



## Signalling with physiological colours: high contrast for courtship but speed for competition



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Dynamic physiological colour change allows animals to alter colours and patterns for communication, camouflage and thermoregulation. Using reflectance spectrometry and digital photography, we found that males of the Indian rock agama, *Psammophilus dorsalis*, can rapidly express intense colours that are different from the neutral state and specific to the social context. The distinct bands on males shifted between yellow and red (dorsal) and between orange and black (lateral) within seconds, and the resulting colour pattern was diametrically different depending on whether males were in courtship or aggressive interactions. Although males showed higher chromatic contrast when courting females, the colour change was faster during competitive encounters with other males. The nature of this social colour communication also differed across populations in anthropogenically disturbed landscapes. Compared to males from rural areas, suburban males were slower to change colour and showed duller and paler colours during staged social encounters. Consistent with other disturbance-induced shifts in phenotypic traits seen in numerous taxa, we provide the first evidence that social signalling through dynamic colour change in terrestrial vertebrates is also affected by urbanization.

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Dynamic physiological colours, which are actively modulated by signallers within seconds to minutes, have been documented in a wide range of taxa from crustaceans and cephalopods to fishes, amphibians and reptiles (Camargo, Visconti, & Castrucci, 1999; Hanlon, 2007; Hemmi, Marshall, Pix, Vorobyev, & Zeil, 2006; Stuart-Fox & Moussalli, 2008; Zylinski, How, Osorio, Hanlon, & Marshall, 2011). Capacity of physiological colour change, however, varies dramatically between species. Aquatic taxa, such as cephalopods and fishes, show remarkable abilities to change body colour and pattern within seconds to minutes (Messenger, 2001; Morris, Mussel, & Ryan, 1995). For most terrestrial species, these physiological colour changes are limited to achromatic changes in contrast with lightening or darkening of the skin (e.g. Camargo et al., 1999; Cooper & Greenberg, 1992; Kindermann, Narayan, Wild, Wild, & Hero, 2013). For a few well-characterized terrestrial vertebrates, physiological colours can shift hues across a wider range of visible wavelengths. In the Chamaeleonidae family, many species are capable of large changes in both achromatic contrast and chromatic contrasts in the red, brown, yellow and green spectral wavelengths

(Ligon & McGraw, 2013; Stuart-Fox & Moussalli, 2008; Teyssier, Saenko, Van Der Marel, & Milinkovitch, 2015). Regardless of the specific colour patterns, physiological colour changes for both aquatic and terrestrial taxa depend on context, shifting for camouflage, thermoregulation and social communication (Messenger, 2001; Stuart-Fox & Moussalli, 2009; Zylinski et al., 2011).

Understanding variation in colour signals has been central to the study of animal communication for decades (Andersson & Andersson, 1998; Dale, 2006; Hamilton & Zuk, 1982). Given that signals have evolved to attract attention and convey information (Hebets & Papaj, 2005; Partan & Marler, 2005), species that use physiological colours for communication are able to use certain colour patterns to convey specific information in different social contexts. For example, in three-spined sticklebacks, *Gasterosteus aculeatus*, males shift the intensity of their red nuptial coloration during both male–male and male–female interactions to convey dominance status and male parental ability (Candolin, 2000). Dwarf chameleons, *Bradypodion* sp., are observed to alter their chromatic contrast to signal dominance or submissiveness during social interactions, regardless of their conspicuousness against the background (Keren-Rotem, Levy, Wolf, Bouskila, & Geffen, 2016; Stuart-Fox & Moussalli, 2008). Dynamic signals can also be used to convey different information to different receivers. Male

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mourning cuttlefish, *Sepia plangon*, can lateralize physiological colour changes, such that one side expresses male courtship patterns, while the other expresses female-mimicked patterns. This dual signalling state allows males to court females, while simultaneously distracting a rival male (Brown, Garwood, & Williamson, 2012). Given that a single body region can express more than one chromatic and achromatic state at any given point in time, signalers that use physiological colours have the potential to convey multiple messages rapidly and dynamically during courtship and aggressive encounters.

Most studies on physiological colours have illustrated the importance of environmental conditions, focusing on induced patterns to enhance crypticity or conspicuousness against different substrates or backgrounds (Clarke & Schluter, 2011; Cole & Endler, 2015; Endler, 1992; Stuart-Fox & Moussalli, 2009; Wong & Candolin, 2015). Individuals should also vary the intensity and brightness of colour patterns for social communication depending on local environmental conditions (e.g. Kelley, Phillips, Cummins, & Shand, 2012; Leal & Fleishman, 2003). For example, in three-spined sticklebacks, algal turbidity influences the expression of the red nuptial coloration, depending on whether a male is poor or good quality (Wong, Candolin, & Lindström, 2007). Similarly, differences in the intensity of light in xeric and mesic habitats seem to influence the brightness of the statically coloured dewlaps on *Anolis cristatellus* (Leal & Fleishman, 2003). Surprisingly very few terrestrial vertebrates have been studied to determine intraspecific population variation in physiological colours across different environmental conditions (but see Boback & Siefferman, 2010). Because they are dynamic, and thus a form of phenotypic plasticity, use of physiological colours can respond to external drivers over very short timescales, and provide a good opportunity to examine how changes in both the physical and social environment influence intraspecific variation in magnitude and range of colour patterns.

Here, we examined the pattern, range and speed of physiological colour change in the Indian rock agama, *Psammophilus dorsalis*, to determine how visual signalling differs between social context and between populations. We explicitly quantified colour changes during social interactions with females as well as males to determine whether this species uses different visual signals for courtship and aggression. *Psammophilus dorsalis* is widely distributed in semiarid open habitats of southern peninsular India, which include human-modified environments. To quantify the range (i.e. capacity) of physiological colour changes during social interactions for this species, we included males from both suburban and rural areas, representing two contrasting environmental conditions. Urbanization alters a large suite of biotic and abiotic factors, from lighting conditions and habitat composition to levels of social competition and predation risk (Kempnaers, Borgström, Loës, Schlicht, & Valcu, 2010; Longcore & Rich, 2004). Mounting evidence suggests that these changes can affect animal communication by affecting the production of signals, transmission efficiency and receiver reception (Rosenthal & Stuart-Fox, 2012). In this paper, we focus on the physiological colour signals themselves, to determine strategies and variation in their use. In doing so, we examine the relative importance of social context and environment in the expression of physiological colour patterns.

## METHODS

### *Study Species and Areas*

*Psammophilus dorsalis* occurs in semiarid habitats, where they are found on rocky boulders and sheet rocks interspersed with scrub vegetation (Radder & Saidapur, 2005), as well as in suburban

habitats (Balakrishna, Batabyal, & Thaker, 2016). In the latter, *P. dorsalis* are generally found in localized clusters around residential construction sites, unbuilt plots and urban gardens. *Psammophilus dorsalis* is sexually dimorphic and males are larger than females (snout–vent length: males = 95–140 mm and females = 75–96 mm). Males also develop conspicuous physiological colours during the breeding season, typically from April to August (Radder & Saidapur, 2005), which become dull at the end of the breeding season.

Adult lizards were collected from study sites of approximately 1 km<sup>2</sup> each, located in and around the city of Bangalore, India. Suburban study sites ( $N = 3$  sites) were located within city limits and rural study sites were located near Antharagange forest range in Kolar district ( $N = 2$  sites). Replicate sites within each habitat were 5–10 km apart, and the suburban and rural habitats were at least 60 km apart. We performed the following experiments during the peak breeding season (April–August) in 2013 and 2014. This species is known to court and fight throughout the breeding season (Deodhar, 2017; Radder, Saidapur, Shine, & Shanbhag, 2006) and has one or two clutches a year (Srinivas, Hegde, Sarkar, & Shivanandappa, 1995), and thus were expected to be socially responsive during the experimental trials. Adult male lizards [ $N = 25$  suburban (7–10 per site) and 25 rural (10–15 per site)] were captured by noosing and brought into the laboratory. All males and females used in the study were sexually mature adults. We ensured that all females were nongravid to minimize variation in receptivity: all females were behaviourally reactive during social trials (e.g. responded to males with head bobs and tail raise).

Wild-caught lizards were housed individually in glass terraria in a dedicated animal housing room that permitted natural temperature and light conditions. Terraria (60 × 30 cm and 25 cm high) were lined with disposable paper towels as the substratum, provided with rocks for refuge, and were covered on all sides to minimize disturbance. Individual incandescent basking lights (60 W), above each terrarium, were turned on from 0800 to 1200 hours, and from 1500 to 1600 hours. Lizards received live ants and field crickets daily for food and water ad libitum and were maintained in the laboratory for 7–9 days. Before the start of the experimental trials, mass (g) and snout-to-vent length (mm) were measured for all individuals using a weighing balance and digital callipers, respectively. All lizards were returned to the site of capture after the experimental trials.

To quantify the effect of social stimulus on colour patterns, we exposed each focal male ( $N = 20$  total suburban and 20 rural, excluding control animals) to a stimulus male and female separately. Stimulus individuals were caught from rural and suburban sites that were different from where focal animals were caught, and therefore were unfamiliar to focal males. Each stimulus individual was randomly paired with two or three focal individuals from the same population. Social interactions were staged under full-spectrum lights (Viva-Lite:B22) in test tanks (95 × 45 cm and 30 cm high), and began with a 30 min acclimatization period, followed by a 30 min interaction period with one of the stimuli. Males in the control treatment ( $N = 5$  suburban and 5 rural) were also kept in the same test tank for 30 min but were not exposed to any social stimuli. Lizards were randomly assigned to control or social test groups, where the order of stimulus (exposure to female or male) was also randomized. All trials were conducted from 0800 to 1200 hours or from 1500 to 1700 hours, which are the peak activity periods for this species in our study areas. Test tanks were kept behind a blind which enabled us to digitally record the social interactions with minimal disturbance (using a Canon EOS550D with 18–55 mm lens) for subsequent quantification of the speed of colour changes (see details below).

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