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

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ARTICLE INFO

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.

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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. chamaeleon*, 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 $\pm$ 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.).

Background matching colour patterns

Pattern L   Pattern O

Courtship colour patterns

Pattern D   Pattern E   Pattern F

Figure 1. Background colour matching patterns (pattern L and O) and courtship colour patterns (pattern D, E and F) of male chameleons.

We visually classified images comprising similar colour, stripes and patches as belonging to the same colour pattern category. Final colour pattern categories were defined by T.K.R. (Fig. 1). Overall, we defined five distinct patterns. During the nonbreeding period chameleons were mostly green (pattern L). However, we observed a seasonal shift in body colour of adult individuals during the breeding season. From June onwards, some of the males and females were brown (pattern O), a trend that increased towards the peak of the breeding season (Keren-Rotem et al., 2016). In the breeding season, during courtship, each male altered its body colour and displayed one of three distinctive temporary colour patterns, which were associated with that individual's seasonal body colour (i.e. green or brown) and with body length. Small brown males used courtship patterns D, medium-size brown males used courtship pattern E, and large green males used courtship pattern F (Keren-Rotem et al., 2016). Pattern categories were then associated with sex and social context. To corroborate our manual classification of images into colour patterns, we employed computer vision techniques, combined with statistical tests, in order to validate the distinguishability of the defined patterns. First, we represented the input image as a vector of thousands of measurements, sometimes referred to as a visual signature (Serre, Wolf, Bileschi, Riesenhuber, & Poggio, 2007; Zhang, Barhomi, & Serre, 2012). Although individual measurement contains very little information, collectively the visual signature captures key aspects of the image's visual appearance. Documentation of the method and codes are posted on github.com/nogaor/Chameleon_classification.

We know that chameleons have the potential for tetrachromatic colour vision, along with other diurnal lizards and birds (Bowmaker, Loew, & Ott, 2005). The structure of our computerized system is based on insights derived from biological vision systems, and includes elements such as hierarchical processing, nonlinear spatial pooling and opponent colour channel processing (Serre et al., 2007; Zhang et al., 2012). The system distinguishes images based on both colour and spatial pattern. We tested distinguishability of patterns in two parallel ways: (1) using colour images for testing distinctiveness of colour in images; and (2) removing colour by converting the RGB images to greyscale images to test distinctiveness of patterns in images. When colour is removed (i.e. when we convert the RGB images to greyscale images) the visual signature of Zhang et al. (2012) degrades to another successful signature,

which has been shown to be effective in various fields of image recognition (Serre et al., 2007). Thus, this new signature is suitable for quantifying the additional information deduced from colour.

The implementation relies heavily on the single opponent descriptor of Zhang et al. (2012), using the authors' code and the default parameters. This encoding is an extension of the C2 grey image descriptor of Serre et al. (2007). The C2 descriptor is defined by computing the maximal similarities to a set of 1000 templates pooled across all image locations. In other words, what is recorded, per image, is the maximal similarity between each of 1000 templates and the best matching image location. The templates are simply selected, as a preliminary step, by sampling 1000 random image locations, taken from all images. Each image and each template is represented, for the purpose of the comparison between an image location and a template, by the C1 representation, which contains the output of Gabor filters on 16 different scales (Serre et al., 2007). The modified C1 layer, used in the single-opponent descriptor, is augmented by eight centre-surround channels (see Zhang et al., 2012). The first two such channels are the red-green channels, in which the surrounding green region is subtracted from a central red region, or vice versa. The other opponent pairs are yellow-blue, the less conventional red-cyan and the luminance-based white-black. The responses of these eight resulting channels are further adjusted by taking only the positive part, i.e. applying the absolute value operator. Specifically, by employing the baseline C1/C2 representation, we were able to observe the distinguishability of spatial patterns independently of colour information.

Next, we measured distinguishability of visual patterns based on statistical classification using direct measurement of the Euclidean distances between visual patterns. We used the Support Vector Machine (SVM; Cortes & Vapnik, 1995), which is a popular binary classification algorithm (LibSVM software package, Chih-Chung & Chih-Jen, 2011), and cross-validated our classification probabilities using the leave-one-out procedure. To distinguish between patterns A and B, we set aside one example from either class, and used the rest as the training set. In this approach the visual signatures of the training set are used in order to train the SVM classifier. This classifier is employed on the single test example and the predicted label is compared to the true label (A and B). This process is repeated multiple times, where at each turn, a different example is taken as the test example. The average success rate is

recorded. For two very different colour pattern classes we would expect this rate to be high, and low for similar classes. The P value of the success rate is computed using permutation tests. In each of 10 000 randomizations, the labels are randomly permuted among all samples, and the distribution of success rates under the null hypothesis that labels and visual appearances are not linked is estimated.

Background Colour Manipulation

To test the crypsis hypothesis, we examined the effect of background colour on chameleon body colour. Our experimental set-up was composed of five artificial 2 m high bushes, identical in shape and size, made out of textile leaves attached to a natural trunk. Each bush was placed in a separate pot (29 cm high and 35 cm in diameter). The foliage of each bush was painted with a different colour, using a nontoxic acrylic paint. These artificially coloured bushes were used as our trial set-up for background preference. We used the following five colours: dark brown, off-white, yellow, green and blue (Enamels 4012, 4002, 4017, 4036, 4025, respectively; Plaid Enterprises, Norcross, GA, U.S.A.) and confirmed these colours using a spectrophotometer. We chose to use these specific colours because they were most often observed on live chameleons, except for the blue, which was used as a non-natural colour for comparison.

Our previous study had shown that during the breeding season some individuals, depending on their social status, demonstrate a long-term shift of body colour from green to brown (Keren-Rotem et al., 2016 from 239 individuals). To exclude confounding behavioural effects associated with breeding, the set of trials related to the effect of background colour manipulation on body colour was conducted during the nonbreeding season, when all participants were green. Each trial involved a single animal and was divided into three consecutive 20 min periods. In the first period we placed an individual on a green artificial bush and recorded its body colour at 5 min intervals. Next, we relocated the animal to another artificial bush whose foliage was in a different, randomly chosen colour, and recorded its body colour the same way. Finally, we returned the animal to the initial green artificial bush, for the last stage of observations. All trials were conducted in sunlight, but we also conducted a series of trials in the shade to test the effect of light intensity. Because the frequency of colour change in sunlight and shade was similar ($\chi^2_1 = 0.108$, $P = 0.743$, $N = 28, 15$ and 13 trials in the sun and shade, respectively) we pooled the two data sets. Air temperatures were measured in the shade and at ground level at the beginning of each trial.

We conducted an additional set of trials in order to examine the effect of ambient temperature and body temperature of individuals on body colour change, in association with background colour manipulation and individual body size. This additional set of trials was conducted during the breeding season using two designs, respective to the individuals that remained green and to those that shifted to brown. First, we placed each of 36 individuals on a green bush for 20 min and then recorded body colour, ambient temperature (measured in the shade and at ground level) and rectal body temperature using a digital thermometer with a thermocouple (Fieldpiece, model ST4). Second, each of an additional 34 individuals was placed on either a green or a brown bush for a 20 min period (we alternated the order such that 17 individuals were randomly placed first on a green bush and the other 17 individuals started the trial sequence on a brown bush), then returned to its cage for a 20 min break, and finally placed on the opposite colour (i.e. green or brown) bush for another 20 min period. At the end of each period (i.e. either a green or a brown bush), we recorded body colour and ambient and rectal temperatures.

Colour Matching Analysis

To test for colour matching between artificial leaves and body colour of the chameleons we trained the SVM classifier using only the relevant colour classes of artificial leaves. The classifier was trained to distinguish between two classes: the green leaf and the brown leaf. The classifier was then applied to the chameleon images, which were tagged as brown if the chameleon was on a brown leaf, and green if the chameleon was on a green leaf. If the colour matched between the chameleon and the leaf, the SVM was expected to classify the chameleon images to the correct class (i.e. green chameleons to green leaves, and brown chameleons to brown leaves). Further, we measured the similarity between green or brown leaves and the colour of the chameleons on these leaves by calculating a Euclidean distance matrix between the descriptors of all leaves and all chameleons. Statistical differences in the mean Euclidean distances between brown and green chameleons and leaves were evaluated using randomization tests.

Male Signalling in the Presence of a Female

In a final set of trials, we individually exposed 35 males of different social statuses (i.e. dominant or subordinate) to two external stimuli simultaneously: foliage painted in an artificial dark-brown background and a social encounter with a female. Each trial was divided into three 20 min consecutive periods. In the first period, we placed each male separately on green artificial foliage and recorded its body colour and pattern at 5 min intervals. Next, we placed the male on dark-brown artificial foliage and again recorded its body colour and pattern in the same way. Finally, we kept the male on the dark-brown plant and placed a female nearby, while again recording the male in the same way. All trials were performed in the breeding season. For these trials, we used 10 different females and presented one of them randomly to each male. All females were of similar medium size. Air temperature in the shade and at ground level was taken at the beginning of each trial. We also documented body weight and body length (SVL) of each trial animal.

Statistical Analyses

Our dependent variable in the various trials was binary: whether the subject changed colour or not. To test the effect of background, female presence, temperature and body length (i.e. independent variables) we used logistic regression. Whenever an individual was used in more than one trial, we accommodated for repeated measures by using logistic regression under the framework of generalized estimation equation (GEE). GEE is a robust extension of generalized linear models (GLM) for correlated data (i.e. mixed model). In all such analyses, the chameleon identity was assigned as a random effect. Statistical tests were performed using JMP 11 (SAS Institute Inc., Cary, NC, U.S.A.) and SPSS 22 (IBM, Armonk, NY, U.S.A.).

Ethical Note

The common chameleon is a protected animal under Israeli law. Collecting chameleons from the wild, handling and keeping them in captivity and conducting our behavioural experiments required a permit from the Israel Nature and Parks Authority, which was granted annually (permit no. 31153/2008, 32296/2009, 37394/2010, 38014/2011, 38579/2012, 40009/2013). We conducted this study in strict accordance with the permit specifications, and in a way that minimized physical stress and harm to the animals.

RESULTS

Male Background Matching

In the first set of trials all participants remained in a green body colour that we defined as pattern L (Fig. 1) both when placed against a green background and when placed against the other background colours (i.e. off-white, yellow and blue). However, we observed a shift to brown body colour, which we defined as pattern O (Fig. 1), when animals were relocated from a green to a dark-brown background (Monte Carlo randomization test: $\chi^2_5 = 28.662$, $P < 0.0001$, $N = 85$) or vice versa ($\chi^2_5 = 19.819$, $P = 0.002$, $N = 85$). Thus, dark-brown foliage was the only background colour that triggered a shift in body colour. This trend was also significant when we compared the frequency of change from green to brown background against the pooled rate from all other background colours together ($\chi^2_1 = 28.4$, $P < 0.0001$, $N = 85$), or vice versa ($\chi^2_1 = 19.2$, $P < 0.0001$, $N = 85$). Because ambient temperature accounted for only 25% of the variation in body temperature ($t_{68} = 4.7$, $P < 0.001$), we examined both variables. The colour shift in males was not affected by their body temperature (logistic regression under the framework of GEE model: $\chi^2_1 = 1.2$, $P = 0.270$, $N = 105$, 70 males) or by body size (SVL; $\chi^2_1 = 0.18$, $P = 0.672$). However, the probability of being brown increased with a rise in ambient temperature (model $\beta \pm SE = 1.00 \pm 0.24$, $\chi^2_1 = 17.0$, $P < 0.0001$; Fig. 2).

High leave-one-out classification success rate, calculated by the SVM algorithm, and randomization tests (0.986 for colour images and 0.877 for greyscale images; Table 1, $N = 109$) revealed that the chameleon green (pattern L) and brown (pattern O) body colours were significantly different. Next, we conducted two statistical tests to match chameleon and bush colours. First, the SVM classifier, which was trained to distinguish between samples of green and brown leaves, correctly separated green or brown chameleons 91% of the time. Second, we tested for a difference in Euclidean distances between several groupings. The mean Euclidean distance between the same colour chameleons and the artificial leaves on the bush on which they perched (e.g. brown chameleons and
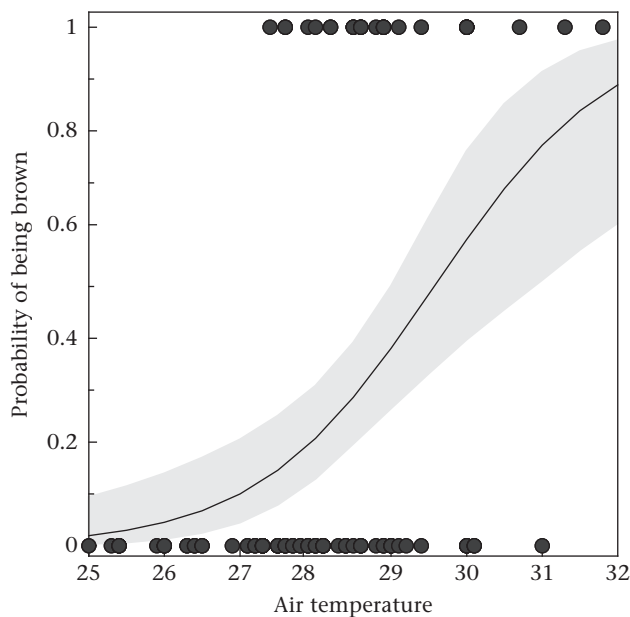
leaves) was not significantly different (Table 2). However, the mean Euclidean distance between the same colour chameleons and artificial leaves was significantly smaller than the mean distance between the colour of the chameleons and the contrasting colour of artificial leaves (i.e. green versus brown or vice versa; Table 2). Taken together, these results suggest that whether on brown or green bushes, chameleons of the same colour as the bush matched the background better than the alternative colour.

Male Signalling in the Presence of a Female

We placed each male separately against a dark-brown background for an acclimation period of 20 min, during which some of the males changed body colour from green (pattern L) to brown (pattern O). Once a female was placed nearby, most males (69%; $\chi^2_1 = 4.83$, $P = 0.028$, $N = 35$ males) shifted to a courtship colour pattern (patterns D, E and F), which was characterized by male body size and social status (Fig. 1), and attempted to copulate with the female. Leave-one-out classification success rate, calculated by the SVM algorithm, revealed that the male brown pattern (O) differed significantly from the three courtship colour patterns (Table 1). The average ($\pm SD$) classification success rate between them was 0.93 ± 0.05 for colour images and 0.87 ± 0.11 for greyscale images.

Males that attempted to mate with a nearby female were also more likely to shift to a courtship pattern (logistic regression: odds ratio = 15.3, $\chi^2_1 = 9.8$, $P = 0.002$, $N = 35$). Male body size also had a significant effect. In males that attempted to copulate, the smaller subordinate males, which used the sneaker mating tactic, tended to shift to a courtship colour pattern in the presence of a female more frequently than the large dominant males that used the mate-guarding tactic (logistic regression: model $\beta \pm SE = -0.91 \pm 0.48$, $\chi^2_1 = 5.4$, $P = 0.020$, $N = 26$; Fig. 3). Ambient temperature had no effect on the rate of shifting to a courtship colour pattern in the presence of a female in any of the male size groups (logistic regression: $\chi^2_1 = 1.4$, $P = 0.24$, $N = 35$).

Table 1
Classification of colour patterns in the common chameleon

Patterns	L	O	D	E	F
Colour images					
L	–	0.986	1.000	0.927	0.833
O	<0.0001	–	0.938	0.881	0.936
D	<0.0001	<0.0001	–	0.867	1.000
E	<0.0001	<0.0001	<0.0001	–	0.966
F	<0.0001	<0.0001	<0.0001	<0.0001	–
Greyscale images					
L	–	0.877	1.885	0.727	0.883
O	<0.0001	–	0.833	0.690	0.723
D	<0.0001	<0.0001	–	0.633	0.771
E	<0.0001	<0.0001	0.046	–	0.690
F	<0.0001	0.010	<0.0001	<0.0001	–

Leave-one-out classification success rate (above diagonal) and P value (below diagonal) between each pair of patterns using the Support Vector Machine (SVM) classifier. The analyses were performed on the same images in colour and greyscale.

Figure 2. The probability of shifting from green (pattern L) to brown (pattern O) as a function of ambient temperature before the breeding season. Confidence intervals are denoted by the grey area.

Table 2
The P value for the difference in mean Euclidean distance between the colour pattern of the chameleons and that of the artificial leaves on green or brown bushes

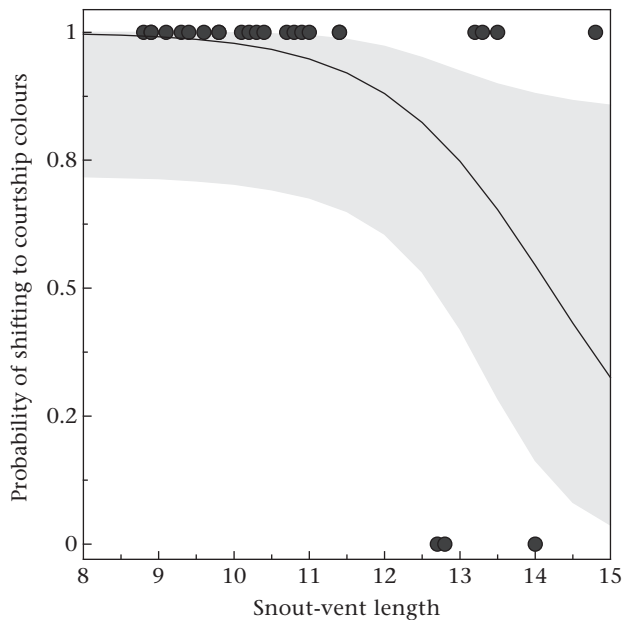| Colour patterns	Green leaves	Brown leaves
Green chameleon	0.247	0.002
Brown chameleon	0.001	0.322

Figure 3. The probability of shifting to a courtship colour pattern in the presence of a female as a function of snout—vent length. Confidence intervals are denoted by the grey area.

Finally, male body weight, controlled for body length, was significantly lower during the breeding season, with large males losing relatively more weight than small males ($F_{1,77} = 8.7$, $P = 0.004$). This difference in controlled weight between small and large males was not observed outside the breeding season ($F_{1,105} = 1.2$, $P = 0.286$).

DISCUSSION

Colour Matching

Our results only partially support the crypsis hypothesis. Against a green background, chameleons preferred to remain at the same shades of green as the background. Similarly, they changed to shades of brown when relocated to a brown bush. Hence, they demonstrated an active ability to match body colour. None the less, they only responded to one specific background change: green to brown or vice versa. The lack of response to the alternative background colours (i.e. off-white, yellow and blue) might challenge the crypsis hypothesis. Although off-white and yellow are colours displayed by some native plants, the natural habitat of the chameleons in our study site is dominated by green and brown colours. Thus, we hypothesized that these individuals may have only responded to background colours that were more familiar. Further investigation into the reflectance spectra and visual sensitivity of chameleons and their predators is required in order to support our hypothesis.

Ambient temperature is known to affect colour change in lizards (in lizards: Norris, 1967; Castrucci, Sherbrooke, & Zucker, 1997; Langkilde & Boronow, 2012; and specifically in chameleons: Durve & Sharma, 1975; Walton & Bennett, 1993; Al-Johany, 1996) through the activation of a melanocyte-stimulating hormone (Fernandez & Bagnara, 1991). During the prebreeding season, we recorded an effect of ambient temperature on change in body colour such that animals tended to become brown with the increase in ambient temperature. Our findings indicate that air temperature, but not body temperature or size, affects this change

in body colour. In a previous study, we showed that adults preferred to perch higher on trees, where they were exposed to direct sunlight and high ambient temperature (>28 °C, Keren-Rotem et al., 2005). Taken together, we suggest that chameleons moderate their ability to change body colours according to perch location and ambient temperature. In contrast to our findings for the prebreeding season, during the breeding season we did not detect any significant effect of ambient temperature on colour change for sexual signalling. Thus, we suggest that while ambient temperature plays an important role in thermoregulation, it is not a thermoregulatory limiting factor for change to courtship colour patterns under natural conditions during the warm breeding season.

Sexual Signalling

Our current experimental work shows that both dominant and subordinate males change body colour during an encounter with females, while ignoring the background colour and Prioritizing on becoming distinctive to females, thus supporting the social signal hypothesis. One possible explanation for prioritizing sexual signalling over background colour matching may be related to male alternative mating tactics (Gross, 1996; Taborsky, Oliveira, & Brockmann, 2008). Small, subordinate male chameleons often attempt to sneakily copulate with females that are guarded by the large dominant males (Cuadrado, 2001). Such sneak attempts may result in agonistic conflicts between the larger dominant males, which are usually the winners, and the smaller subordinate males, which are systematically excluded from courting and mating with females (Cuadrado, 2001). Thus, a sneaker male that has an opportunity to court a female that is not being guarded by a dominant male should signal quickly while ignoring background matching, and act before the guarding male or a predator approaches. This may also be why the smaller subordinate males changed body colours to courtship colours more frequently than the larger dominant males. The higher differential rate of colour change in subordinate males refutes our prediction that subordinates (i.e. small and medium-size males) would prefer to remain cryptic in the predominant background and avoid the conspicuousness of sexual signalling (Fig. 3).

Signalling to females has been suggested to be costly to the signaller, because it makes it more conspicuous to predators (Zahavi, 1975). Under these circumstances, signal rate might serve as an honest indicator of male quality (Martin & Forsman, 1999; Langkilde & Boronow, 2012). However, the larger males employ a different mating tactic to that of the smaller ones: they guard the females (Cuadrado, 2001) and remain in the immediate vicinity of them (<50 cm away; Keren-Rotem et al., 2016) continuously throughout the breeding season (Cuadrado, 2001). During the breeding season the dominant males in our study population lost significantly more body weight than the subordinate males, possibly due to the investment in female guarding. The mating tactic of large males may thus imply an energetic bottleneck during the breeding period, and, if signalling is costly, a small adaptive advantage in frequent sexual signalling to the guarded female.

Overall, our results suggest that chameleons handle the conflict between natural and sexual selection by means of rapid and temporary body colour changes, which are driven more strongly by a need for sexual signalling than by a need for crypsis. We thus clearly demonstrate that a trade-off between crypsis and sexual signalling takes place in animals that employ rapid and temporary body colour change for both needs. Most importantly, our results support the hypothesis that the specific mating tactic of the male influences its decision to remain cryptic or to employ sexual signalling.

Acknowledgments

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