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Male preference for sexual signalling over crypsis is associated with alternative mating tactics

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Changing body colour in animals generally reflects a conflict between two selection pressures, camouflage and social signalling. Chameleons are among the few organisms that resolve this conflict by rapid and temporary change in body colour for both background matching and social display. Male common chameleons, *Chamaeleo chamaeleon*, employ two alternative mating tactics, dominants and subordinates, both of which are associated with long-term body colour patterns and instantaneous colour displays during social encounters. Hence, males present a good model in which to study the influence of mating tactic on the decision of whether to remain cryptic or to signal. We exposed individuals to two conflicting external stimuli: background manipulations, which challenge camouflage, and the presence of a female, which stimulates sexual signalling. No individuals of either mating tactic responded to background manipulation except when the shift was from green to brown background or vice versa. Ambient temperatures affected colour matching but not sexual signalling, while body temperature affected neither. Males ignored the background colour and prioritized being distinctive when encountering females. As such, males were more likely to engage in sexual signalling than crypsis. Subordinate sneakers signalled females more frequently than the dominant, female-guarding males, suggesting that sneakers rapidly signal females their intentions when the dominant is out of range. Conversely, dominant males may gain little by frequent signalling to the females they guard, while possibly gaining more by diverting this energy towards mate guarding. Our results suggest that specific male mating tactics strongly influence the decision to use crypsis or sexual signalling.

Evolutionary change in body colour is controlled by two conflicting processes. Natural selection drives changes in body colours towards camouflage and crypsis, while sexual selection exerts pressures towards bright colours that create contrasts between the animal and the background against which it is typically viewed. (Darwin, 1871; Endler, 1992). Stuart-Fox and Moussalli (2008) referred to these two selection pressures as the crypsis and the social signalling hypotheses. They defined the crypsis hypothesis as the positive association between the variance in background coloration and the change in body colour that animals need to make in order to remain cryptic; and the social signalling hypothesis as the positive association between the change in body colour and signal conspicuousness expressed by the visual contrast between the animal's display colours and both its adjacent body regions and the vegetation background.

Several lizard species have developed a different and remarkable behaviour that tackles this conflict by rapidly changing their body colour for brief intervals in response to environmental stimuli, before returning to the primary body colour state (Cooper & Greenberg, 1992; Thurman, 1988). Such an evolutionarily adaptive strategy involves two principles. The first is background matching, which allows for rapid matching with the predominant background while the animal is moving between alternative microhabitats (Cooper & Greenberg, 1992; Fernandez & Bagnara, 1991; Wente & Phillips, 2003). The second is a brief flashing of body colour display, which is conspicuous against the background and designed primarily for signalling to conspecifics (Cuadrado, 1998; Greenberg, 2002; Martin, 1992; Stuart-Fox & Moussalli, 2008) while minimizing exposure to predators (Stuart-Fox & Moussalli, 2008).

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Among lizards, chameleons have been characterized in numerous studies by their ability to rapidly change body colour, associated with both background matching (Cooper & Greenberg, 1992; Cuadrado, 1998; Durve & Sharma, 1975; Stuart-Fox & Moussalli, 2009) and social signalling (Kelso & Verrell, 2002; Ligon & McGraw, 2013; Martin, 1992; Stuart-Fox & Moussalli, 2008). None the less, most studies on rapid and temporary body colour change for camouflage and communication in various taxa, including chameleons, have focused either on crypsis (e.g. colour matching) or on social (e.g. signalling to mates) selection processes, while the trade-off between these selective forces during conflicting stimuli (i.e. the need for crypsis and social signalling at the same time) is not well understood.

Our model animal in this study was the common chameleon, *Chamaeleo chamaeleon*, an arboreal animal that is highly adapted to life on plants. It inhabits park forests and plantations in the Mediterranean region of Israel (Bouskila & Amitai, 2001) and southern Spain (Hódar, Pleguezuelos, & Poveda, 2000). The adults occupy a variety of tall woody trees and bushes, while the young hatchlings perch on small bushes and low grasses. At the age of several months, the young leave the near ground level microhabitat and move into the same microhabitat occupied by the adults (Keren-Rotem, Bouskila, & Geffen, 2005). However, perch height is very variable among both subadults and adults, depending on individual body size and social status (Keren-Rotem, Levy, Wolf, Bouskila, & Geffen, 2016). Adults vary in body colours and patterns, which change according to context (e.g. sex, social status, social interactions, microhabitat and season; Keren-Rotem et al., 2016).

In our study area, chameleons are active mostly during the warm months (May–November). No significant differences in snout–vent length (SVL) and tail length were found between the sexes (Keren-Rotem et al., 2005). Mating occurs in July–September, and during October–November females deposit 14–47 eggs, which remain underground for 10 months of incubation and hatch in late August and September (Keren, 2001).

The common chameleon is known both to colour match (Cuadrado, Martin, & López, 2001) and to signal during social encounters (Cuadrado, 1998; Keren-Rotem et al., 2016). In a previous study, we documented an association between long-term body colour in males and their mating tactic (Keren-Rotem et al., 2016). In this species, males used two alternative mating tactics: the small, subordinate, brown-coloured males adopted sneaking tactics, in which they attempted to copulate with guarded females during the absence of the dominant female-guarding male, while the large, dominant, green-coloured males engage in mate guarding of reproductive females (Keren-Rotem et al., 2016). None the less, both male classes briefly flashed different colour patterns in correspondence with their mating tactic when encountering a female during the mating season. Hence, the common chameleon males present a good model to investigate the trade-off between the need for body colour change for camouflage and that for social communication.

Given the likely trade-off between crypsis and social communication in *C. chameleon*, we postulated that the specific seasonal body colour of males, which is associated with a specific mating tactic, might influence the decision as to whether to remain concealed or to signal during a social encounter. To test this hypothesis, we exposed males to two conflicting external stimuli, background change and the presence of a female. We predicted that both stimuli would trigger individuals to change their body colour and pattern, while the different mating tactics of dominants and subordinates would reflect the motive for change. Specifically, we predicted that dominant males would prioritize using distinctive colours for social interaction over colour matching in order to reflect their honest signalling and higher quality. In contrast, subordinate males would show the opposite preference, and use distinctive colours to signal to conspecifics less frequently than dominant males.

METHODS

Study Site and Data Collection

We conducted the study along the Maharal creek on the Mediterranean coast, at the foothills of Mt Carmel in Israel (32°38′N, 34°58′E). The study site is a relatively dry habitat of Mediterranean woodland. In summer, mean maximum and minimum daily temperatures are 30 and 21 °C, respectively, and relative humidity averages about 70%. Mean annual rainfall is 550 mm, and all precipitation falls during the winter months (November–March; Keren-Rotem et al., 2005). Fieldwork was carried out between May and December during 2008–2013. We conducted 15–20 surveys annually in order to collect animals for our behavioural experiments.

We collected chameleons from vegetation using a spotlight at night, when they are sleeping and their body is light in colour and reflective. To minimize stress, each captured chameleon was kept for less than 24 h in individual 35 × 20 cm terraria. All the terraria were placed in a shady area and inside a screen cage to prevent predation. Keeping the terraria outdoors exposed the animals to the same air temperature and humidity conditions as in their natural environment. We did not provide food or water during the short period in which the chameleons were kept in captivity. All animals were measured, weighed, sexed and released back at the capture site the following day. We individually marked all chameleons just before their release by clipping off the tip of one to three nails using a fingernail cutter. Clipping off the nail tips of an individual took a few seconds, and animals held by hand showed little resistance to it. Clipped fingernails regrow a blunt tip, which does not affect the animals' ability to climb branches (Cuadrado, 2000).

Recording and Classification of Colour Patterns

We documented body colours and patterns during the morning hours. We placed each individual separately on a 2 m long measuring stick, located horizontally 1 m above the ground. The stick had smooth polycarbonate rolls affixed to each end, which prevented the animals from descending it. Each individual was placed in turn on the middle of the stick and its colour and pattern on both sides of the body were documented as digital images. The animals often walked naturally along the stick, a position that allowed us to record their full natural colour patterns (see Fig. 1).

Images were also used for measuring the SVL of animals while on the stick in a fully extended position. The accuracy of this measuring method had been verified in a preliminary study using three independent images of each of 10 individuals (mean ± SD: 0.79 ± 0.079 mm). SVL measurements taken using callipers or a measuring tape were less accurate since the animals are highly flexible and tend to curl up when handled.

We used a Canon D3 digital camera with a macro lens (100–400 SMU L). Photos were saved as RAW formatted files (7.5 Mb, 3504 × 2336 pixels). The camera was placed on a tripod 2 m from the focal animals. Photos were taken under natural sunlight, without a flash. Each photo included a colour standard in the form of a white ruler running along the horizontal stick. We standardized image colours by a 'white standard' (approach resembles that of Stevens, Párraga, Cuthill, Partridge, & Troscianko, 2007) relevant only to our study, using the spectral reflectance of the white ruler and the Photoshop software (version 7, Adobe Systems, Inc.).