01	0.05 (0.01)	4.71	<0.001	-0.06 (0.01)	-4.13	<0.001
Gerbillus gerbillus (N = 58)									
(Intercept)	-4.40 (0.17)	-27.04	<0.001	-2.67 (0.14)	-18.77	<0.001	-2.76 (0.12)	-22.12	<0.001
Spatial Scale	0.13 (0.01)	14.1	<0.001	-0.01 (0.02)	-0.65	0.52	-0.004 (0.01)	-0.37	0.71
Temporal Scale	0.05 (0.01)	5.09	<0.001	-0.04 (0.02)	-2.49	0.013	0.05 (0.01)	3.49	<0.001
Spatial2	-0.15 (0.01)	-18.04	<0.001	-0.04 (0.01)	-2.8	0.005	-0.10 (0.01)	-8.60	<0.001
Temp.2	-0.03 (0.01)	-2.94	0.003	-0.01 (0.02)	-0.47	0.64	-0.01 (0.02)	-0.57	0.57
Jaculus jaculus (N = 40)									
(Intercept)	-4.83 (0.09)	-53.64	<0.001	-2.18 (0.09)	-26.04	<0.001	-2.52 (0.10)	-24.54	<0.001
Spatial Scale	0.11 (0.01)	7.68	<0.001	-0.08 (0.02)	-4.32	<0.001	0.04 (0.01)	2.73	0.006
Temporal Scale	0.02 (0.02)	1.52	0.13	-0.16 (0.02)	-8.47	<0.001	-0.0007 (0.02)	-0.05	0.96
Spatial2	-0.05 (0.01)	-3.78	<0.001	-0.11 (0.02)	-6.51	<0.001	-0.13 (0.01)	-9.17	<0.001
Temp.2	0.07 (0.02)	3.41	<0.001	-0.04 (0.02)	-1.62	0.11	-0.06 (0.02)	-3.15	0.002
Gerbillus tarabuli (N = 37)									
(Intercept)	-4.24 (0.20)	-21.35	<0.001	-2.37 (0.07)	-34.74	<0.001	-2.60 (0.11)	-20.61	<0.001
Spatial Scale	0.16 (0.01)	12.77	<0.001	0.14 (0.03)	5.11	<0.001	-0.18 (0.02)	-8.93	<0.001
Temporal Scale	0.04 (0.01)	2.72	0.006	0.14 (0.03)	5.34	<0.001	0.24 (0.02)	11.14	<0.001
Spatial2	-0.17 (0.01)	-15.83	<0.001	0.06 (0.02)	2.53	0.01	-0.22 (0.02)	-11.52	<0.001
Temp.2	-0.08 (0.01)	-5.40	<0.001	0.09 (0.03)	2.84	0.005	0.11 (0.03)	4.20	<0.001
Gerbillus amoenus (N = 32)									
(Intercept)	-4.33 (0.07)	-58.74	<0.001	-2.87 (0.11)	-27.19	<0.001	-2.94 (0.5)	-5.85	<0.001
Spatial Scale	0.09 (0.01)	8.15	<0.001	0.04 (0.02)	1.94	0.05	-0.15 (0.02)	-8.05	<0.001
Temporal Scale	-0.02 (0.01)	-2.6	0.009	0.09 (0.02)	4.48	<0.001	0.25 (0.02)	12.95	<0.001
Spatial2	-0.10 (0.01)	-10.64	<0.001	0.01 (0.02)	0.48	0.63	-0.03 (0.02)	-1.70	0.09
Temp.2	-0.06 (0.01)	-4.75	<0.001	-0.10 (0.03)	-3.72	<0.001	0.09 (0.02)	3.74	<0.001

The results, from a mixed model analysis for *Gerbillus tarabuli* (N = 37) species for mismatches in hue showed that both quadratic and linear terms were significant for spatial scale, linear was positive [β = 0.16 (0.01)] and quadratic was negative [β = -0.17 (0.01)]. For temporal scale linear term was weak [β = 0.04 (0.01)] but quadratic was significant and negative [β = -0.08 (0.01), Table 2]. The results for analysis for mismatch in saturation showed significant positive linear [β = 0.14 (0.03)] but insignificant quadratic [β = 0.06 (0.02)] terms for spatial scale. For temporal scale it showed positive linear [β = 0.14 (0.03)] but insignificant quadratic terms [β = 0.09 (0.03)]. The results for analysis for mismatch in brightness, showed both significant and negative linear [β = -0.18 (0.02)] and quadratic terms [β = -0.22 (0.02)] for spatial scale. For temporal scale, it showed positive and significant linear [β = 0.24 (0.02)] and quadratic terms [β = 0.11 (0.03)].

Figure 9. Graphical representation of the β results in several generalized linear mixed model tests on 5 different species using HSV mismatches as dependent variable and scaled spatial scale as continuous predictors, including both linear and quadratic terms.

The results, from a mixed model analysis for *Gerbillus amoenus* (N = 32) species for mismatches in hue showed that both quadratic and linear terms were significant for spatial scale, linear was positive [β = 0.09 (0.01)] and quadratic was negative [β = -0.06 (0.01)]. For temporal scale linear term was insignificant [β = -0.02 (0.01)] but quadratic term was significant and negative [β = -0.06 (0.01), Table 2]. The results for analysis for mismatch in saturation showed insignificant linear [β = 0.04 (0.02)] and quadratic [β = 0.01 (0.02)] terms for spatial scale. For temporal scale, it showed positive significant linear [β = 0.09 (0.02)] but negative quadratic terms [β = -0.10 (0.03)]. The results for analysis for mismatch in brightness, showed negative linear [β = -0.15 (0.02)] and insignificant quadratic [β = -0.03 (0.02)] terms for spatial scale. For temporal scale, it showed significant positive linear [β = 0.25 (0.02)] and quadratic terms [β = 0.09 (0.02)].
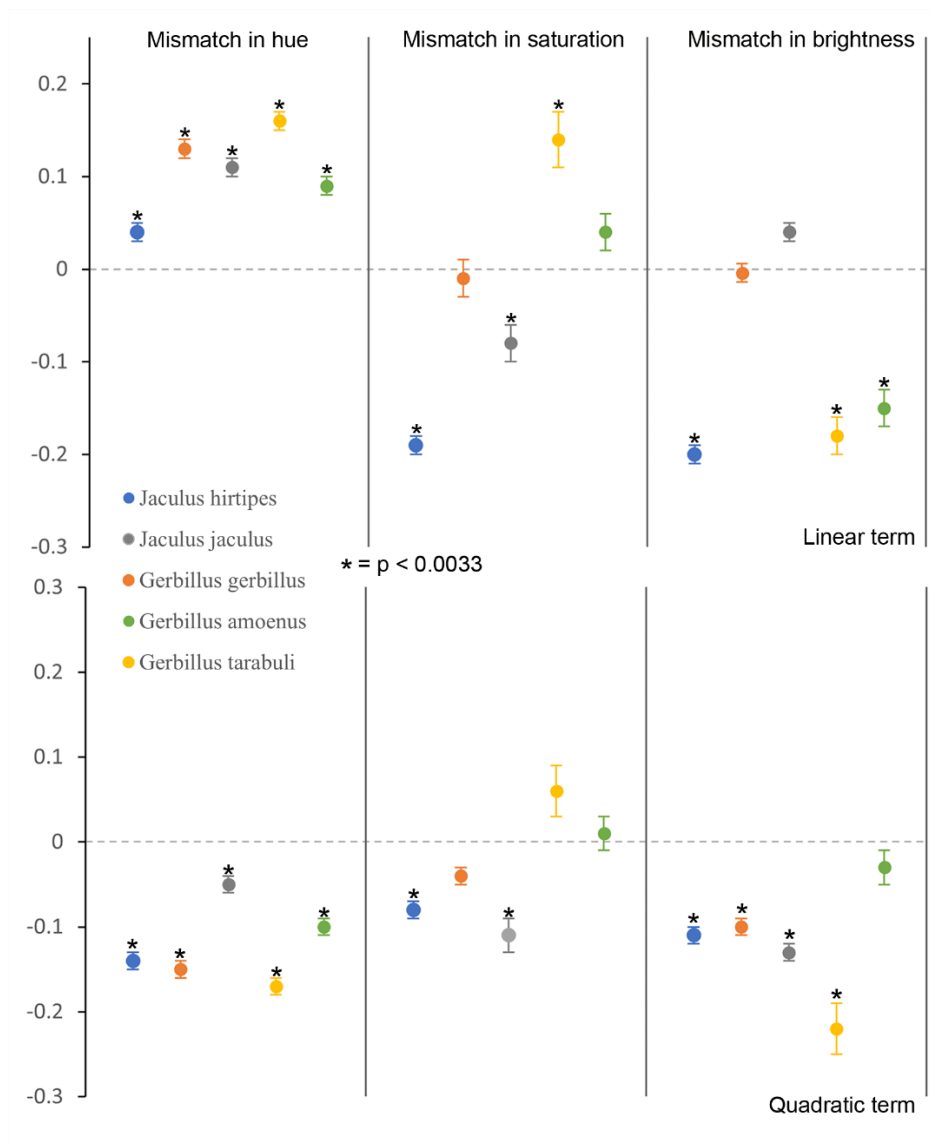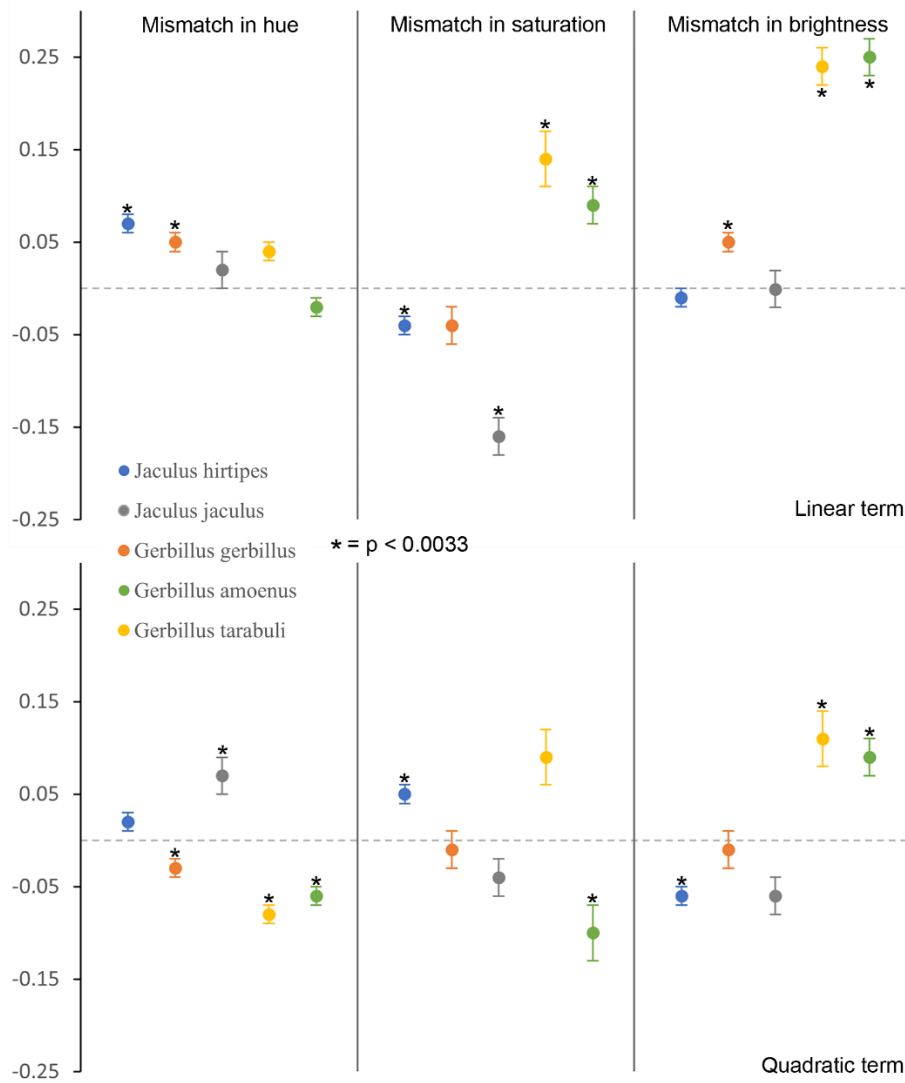
Figure 10. Figure 7. Graphical representation of the β in several generalized linear mixed model tests on 5 different species using HSV mismatches as dependent variable and scaled temporal scale as continuous predictors, including both linear and quadratic terms.
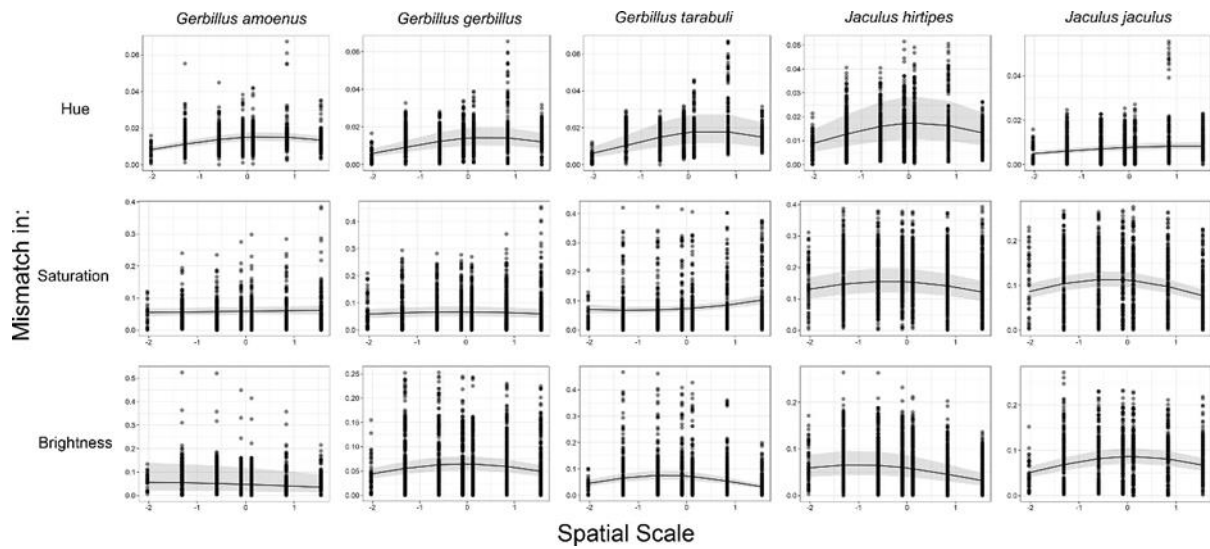
Figure 11. Graphical representation of the results for 5 mixed model analyses with the mismatch in hue, saturation or brightness as dependent variables, and spatial scale as continuous predictors, on the 5 studied species. It shows the evolution and prediction the model estimated.
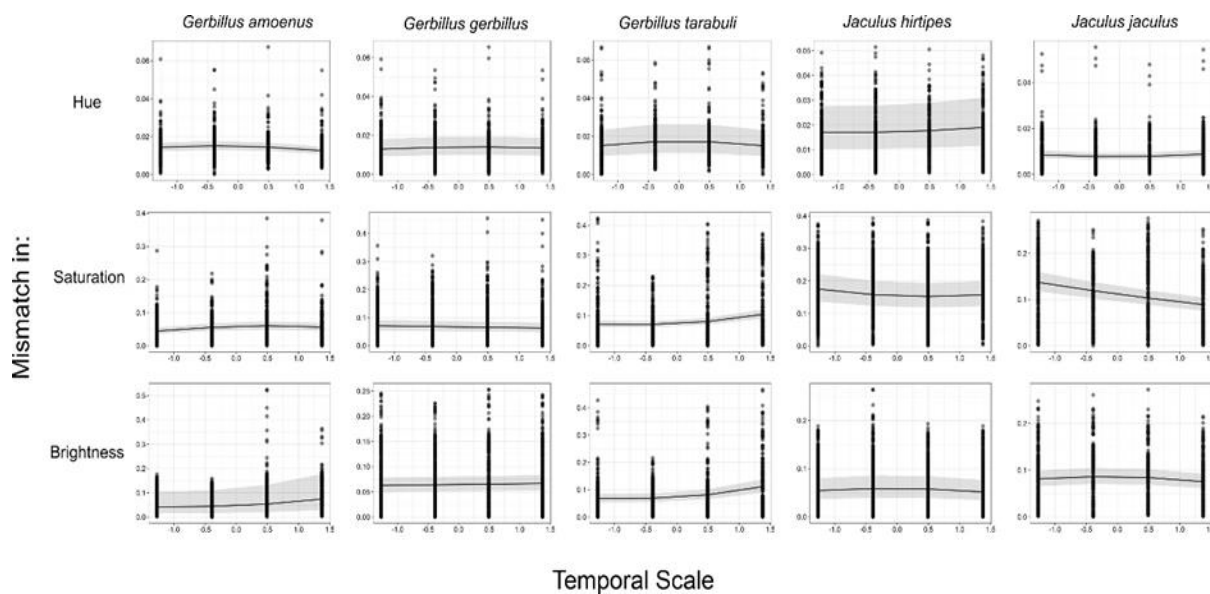
Figure 12. Graphical representation of the results for 5 mixed model analyses with the mismatch in hue, saturation or brightness as dependent variables, and spatial scale as continuous predictors, on the 5 studied species. It shows the evolution and prediction the model estimated.

Discussion

Rodents' community from Sahara-Sahel provides a fruitful model system to study how animals adapt to their habitat (Boratyński et al., 2017; Boratyński et al., 2014). Benefiting from that, here we have presented results from analyses on camouflage in sixteen Sahara-Sahel rodent species, conducted on in total of 295 individuals, and showed that species differed in their spatial and temporal resolution of the camouflage adaptation. We also discovered that different colour characteristics (hue, saturation, and brightness) have variable importance among studied species, perhaps reflecting species activity patterns and other ecological properties. Nevertheless, there are striking patterns shared among species in how the habitat colour matching developed. All species showed that accuracy of camouflage in hue, the colour of dorsal fur, generally decreased with increasing the geographical scale of analyses. However, this effect was complicated by important quadratic terms of spatial scale, suggesting that in addition to the optimized local scale of camouflage (1-100 m) species also match relatively well habitat perceived on very global scale (10-100 km). In contrast, the amount of reflected light by dorsal fur, brightness, matched better the habitat in very global spatial scales, in all species which had data of enough power for analyses (N > 30).

The general pattern in the spatial scale of brightness camouflage reveals that three (*Jaculus hirtipes*, *Gerbillus tarabuli* and *Gerbillus amoenus*), out of five studied species, have developed generalist strategy when it comes to matching brightness, as they show better camouflage in the broad spatial scale. This might be due to light and reflectance conditions being relatively homogenous on the desert surface, making it better and less energetically expensive to match the brightness of a large spatial scale than the small intricate light conditions of a local niche. The species which showed the strongest brightness camouflage were: Jaculus hirtipes and Gerbillus tarabuli (Table 2) (Figure 3). Analysing brightness camouflage on a temporal scale, we can see two distinct findings. The first, shared among *Gerbillus amoenus* and *Gerbillus tarabuli*, showed us that these species were better adapted to brightness camouflage a few years (1-2) before capture (Table 2) (Figure 4). This might be related to the observations of 1-2 years delayed population responses in *Gerbillus* rodents, following increasing habitat productivity (Barros et al., 2018), suggesting the selection response observed on captured individuals is related to rather past than current selective pressures. The second pattern, belonging to *Jaculus hirtipes*, revealed that they better match their habitat brightness at the year of capture, instead of previous years (Table 2) (Figure 4). The different patterns observed here can, also, be speculated to reflect the mobility of the studied species as well as the longevity and/or time of reproduction, perhaps happening later in *Jaculus* lives than in the Gerbillus species. Moreover, the results for the study of brightness as a camouflage tactic show promising results and invoke several questions, such as: why all species, with brightness

camouflage, evolved to a generalist strategy, matching the habitat brightness on a broad scale? and how the different species life histories contribute to the determination of brightness camouflage?

We have found that every species developed a specialist camouflage strategy for matching local habit hue in detriment of the large spatial scales, developing a specialist strategy in this colour property (Table 3) (Figure 3). The species that presented the strongest specialist tactic for hue camouflage were: *Gerbillus gerbillus* and *Gerbillus tarabuli*. This might be due to predators' vision models only encompassing spatial scales considered small in our scale (1m to 100km). This way, rodents responding to this selection pressure would try to match the background visible to the predator, resulting in a specialist strategy matching camouflage on the local scale (1-100m). In the temporal scale of hue camouflage, 2 species (*Jaculus hirtipes* and *Gerbillus gerbillus*), revealed that they better matched their habitat at the same year they were captured, when compared to prior years (Figure 4). The question is if *Gerbillus* genera present more specialization than *Jaculus.* Our results show some evidence on this, but more research needs to be made.

Saturation fur matching seems to be less important for camouflage in most of the studied species of the North African rodents. It was only detectable for the *Jaculus* genus that showed camouflage in the broad spatial scale in saturation, suggesting a generalist strategy (Table 2) (Figure 3). An explanation for this could come from the fact that *Jaculus* species are typically known for being more mobile and active (Happold, 2013), being able to move several kilometres each day, therefore, needing to traverse several different background patches.

Through our study it became apparent that the different colour properties (hue, saturation and brightness) showed remarkable differences for camouflage strategies (Table 2) (Figures 3 and 4). This complicates the perception of how specialist or generalist strategies could be defined. For instance, a specialist strategy was previously understood as when the animal matches one habitat background well at the expense of the others (Cuthill, 2019). Alternatively, animals can adapt colourations to resemble multiple backgrounds simultaneously, a generalist strategy (Michalis et al., 2017). For instance, our results not only confirm this theory but further the knowledge in this field, providing the novel concept that camouflage strategies are dependent on the studied colour parameters (Table 2). As such, some rodent species (i.e., *Jaculus hirtipes*) seemed to have a specialist tactic in hue camouflage, matching it very well on the local scale, but on the other colour properties (saturation and brightness) reflected a generalist strategy, better matching these properties on the broad spatial scale. As hue represents the colour observed on the animal, it makes sense to be the primary camouflage colour parameter for each studied species. This phenomenon can be due to the predator's

vision abilities being more biased to recognise hue, leading prey to develop better camouflage in hue (Nokelainen, Brito, et al., 2020). Brightness could be considered as the second most important camouflage property due to being a relevant characteristic in 18 out of 25 analyses (hue having: 21/25 and saturation only in: 16/25) (Table 2) (Figures 3 and 4). As brightness describes the perceived reflected light by the observer it can be important due to animal behaviour. As the Sahara-Sahel rodents usually are active during night (Boratyński et al., 2017), on dim light conditions, brightness, or the light reflected, can be an important parameter for the prey to stay hidden and avoid being exposed against the murky background. Likewise, hue, or colour, is not well perceived in low light conditions (at night) by predators. Saturation, in contrast, seems to be the weakest colour parameter in determining camouflage adaptation. It is the only studied camouflage property which a species, *Gerbillus gerbillus,* revealed no connection, meaning that this species shows no saturation camouflage, not matching saturation at any spatial or temporal scale. Saturation is the intensity of how the colour is perceived, the higher the saturation the more vivid the colour, the lower the saturation, the closer it is to grey (Ajmal et al., 2018). Saturation could be not as important as the other studied camouflage parameters, as some predators vision models could interpret saturation poorly (Kelber & Osorio, 2010).

With this study, we did not directly measure how rodent species make use of and behave in their natural habitat, yet through the results, we obtained in the spatial scale it is possible to compare and infer the connection between morphological and behavioural adaptation. Our results show that there are significant differences in the way the studied species adapted to their environment (Table 2). For instance, our research shows some clues that species genus can group similar responses, i.e., our results showed that the *Jaculus* genus shared similar responses in saturation camouflage, and the *Gerbillus* genus in brightness camouflage (Table 2) (Figures 3 and 4). These differences can be interconnected with animal behaviour and life story. As an example, more mobile species, such as Jaculus (Happold, 2013), should cover bigger distances and cross more varied backgrounds, therefore, it would be advantageous to develop a generalist strategy. Such speculation is confirmed by our results, *Jaculus hirtipes* developed a generalist tactic in saturation and brightness camouflage. It is possible to find suggestive links of morphological adaptations with behavioural ones. Essentially behavioural studies are needed to be integrated with camouflage analyses to further our knowledge in this field, furthermore, research in this area would greatly benefit from the development of technology, such as efficient rodent GPS trackers.

Conclusions

Some species differences in spatial resolution of camouflage adaptation were made obvious with this research. When analysing hue, all species showed a specialist strategy, prioritizing short spatial scales. When analysing saturation, the *Jaculus* genus showed a preference for a generalist strategy (larger spatial scales) and *Gerbillus tarabuli* demonstrated a stronger specialist tactic. When analysing brightness, 3 species (*Jaculus hirtipes*, *Gerbillus tarabuli* and *Gerbillus amoenus*) showed a preference for matching large spatial scales, developing a generalist strategy, and 2 species (*Gerbillus gerbillus* and *Jaculus jaculus*) showed that they matched better the extremities of spatial scale. Therefore, we can conclude that division between generalist vs specialist camouflage strategies might not be as straightforward as we previously thought. It became evident that animals developed different camouflage strategies depending on the colour properties studied (hue, saturation, and brightness). Consequently, the same animal could have developed a generalist strategy in one camouflage property, such as hue, and a specialist strategy in another, such as brightness. Could this be because animals developed variable camouflage strategies depending on the type and timing (considering prey ontogeny) of the selection applied by the diversity of predators? Depending on the predators' visual abilities (Nokelainen, Brito, et al., 2020) selection on hue, saturation or brightness could prevail over the other parameters. Could it be that such diverse colour adaptations help the diverse Sahara-Sahelian community of rodents to coexist in sympatry (Barros et al., 2018)? Our research also allowed to notice that time resolution is something important to consider for adaptation. Life history strategies (e.g., fast vs slow reproduction), behaviours and species mobility could all be related to the timing of selection pressures on the rodents' camouflage. For instance, our model system, especially *Gerbillus* rodents, showed a strong population response (around one year delays) to past productivity bursts in otherwise harsh desert environment (Barros et al., 2018). Such effect together with presented here novel results suggests that selection might be strongest in the early ages of physiologically able to reproduce individuals. This requires future research focusing on the strength of selection during ontogenetic development and the effectiveness of that selection on young (before reproduction) and older animals. With the development of technology and further research it can be possible to learn and find out more about how camouflage is linked with spatial and temporal scales, and how it responds to environmental inputs. Animals adapt to the environment, and as evidenced in this research such adaptive responses can be complex. Anthropogenic climate change pose threats toward animal species with strong and complex, thus lacking flexibility, adaptations, and might eventually lead to the extinction of many species. Research like this is important to understand how animals could respond to the changing environment and if they would be able to survive and persist in new scenarios.

Bibliography

Ajmal, A., Hollitt, C., Frean, M., & Al-Sahaf, H. (2018, 19-21 Nov. 2018). *A Comparison of RGB and HSV Colour Spaces for Visual Attention Models.* Paper presented at the 2018 International Conference on Image and Vision Computing New Zealand (IVCNZ).

Akpodiogaga-a, P., & Odjugo, O. (2010). General Overview of Climate Change Impacts in Nigeria. *Journal of Human Ecology, 29*(1), 47-55. doi:10.1080/09709274.2010.11906248

Barros, M. I., Brito, J. C., Campos, J. C., Mappes, T., Qninba, A., Sousa, F. V., & Boratyński, Z. (2018). The effect of rainfall on population dynamics in Sahara-Sahel rodents. *Mammal Research, 63*(4), 485-492. doi:10.1007/s13364-018-0377-x

Behera, M. D., Matin, S., & Roy, P. S. (2014). Biodiversity of Kargil Cold Desert in the Ladakh Himalaya. In S. i. Nakano, T. Yahara, & T. Nakashizuka (Eds.), *Integrative Observations and Assessments* (pp. 253-274). Tokyo: Springer Japan.

Bontrager, M., Muir, C. D., Mahony, C., Gamble, D. E., Germain, R. M., Hargreaves, A. L., . . . Angert, A. L. (2020). Climate warming weakens local adaptation. *bioRxiv*, 2020.2011.2001.364349. doi:10.1101/2020.11.01.364349

Boomsma, J. J. (2016). Fifty years of illumination about the natural levels of adaptation. *Current Biology, 26*(24), R1250-R1255. doi:https://doi.org/10.1016/j.cub.2016.11.034

Boratyński, Z., Brito, J. C., Campos, J. C., Cunha, J. L., Granjon, L., Mappes, T., . . . Serén, N. (2017). Repeated evolution of camouflage in speciose desert rodents. *Scientific Reports, 7*(1), 3522. doi:10.1038/s41598-017-03444-y

Boratyński, Z., Brito, J. C., Campos, J. C., Karala, M., & Mappes, T. (2014). Large Spatial Scale of the Phenotype-Environment Color Matching in Two Cryptic Species of African Desert Jerboas (Dipodidae: Jaculus). *PLOS ONE, 9*(4), e94342. doi:10.1371/journal.pone.0094342

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

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

Brito, J. C., Godinho, R., Martínez-Freiría, F., Pleguezuelos, J. M., Rebelo, H., Santos, X., . . . Carranza, S. (2014). Unravelling biodiversity, evolution and threats to conservation in the Sahara-Sahel. *Biol Rev Camb Philos Soc, 89*(1), 215-231. doi:10.1111/brv.12049

Brito, J. C., Tarroso, P., Vale, C. G., Martínez-Freiría, F., Boratyński, Z., Campos, J. C., . . . Carvalho, S. B. (2016). Conservation Biogeography of the Sahara-Sahel: additional protected areas are

needed to secure unique biodiversity. *Diversity and Distributions, 22*(4), 371-384.
doi:https://doi.org/10.1111/ddi.12416

Caro, T. (2005). The Adaptive Significance of Coloration in Mammals. *BioScience, 55*(2), 125.
doi:10.1641/0006-3568(2005)055[0125:tasoci]2.0.co;2

Caro, T., & Mallarino, R. (2020). Coloration in Mammals. *Trends in Ecology & Evolution, 35*(4), 357-
366. doi:10.1016/j.tree.2019.12.008

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range Shifts of Species
Associated with High Levels of Climate Warming. *Science, 333*(6045), 1024-1026.
doi:doi:10.1126/science.1206432

Cuthill, I. C. (2019). Camouflage. *Journal of Zoology, 308*(2), 75-92. doi:10.1111/jzo.12682

Cuthill, I. C., Stevens, M., Sheppard, J., Maddocks, T., Parraga, C. A., & Troscianko, T. S. (2005).
Disruptive coloration and background pattern matching. *Nature, 434*(7029), 72-74.
doi:10.1038/nature03312

Davies, J., Poulsen, L., Schulte-Herbrüggen, B., Mackinnon, K., Crawhall, N., Henwood, W., . . . Gudka,
M. (2012). *Conserving Dryland Biodiversity. xii+ 84p*.

Davis, M. B., & Shaw, R. G. (2001). Range Shifts and Adaptive Responses to Quaternary Climate
Change. *Science, 292*(5517), 673-679. doi:doi:10.1126/science.292.5517.673

Di Bernardi, C., Thierry, A.-M., Eide, N. E., Bowler, D. E., Rød-Eriksen, L., Blumentrath, S., . . . Landa,
A. (2021). Fitness and fur colouration: Testing the camouflage and thermoregulation
hypotheses in an Arctic mammal. *Journal of Animal Ecology, 90*(5), 1328-1340.
doi:https://doi.org/10.1111/1365-2656.13457

Diffenbaugh, N. S., & Field, C. B. (2013). Changes in Ecologically Critical Terrestrial Climate
Conditions. *Science, 341*(6145), 486-492. doi:doi:10.1126/science.1237123

Durant, S. M., Pettorelli, N., Bashir, S., Woodroffe, R., Wacher, T., Ornellas, P. D., . . . Baillie, J. E. M.
(2012). Forgotten Biodiversity in Desert Ecosystems. *Science, 336*(6087), 1379-1380.
doi:doi:10.1126/science.336.6087.1379

Endler, J. A. (1978). A Predator's View of Animal Color Patterns. In M. K. Hecht, W. C. Steere, & B.
Wallace (Eds.), *Evolutionary Biology* (pp. 319-364). Boston, MA: Springer US.

Giannoni, S. M., Dacar, M., Taraborelli, P., & Borghi, C. E. (2001). Seed hoarding by rodents of the
Monte Desert, Argentina. *Austral Ecology, 26*(3), 259-263.
doi:https://doi.org/10.1046/j.1442-9993.2001.01112.x

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

Hadley, N. F. (1972). Desert Species and Adaptation: Plants and animals in arid environments show many striking similarities in their morphological and physiological adaptations. *American Scientist, 60*(3), 338-347. Retrieved from http://www.jstor.org/stable/27843134

Haim, A., & Izhaki, I. (1995). Comparative physiology of thermoregulation in rodents: adaptations to arid and mesic environments. *Journal of Arid Environments, 31*(4), 431-440. doi:10.1016/s0140-1963(05)80126-0

Happold, D. C. D. (2013). Mammals of Africa Volume III Rodents, Hares and Rabbits. In D. C. D. Happold (Ed.), *Mammals of Africa : Rodents, Hares and Rabbits* (1 ed., Vol. III, pp. 137-138). London: Bloomsbury Publishing.

Kang, C.-K., Moon, J.-Y., Lee, S.-i., & Jablonski, P. G. (2013). Moths on tree trunks seek out more cryptic positions when their current crypticity is low. *Animal Behaviour, 86*(3), 587-594. doi:https://doi.org/10.1016/j.anbehav.2013.06.014

Kelber, A., & Osorio, D. (2010). From spectral information to animal colour vision: experiments and concepts. *Proceedings of the Royal Society B: Biological Sciences, 277*(1688), 1617-1625. doi:doi:10.1098/rspb.2009.2118

Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography, 38*(1), 15-28. doi:https://doi.org/10.1111/ecog.00967

Mahmoud, S. H., & Gan, T. Y. (2018). Impact of anthropogenic climate change and human activities on environment and ecosystem services in arid regions. *Science of The Total Environment, 633*, 1329-1344. doi:https://doi.org/10.1016/j.scitotenv.2018.03.290

Mares, M. A. (1993). Desert Rodents, Seed Consumption, and Convergence. *BioScience, 43*(6), 372-379. doi:10.2307/1312045

Merilaita, S. (2011). *Animal Camouflage: Mechanisms and Function* (M. Stevens & S. Merilaita Eds.). Cambridge: Cambridge University Press.

Merilaita, S., Scott-Samuel, N. E., & Cuthill, I. C. (2017). How camouflage works. *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*(1724), 20160341. doi:doi:10.1098/rstb.2016.0341

Merilaita, S., Scott-Samuel, N. E., & Cuthill, I. C. (2017). How camouflage works. *Philosophical Transactions of the Royal Society B-Biological Sciences, 372*(1724). doi:10.1098/rstb.2016.0341

Michalis, C., Scott-Samuel, N. E., Gibson, D. P., & Cuthill, I. C. (2017). Optimal background matching camouflage. *Proceedings of the Royal Society B: Biological Sciences, 284*(1858), 20170709. doi:doi:10.1098/rspb.2017.0709

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

Mulroy, T. W., & Rundel, P. W. (1977). Annual Plants: Adaptations to Desert Environments. *BioScience, 27*(2), 109-114. doi:10.2307/1297607

Murphy, N. P., Breed, M. F., Guzik, M. T., Cooper, S. J. B., & Austin, A. D. (2012). Trapped in desert springs: phylogeography of Australian desert spring snails. *Journal of Biogeography, 39*(9), 1573-1582. doi:https://doi.org/10.1111/j.1365-2699.2012.02725.x

Nokelainen, O., Brito, J. C., Scott-Samuel, N. E., Valkonen, J. K., & Boratyński, Z. (2020). Camouflage accuracy in Sahara–Sahel desert rodents. *Journal of Animal Ecology, 89*(7), 1658-1669. doi:10.1111/1365-2656.13225

Nokelainen, O., Sreelatha, L. B., Brito, J. C., Campos, J. C., Scott-Samuel, N. E., Valkonen, J. K., & Boratyński, Z. (2020). Camouflage in arid environments: the case of Sahara-Sahel desert rodents. *Journal of Vertebrate Biology, 69*(2), 1-12, 12. Retrieved from https://doi.org/10.25225/jvb.20007

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V., Underwood, E. C., . . . Morrison, J. C. (2001). Terrestrial Ecoregions of the World: A New Map of Life on EarthA new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience, 51*(11), 933-938.

Ott, S. R., & Rogers, S. M. (2010). Gregarious desert locusts have substantially larger brains with altered proportions compared with the solitarious phase. *Proceedings of the Royal Society B: Biological Sciences, 277*(1697), 3087-3096. doi:doi:10.1098/rspb.2010.0694

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., . . . Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science, 355*(6332), eaai9214. doi:doi:10.1126/science.aai9214

Peterson, M. L., Doak, D. F., & Morris, W. F. (2019). Incorporating local adaptation into forecasts of species' distribution and abundance under climate change. *Global Change Biology, 25*(3), 775-793. doi:https://doi.org/10.1111/gcb.14562

Price, N., Green, S., Troscianko, J., Tregenza, T., & Stevens, M. (2019). Background matching and disruptive coloration as habitat-specific strategies for camouflage. *Scientific Reports, 9*. doi:10.1038/s41598-019-44349-2

Ramirez-Delgado, V. H., & del Castillo, R. C. (2020). Background matching, disruptive coloration, and differential use of microhabitats in two neotropical grasshoppers with sexual dichromatism. *Ecology and Evolution, 10*(3), 1401-1412. doi:10.1002/ece3.5995

Renaud, S., Michaux, J., Schmidt, D. N., Aguilar, J.-P., Mein, P., & Auffray, J.-C. (2005). Morphological evolution, ecological diversification and climate change in rodents. *Proceedings of the Royal Society B: Biological Sciences, 272*(1563), 609-617. doi:doi:10.1098/rspb.2004.2992

Rosenzweig, M. L., & Winakur, J. (1969). Population Ecology of Desert Rodent Communities: Habitats and Environmental Complexity. *Ecology, 50*(4), 558-572. doi:https://doi.org/10.2307/1936246

Sillero-Zubiri, C., & Gottelli, D. (1995). Diet and feeding behavior of Ethiopian wolves (Canis simensis). *Journal of Mammalogy, 76*(2), 531-541.

Tankus, A., & Yeshurun, Y. (2001). Convexity-Based Visual Camouflage Breaking. *Computer Vision and Image Understanding, 82*(3), 208-237. doi:https://doi.org/10.1006/cviu.2001.0912

Team, R. C. (2021). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*. Retrieved from https://www.R-project.org/.

Troscianko, J., & Stevens, M. (2015). Image calibration and analysis toolbox – a free software suite for objectively measuring reflectance, colour and pattern. *Methods in Ecology and Evolution, 6*(11), 1320-1331. doi:https://doi.org/10.1111/2041-210X.12439

Williams, J. B., & Tieleman, B. I. (2005). Physiological Adaptation in Desert Birds. *BioScience, 55*(5), 416-425. doi:10.1641/0006-3568(2005)055[0416:Paidb]2.0.Co;2

Wilson, D. E., & Reeder, D. M. (2005). *Mammal species of the world: a taxonomic and geographic reference* (Vol. 1): JHU Press.

Zhou, C., & Wang, K. (2016). Land surface temperature over global deserts: Means, variability, and trends. *Journal of Geophysical Research: Atmospheres, 121*(24), 14,344-314,357. doi:https://doi.org/10.1002/2016JD025410