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Camouflage in arid environments: the case of Sahara-Sahel desert rodents

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Abstract. Deserts and semi-deserts, such as the Sahara-Sahel region in North Africa, are exposed environments with restricted vegetation coverage. Due to limited physical surface structures, these open areas provide a promising ecosystem to understand selection for crypsis. Here, we review knowledge on camouflage adaptation in the Sahara-Sahel rodent community, which represents one of the best documented cases of phenotype-environment convergence comprising a marked taxonomic diversity. Through their evolutionary history, several rodent species from the Sahara-Sahel have repeatedly evolved an accurate background matching against visually-guided predators. Top-down selection by predators is therefore assumed to drive the evolution of a generalist, or compromise, camouflage strategy in these rodents. Spanning a large biogeographic extent and surviving repeated climatic shifts, the community faces extreme and heterogeneous selective pressures, allowing formulation of testable ecological hypotheses. Consequently, Sahara-Sahel rodents poses an exceptional system to investigate which adaptations facilitate species persistence in a mosaic of habitats undergoing climatic change. Studies of these widely distributed communities permits general conclusions about the processes driving adaptation and can give insights into how diversity evolves.

Key words: Africa, background matching, crypsis, predation, protective colouration

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Introduction

Deserts and semi-deserts are characteristically open environments with limited vegetation coverage. They are harsh environments, severely limited by annual precipitation (Holt et al. 2013, Vale & Brito 2015), and therefore, desert organisms have been studied from the perspective of adaptation to arid conditions (Kotler & Brown 1988, Brito et al. 2014). Due to a lack of vegetation (or surface structures), exposed desert habitats provide an opportunity to understand natural selection under extreme conditions (Dice 1947, Brown et al. 1988, Kotler & Brown 1988, Nachman et al. 2003, Hoekstra et al. 2006, Brito et al. 2014, Boratyński et al. 2014, Bleicher et al. 2018).

Selection, broadly defined as differential fitness of individuals caused by differences expressed in their phenotypes, is a key mechanism of evolution driving adaptive change (Bell 2008). In this process, natural sorting of the genetic constituents of

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individuals at the phenotypic level occurs (Reznick 2016). Selection can shape phenotypic variation due to covariation, for example, between prey phenotypic features and predation pressure, as in desert rodents (Kotler & Brown 1988, Hoekstra et al. 2006, Boratyński et al. 2017, Bleicher et al. 2018). Therefore, predator-induced selection can drive evolution of prey anti-predatory adaptations, such as high mobility and saltation behaviour (Alhajeri 2016), bullar hypertrophy (i.e. an auditory morphology in bone structure) aiding auditory sensation and detection of approaching predators (Alhajeri & Steppan 2018), and phenotype-environment convergence for visual crypsis (Caro 2005, Boratyński et al. 2014).

In this review, we focus on North African desert rodents and summarize the current understanding of visual camouflage adaptation in the Sahara-Sahel rodent community. Spanning a large biogeographic extent in North Africa (Fig. 1), and comprising a marked taxonomic diversity (Alhajeri et al. 2015, Boratyński et al. 2017), the Sahara-Sahelian rodent community represents one of the most compelling cases of camouflage adaptation in the wild (Nokelainen et al. 2020). As the community faces extreme (in terms of temperature and dryness) and heterogeneous selection pressures (Kotler & Brown 1988), testing of ecological predictions of ongoing climate and landscape changes is possible. We discuss how this study system can contribute to our understanding of the processes that shape adaptation under ongoing environmental change.

State-of-the-art

One of the most pervasive selection pressures in open habitats is selection driving evolution of anti-predator adaptations, particularly selection for visual concealment from predators or camouflage (Stevens & Merilaita 2009, Boratyński et al. 2014, 2017, Merilaita et al. 2017). In order to avoid detection and recognition, animals often share visual characteristics, including lightness, colour and pattern, with that of their environment (Cott 1940, Stevens & Merilaita 2011, Nokelainen & Stevens 2016). Camouflage is a widespread anti-predator strategy found across many taxa and is not restricted to desert environments. However, as camouflage helps animals to escape from predators, it is particularly important to survival in exposed habitats, where opportunities for hiding in physical structures (such as trees or vegetation) are limited (Dice 1947, Kaufman 1974, Vignieri et al. 2010). It is worth mentioning that to counteract the natural lack of shelters, many rodents can make burrows, which helps them to escape predators (Rios & Álvarez-Castañeda 2012), or are nocturnal.

Camouflage in the Sahara-Sahel desert rodent community presents a fine-tuned example of background matching in geographically widespread taxa (Boratyński et al. 2014, 2017). Both the colour and the pattern of 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 et al. 2020). Animal-

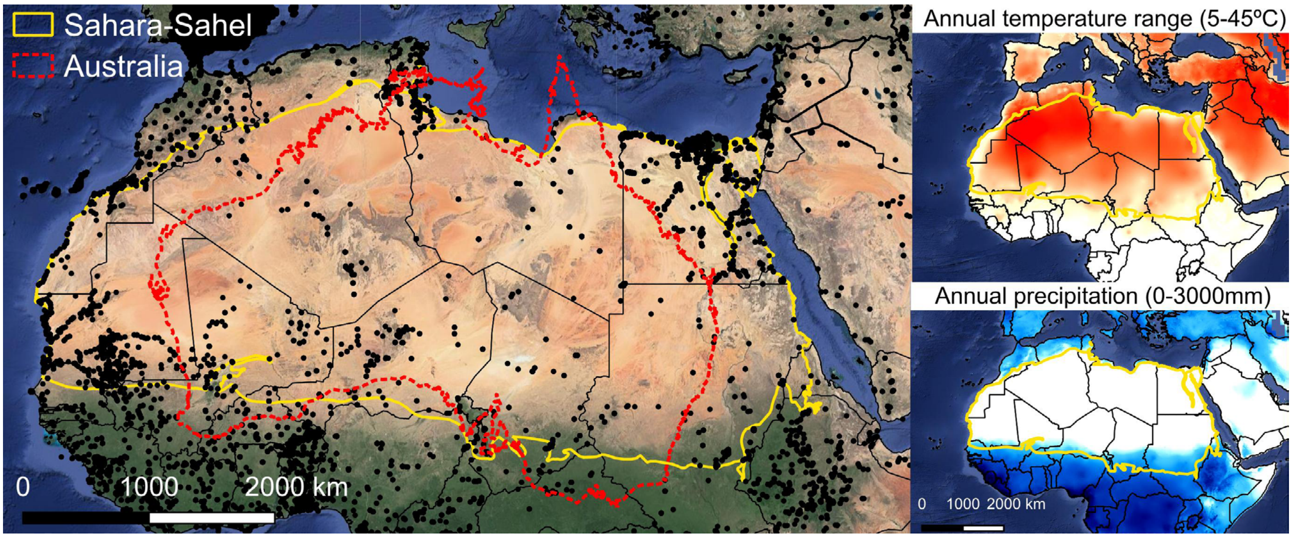

Fig. 1. Rodent species geographic locations (black dots) obtained from the Global Biodiversity Information Facility indicating limited information for most of the Sahara-Sahel (left panel). Inserted outline of Australia (red) is presented on the same scale as the Sahara-Sahel (yellow), for size comparison. Average annual temperature range (top-right) and average yearly precipitation in North Africa (bottom-right).

to-background differences are generally low in Sahara-Sahel rodents at large spatial scales (i.e. such as when animals are being compared between all the backgrounds that the species uses), supporting the hypothesis of a generalist camouflage strategy. However, some species (e.g. *Jaculus hirtipes*) may match best their local habitat (Nokelainen et al. 2020), suggesting the importance of behaviour in improving camouflage and habitat specialization (Stevens & Ruxton 2019). However, a controlled verification of that process is required. It has also been shown that camouflage has evolved repeatedly in Sahara-Sahel rodents, even among related *Gerbillus* species (Boratyński et al. 2017), which suggests that it is an evolutionary labile adaptation, and possibly linked to the repeated changes between semi-arid to hyper-arid habitats over the history of the Sahara-Sahel (Brito et al. 2014, Boratyński et al. 2017, Alhajeri & Steppan 2018).

The ongoing environmental changes in the Sahara-Sahel expose organisms to spatially and temporally heterogeneous selection (Kotler & Brown 1988, Brito et al. 2014). Thus, many species face the constant risk of mismatching their habitat (Merilaita et al. 1999, 2001, Michalis et al. 2017). In theory, animals may evolve several optimal camouflage patterns (Merilaita et al. 1999, 2001, Michalis et al. 2017), potentially specializing to match their most often used micro-habitat. However, if several habitat types are sufficiently similar, an outcome would be a reduction in the conflict between matching different background types, and thus, a generalist strategy may outperform specialism (Merilaita et al. 2001, Houston et al. 2007, Hughes et al. 2019). In this context, trade-offs between specialist and generalist camouflage adaptation can emerge from species' differences in exploratory and personality traits, which will influence the range of micro-habitats visited. While there are potential benefits of exploratory and bold behaviour (e.g. higher chances of encountering novel resources), the predation costs may also be high (Dingemanse & Reale 2005, Nicolaus et al. 2016, but see Moiron et al. 2020).

Co-evolution between complex behavioural strategies as well as spatial and temporal scales of adaptations are theoretically predicted (Stevens & Ruxton 2019), but less often tested in wild animal communities. As Sahara-Sahel desert rodents compromise camouflage accuracy across different habitat types (Nokelainen et al. 2020), they present a good model to investigate how phenotype-environment matching evolves in the community at variable spatial as well as temporal scales (Boratyński et al. 2014, 2017). For example, some rodents may specialize on specific micro-habitats and integration of colour quantification methods may prove useful in revealing habitat specialization and intra-community interactions. Recent methodological advances enable the measurement of animal-to-background matching more objectively (Troscianko & Stevens 2015, Van Den Berg et al. 2019) and the quantification of how camouflage may deceive ecologically relevant sensory systems.

Perspectives

We outline how desert rodents are a particularly valuable study system to tackle the following open questions, all of which are applicable to desert habitat: 1) How do animals cope with habitat heterogeneity over different spatial scales? 2) How does seasonality determine the evolution of camouflage? 3) How does rodent behaviour (e.g. through mobility, dominance structure, life-history strategies) dictate the efficacy of anti-predator strategies? 4) How does behavioural (e.g. diurnal, crepuscular or nocturnal) and cognitive processing of predators facilitate camouflage efficacy? Although these questions may apply to other environments and/or study systems, we focus on desert rodents of Sahara-Sahel as a working example.

How do animals cope with habitat heterogeneity over different spatial scales?

The Sahara-Sahel region is a vast biogeographic entity in North Africa (Fig. 1). Species occupying this environment are assumed to have variable home ranges and mobility, and thus face different camouflage requirements. The terrain does not consist of pure sand habitats; rather, in addition to dunes, there are seasonal river habitats of varied levels of mud, clay and rock, shrublands, rocky plates and outcrops, combined with altitudinal variation in habitat type (Brito et al. 2014, Campos & Brito 2018). Consequently, desert rodents have repeatedly evolved variable levels of background matching (Boratyński et al. 2017). Animals may have adopted versatile camouflage tactics and behaviours where effective concealment requires matching different types of lightness, colour and pattern (i.e. substrate granularity). For example, they may have evolved a generalist strategy, which can be viewed as "imperfect camouflage" (Hughes et al. 2019), representing a compromise to match different visual backgrounds (Nokelainen et al.

2020). Alternatively, they may become camouflage specialists, which should constrain the location and/or habitat use of a given species through increased vulnerability (Merilaita et al. 1999, 2001, Kjernsmo & Merilaita 2012, Michalis et al. 2017). Camouflage specialists are predicted to be less vulnerable than camouflage generalists within the habitat to which they have specialized, but the specialist species are constrained in their use of the habitat types, as they suffer greater vulnerability to predators outside their specialized habitat.

How does seasonality determine the evolution of camouflage in arid environments?

Although seasonality has a well-documented impact on animal camouflage (e.g. through seasonal polyphenism), how seasonality in desert landscapes may influence camouflage efficacy is less well understood. The other issue on drylands is that low predictability (or repeatability) of seasons, e.g. extended periods without rainfall, sometimes lasting several years, is not unusual (Foley et al. 2003, Dardel et al. 2013). While a particular habitat may superficially appear similar based just on visual appearance, the resources available may change through the seasons (i.e. wet *vs.* dry season) and this change may drive animals to move, thereby exposing them to different camouflage requirements. Thus, we may again predict that species forced to use large areas should be more generalist habitat users, whereas species that are more sedentary may have evolved to utilize particular types of habitat (e.g. mountain endemics or tight niche utilizers).

How does rodent behaviour dictate the efficacy of anti-predator strategies?

Although camouflage has traditionally been considered as a phenotypic trait to be associated with the local environment, evidence is accumulating that behaviour in a particular habitat may play a crucial role how well camouflage works (Stevens & Ruxton 2019). For example, movement has been shown to be an issue for camouflage because predators tend to focus their attention on moving targets (Hall et al. 2013). When detected, a mobile species can either try to evade predators by running to a shelter (Fig. 2a), or by manoeuvring while escaping (Fig. 2b). Camouflage in species adopting this behaviour should be poorer than in those species that evade predators by remaining stationary and relying on "freeze" behaviour (Fig. 2c). In addition, when the movement of prey ceases it is important to stop in a location that minimises vulnerability. Likewise, more bold (or dominant and exploratory) animals may be exposed more than shy (or subordinate) animals but, on the other hand, more dominant individuals may be better competitors and may force subordinates to move. It is possible that behavioural strategies mirror complex life-history interactions that may be difficult to tease apart without integration of phylogenetic, experimental and statistical approaches (Moiron et al. 2020).

To sum up, we predict that more mobile animals, and those with large home ranges spanning heterogenous environments, should adopt a more generalist and/or compromise camouflage strategy. Less mobile, more sedentary or less competitive species should rely on more specialized camouflage (Merilaita et al. 2017, Fennell et al. 2019, Hughes et al. 2019). Animals having larger home ranges would more likely have a need to cross several different types of micro-habitats in comparison to less mobile individuals/species with smaller ranges. It would be valuable to test how different proxies of mobility

Fig. 2. Visual representation of animals and their respective micro-habitats. Panels (a-g) illustrate different visual appearances of animals and how well fur colouration matches their respective background colour and pattern. Note the microhabitat granularity. For objective photography purposes reflectance standards were included. a) *Gerbillus nigeriae*, 21 km NW from Kenkossa, Mauritania, 20.11.2012; b) *G. amoenus*, 85 km E from Msied, Morocco, 07.02.2016; c) *G. amoenus*, 31 km NW from Ouadane, Mauritania, 31.10.2011; d) *Pachyuromys duprasi*, 17 km SW from Aouint Lahna, Morocco, 03.02.2016; e) *Jaculus jaculus*, 4 km S from El Hagounia, Morocco, 11.02.2016; f) *J. hirtipes*, 35 km E from Abteh, Morocco, 09.02.2016; g) *G. gerbillus*, 120 km W from Choum, Mauritania, 24.10.2011 (photo Z. Boratyński).

Fig. 3. Representation of three behavioural strategies that may influence how camouflage counters predator perception in combination with movement: a) run and hide (*Gerbillus* sp., 43.5 km W from Kenkossa, Mauritania, 01.09.2015), b) run fast and manoeuvre sharply during evasion (*Jaculus hirtipes*, 185 km SE from Dakhla, Morocco, 06.01.2018), or c) sit and wait (*Pachyuromys duprasi*, 49 km S from Assa, Morocco, 07.02.2016). Each strategy may have consequences for how accurately the rodent matches its background and, as a consequence, the effectiveness of its camouflage in the respective environments (photo Z. Boratyński).

(such as ability to saltation, length of the hind foot and/or tail), as used in previous studies (Alhajeri et al. 2015, Alhajeri 2016, Alhajeri & Steppan 2018), correlate with the degree of crypsis and/or with different personality types (Moiron et al. 2020).

How do behaviour and cognitive processing of predators facilitate camouflage efficacy?

Animals use their vision to acquire information or to reduce uncertainty in their environment (Maynard Smith & Harper 2004, Stevens 2013). Thus, reducing the capability of a predator to acquire this information reliably is crucial for prey using visual camouflage (Mokkonen & Lindstedt 2015, Merilaita et al. 2017). The visual appearance of the prey in a given environment is important, but also how predators acquire and process visual information (i.e. retinal sensitivities to different wavelengths, visual acuity, neural transmission and processing of information in the visual cortex of the brain) will influence their decision making in prey search (Endler & Mappes 2017, Cuthill et al. 2019). The process of "seeing" colour can be simplified into the following stages: viewing conditions, colour representation, perception and cognitive processing of the receiver (White & Kemp 2015). Changes in any of these can alter the efficacy of camouflage, favour different camouflage tactics and shape the strength of selection (Endler 1992, Price 2017).

In deserts, the most notable changes in viewing conditions are mostly those over the course of

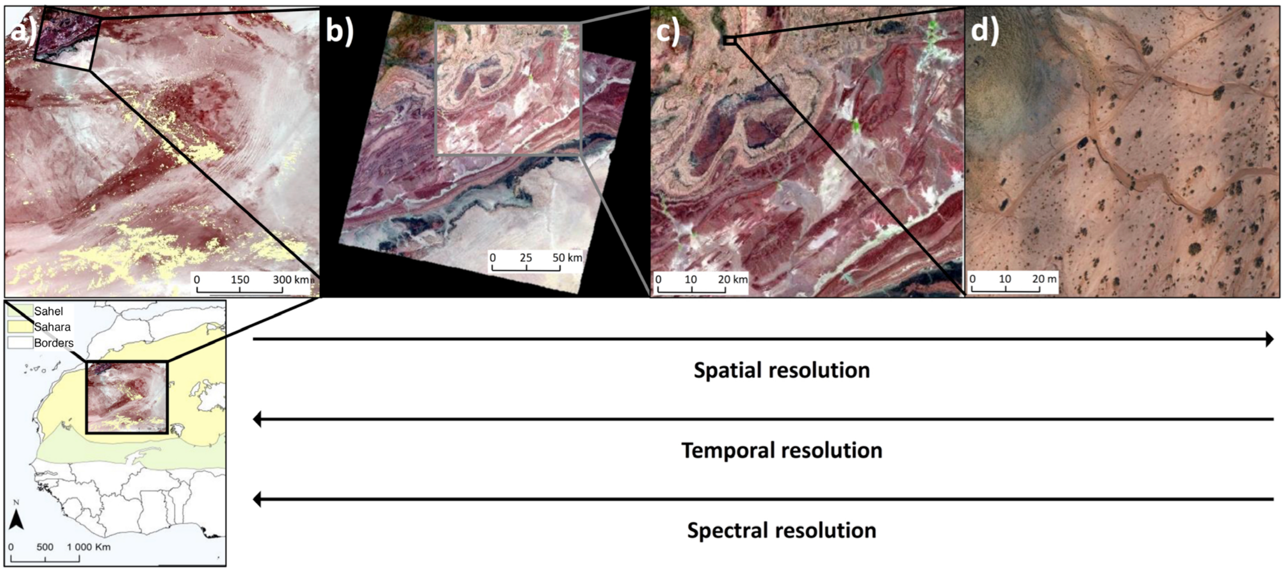

Fig. 4. Schematic representation of the differences among remote sensing devices used in habitat colouration studies, in terms of spatial, temporal and spectral resolutions. Differences are exemplified with satellite images obtained from distinct sources a) MODIS-Terra, image acquired in 2019/05/27; b) Landsat 8, image acquired in 2019/05/22; c) Sentinel-2, image acquired in 2019/05/27) and with an aerial photograph d) obtained by an UAV (image acquired in 2020/01/06). Satellite images were obtained through EarthExplorer interface from the United States Geological Survey (https://earthexplorer.usgs.gov/).

the day; diurnal predators have much more light available for visual processing in comparison to nocturnal animals, which have to cope with (scotopic) low light intensities. Broadly speaking, matching the colour spectrum is assumed more important for diurnal and crepuscular animals, whereas luminance matching may be more important for nocturnal animals (Kelber 2006, Kelber & Lind 2010). It should be noted that although we can make detailed measurements of colour and reflectance to build up receiver-independent estimates of animal-to-background matching, the visual perception of predators may differ; visual acuity varies greatly among species; as does their ability to process light at different wavelengths (Kelber et al. 2003, Caves et al. 2018). Humans are trichromats (i.e. we see three different chromatic ranges perceived as red, green and blue) and have good visual acuity. Many mammals are dichromats, lacking long wavelength receptors and sharp visual acuity, which can improve the efficacy of certain camouflage types against mammalian predators. Birds are typically tetrachromats, can process the ultraviolet part of the spectrum, and the visual acuity of raptors outperforms ours, driving strong selection for crypsis on day-active prey. However, most desert rodents are crepuscular or nocturnal. For these species, owls pose a particular risk (San-jose et al. 2019), as they can process luminance information in low light conditions (Wu et al. 2016). Finally, visual input alone cannot explain why certain camouflage types predominate. As visual information is processed through the psycho-physiological landscape of the receiver (Stevens 2007, Skelhorn & Rowe 2016), it is plausible that higher-level cognitive processing and predator psychology influences the effectiveness of camouflage.

Prospects

Current methodologies allow detailed insight into wild rodents: 1) phenotypic variation in fur colouration, 2) visual structure of their habitats, 3) individual variation in shyness/boldness and exploratory behaviours, 4) mobility and home range sizes, and 5) targeting inheritance and expression mechanisms of the above traits, thus allowing a reconstruction of their evolutionary history and testing their adaptive significance. These can be applied to natural populations on individuals in their native habitats.

Animal colouration can be accurately estimated in a controlled way, even under field conditions (Fig. 3). To measure the level of camouflage adaptation, digital images of an animal's dorsum, along with the background where they were captured and a colour standard (e.g. Spectralon, X-Rite), can be taken with a full spectrum camera (Stevens et al. 2007, Johnsen 2016). Saved images in RAW format, corrected for white balance, can be analysed with open-source software (e.g. Image Calibration and Analysis Toolbox, Image-J; www.jolyon.co.uk; www.empiricalimaging.com; Troscianko & Stevens 2015, Van Den Berg et al. 2019) based on quantified camera responses to a set of grey standards (Stevens et al. 2007, Troscianko et al. 2017, Price et al. 2019). Multispectral image analysis is a powerful tool to study animal colouration. It allows the analysis of entire visual scenes, such as fur colouration compared to background (Fig. 3), and utilizes several colour metrics to enable quantification of colours and patterns simultaneously (Gómez et al. 2018, Hawkes et al. 2019).

Habitat appearance in variable spatial and temporal scales can be estimated with available remote sensing methodologies based on aerial and satellite imagery (Fig. 4). To measure the spatial scale of camouflage adaptation, e.g. habitat specialist versus habitat generalist strategies, aerial images of a mosaic of habitats along with a colour standard (e.g. large X-Rite), can be taken using commercially available, and affordable, drones (e.g. Mavic Pro, equipped with DJI camera; Fig. 4). The series of digital images allow analysis of the entire visual scene, composed of a mosaic of habitats, in a similar fashion to analyses of standard digital images taken with hand held cameras. Camouflage over a large geographical scale can be studied using publicly available satellite imagery (e.g. NASA Landsat satellite series or MODIS Terra, both available at EarthExplorer interface from the United States Geological Survey: https://earthexplorer.usgs.gov/; Fig. 4). Low cloud coverage images should be selected and appropriate atmospheric corrections should be applied to standardize satellite imagery (Chander et al. 2009). The time periods of satellite images, and their spatial resolution (e.g. 30 m for Landsat) can be selected to target specific research questions, e.g. related to seasonal variation or long-term habitat changes observed over years/decades, or specific spatial relevance for given species (Boratyński et al. 2014, 2017).

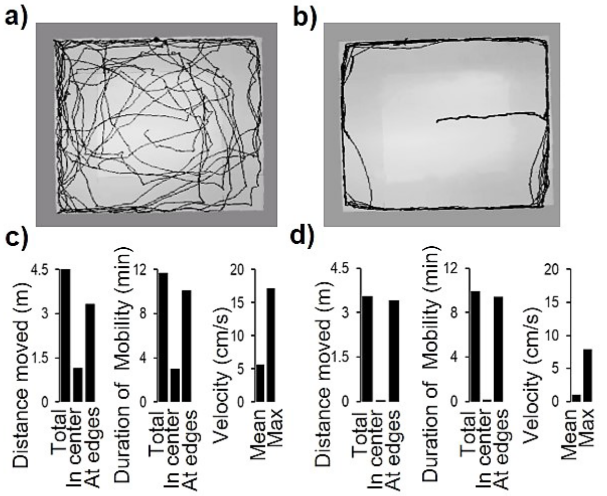

Fig. 5. Conceptual representation of an open arena test to study animal behaviour, and its visualization: a) an automatically recorded track for a bold animal, with mobility in both the centre and edges of the arena; and b) a track for a shy animal, with mobility mainly at the edges of the arena; c) results for selected variables after tracking the bold animal (from panel a); and d) variables after tracking the shy animal (from panel b).

Behavioural patterns and animal personality types can be studied in wild individuals in combination with *in situ* camouflage experiments (Fig. 5). To estimate how personality and exploratory behaviours can interfere with camouflage accuracy measured over variable spatial scales (i.e. if personality correlates with background choice, or if species have evolved habitat specialization), a standard rodent open field test can be applied (Cummins & Walsh 1976, Gould et al. 2009, Montiglio et al. 2010, Šíchová et al. 2014, Mazzamuto et al. 2019). Trials can even be performed inside a modified field vehicle, if necessary, and affordable cameras can be used to record videos of animal behaviour (e.g. GoPro). Available software facilitates quantification of various aspects of animal behaviour, such as mobility and shyness-boldness, using commercial automatic tracking systems (e.g. Ethovision XT, Noldus) or their open-source alternatives (e.g. EthoWatcher or OpenControl; Aguiar et al. 2007). Individual traits related to running speed, distances and trajectories of movements can be related to spatial extent and accuracy of camouflage. Accurate GPS tracking, with microtransmitters, will allow not only the analysis of point data (e.g. capturing locations) to test the match between phenotype and habitat, but also provide a measure of habitat selection in free-ranging animals through behavioural analyses. The ICARUS system is currently being tested, and when available (and affordable) it will revolutionize behavioural, spatial and mobility studies in wild populations, including small animals (http://www.icarusinitiative.org; Wikelski et al. 2007, Pennisi 2011, Wikelski 2013, Wikelski & Tertitski 2016).

Associated with ecological research, molecular studies can provide a much broader perspective if conducted in conditions that are as natural as possible (Mitchell-Olds et al. 2008, Pardo-Diaz et al. 2015). Transcriptomic and genomic tools developed for model laboratory rodents can potentially be applied to wild Sahara-Sahelian species. In this way, gene expression variation in fur colour and behavioural traits between habitat specialists and generalists can be investigated. Sensitive samples can be preserved in the field in specialized solutions (e.g. RNAlater) and mobile freezers. Rodent genomes (model and non-model) are readily available to aid the mapping of novel sequences of wild species. Subtle differences in gene expression patterns between related species can be now tackled with co-expression network analyses (Pardo-Diaz et al. 2015, Voigt et al. 2017, Gysi et al. 2018, Fu et al. 2019). Evolutionary-ecological functional genomics allow identification of the molecular mechanisms underlining camouflage, and enables targeting coevolution of "non-visible" traits (e.g. physiology or immunology correlates). Genomics information can aid phylogenetic reconstruction, especially in diverse and problematic groups, such as *Gerbillus* rodents, where traditional marker based phylogenetics has proven difficult (Ndiaye et al. 2016a, b). Accurately reconstructed species relatedness is imperative for comparative analyses of coevolution between species' quantitative traits (Weber & Agrawal 2012, Boratyński 2020), such as mobility, camouflage and habitat use.

Discussion

We are entering an exciting time when integrative studies can be applied to diverse animal communities and wild populations. African rodent communities inhabiting open habitats, such as the Sahara-Sahel or Namibian desert, constitute excellent model systems. The value of Sahara-Sahel rodents is that the study system presents an opportunity to test adaptations facilitating species' persistence in a mosaic of habitats over dynamically changing conditions (i.e. environmental change). Human-induced climate change has had negative effects on biodiversity worldwide (Bellard et al. 2012). Whenever the velocity of change is too fast for evolution to keep pace, individuals risk becoming poorly adapted to their environment, which might lead to population declines and extinction (Urban 2015). The velocity of climate change is highest in arid areas (Loarie et al. 2009), but behavioural flexibility may allow organisms to respond rapidly to environmental change, and thereby facilitate survival under changed conditions (Catullo et al. 2019). While arid areas, such as the Sahara-Sahel, are characterized by low rainfall that limits biodiversity (Huxman et al. 2004), these environments can be surprisingly diverse in habitats and species, and support high levels of endemism (Brito et al. 2016, Guerreiro et al. 2016).

The remoteness of many arid areas has hitherto constrained research. Limited research on remote deserts means that there is a risk that arid-adapted biodiversity might disappear before being described (Brito et al. 2014, Vale & Brito 2015). However, field expeditions are now being undertaken to collect data on individual and species characteristics, including behaviour, to objectively record the visual appearance (e.g. lightness, colour, pattern granularity) of animals and their habitat. This approach is supported by technological advances, such as access to free and high-resolution satellite imagery, the availability of small, rugged and high-quality cameras for recording animal behaviour under field conditions, and video tracking systems for automated monitoring of behaviour. As quantifying camouflage has become straightforward and accessible, it is now a matter of applying the available tools to wildlife research in order to understand how biologically relevant receivers may perceive animals and shape phenotypic evolution. Advances in any of these areas of research will guide our understanding of the ecology of adaptation.

Camouflage is a composite phenotypic trait that is determined by the genetic composition of its carrier and mirroring a complex variation in morphology (e.g. allometry, structures and/or colours), behaviour (e.g. mobility level, boldness/shyness) and physiology (e.g. capability for mobility or thermoregulation), all of which can be targeted by selection in a given environment. To understand what maintains heritable variation in the wild we need integrated research on phenotypic evolution (Caro & Mallarino 2002), including camouflage, which is ubiquitous in desert rodent communities. Studies of widely distributed animal communities, such as those spanning the Sahara-Sahel, will permit broad conclusions to be drawn on the processes driving adaptation and providing a better understanding about how natural diversity evolves.

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