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Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Influence of light intensity and substrate color on dorsal gray color change in *Phrynocephalus helioscopus* and *Phrynocephalus grumgrzimailoi*

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ARTICLE INFO

Keywords:

Agama lizard
Gray gradient
Light intensity
Background matching

ABSTRACT

Body coloration is a functional adaptation that increases reproductive success or decreases the predation risk in animals. To understand the effect of light and substrate on coloration, we investigated the dorsal gray change in *Phrynocephalus helioscopus* and *Phrynocephalus grumgrzimailoi* maintained in habitats with a different light intensity and different substrate. We measured their gray gradient under different light and substrate conditions to establish the functional meaning of color change. We found that (1) in these two species, the gray level of dorsal gray decreased when they were housed on a light substrate with a high light intensity, (2) they increased their dorsal gray color when they were housed on a dark substrate with a low light intensity, and (3) *P. helioscopus* became darker than *P. grumgrzimailoi* with increasing light intensity but became brighter as the substrate darkened. These results imply that light intensity and substrate treatments induced strong color change responses. *Phrynocephalus helioscopus* used light and *P. grumgrzimailoi* used substrate as their main color change cues. *Phrynocephalus grumgrzimailoi* was likely to actively avoid predation while *P. helioscopus* has a thermoregulatory adaptation. We suggested that both light and substrate are important for color changing and camouflage capability in these lizards.

1. Introduction

Body coloration is an adaptive response to a number of selection pressures, such as isolation between sympatric species, defense against predators (Endler, 1978; Cooper and Greenberg, 1992; Merilaita and Lind, 2005; Stuart-Fox and Moussalli, 2008), endurance of “wear and tear” in harsh environments, reproduction (Norris, 1967; Butcher and Rohwer, 1989; Collins et al., 2000), and social interactions (Ross, 1995; Stuart-Fox et al., 2006a; Stuart-Fox and Moussalli, 2008). Species capable of physiological color change may alter their coloration in response to external conditions, and many species have independently evolved the ability to modify their body color over a period of seconds or minutes. These rapid changes are generally associated with intraspecific communication (Adamo and Hanlon, 1996; O'Connor et al., 1999), background matching (Osorio and Vorobyev, 1997), thermoregulatory purposes (Brown and Sandeen, 1948), and light intensity (Vroonen et al., 2012).

Color changes have been studied extensively in many different taxa, such as cephalopods (Whiteley et al., 2011), insects (Parkash et al., 2009), arachnids (Llandres et al., 2013), crustaceans (Thurman, 1988), fish (Hanlon et al., 1999; O'Connor et al., 1999; Mäthger et al., 2003), amphibians (King et al., 1994), and reptiles (Norris and Lowe, 1964; Stuart-Fox and Ord, 2004; Stuart-Fox et al., 2006a; b; Vroonen et al., 2012). Physical color change has been described in Agamidae lizards, and it is related to thermoregulation, background matching, and communication, and most of them are able to take spectrophotometric readings to characterize their dorsal body coloration (Madsen and Loman, 1987; Zucker, 1994a; b; Stuart-Fox and Ord, 2004; Stuart-Fox et al., 2006a; b; Zaidan and Wiebusch, 2007; Stuart-Fox and Moussalli, 2008, 2009; Vroonen et al., 2012). However, the co-effect of light and substrate background color on color change of the sand lizard remains unknown.

In general, lizards in arid habitats usually adopt specific strategies to survive the harsh environment, such as crypsis, the ability to match the

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<https://doi.org/10.1016/j.jaridenv.2018.07.004>

Received 28 December 2017; Received in revised form 21 June 2018; Accepted 9 July 2018

Available online 13 July 2018

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surrounding substrate, and conceal itself (Luke, 1989; Rosenblum, 2006). Two Agamid lizards, the sunwatcher toadhead agama *Phrynocephalus helioscopus* and spotted toadhead agama *Phrynocephalus grumgrzimailoi*, are common lizards in the Junggar Basin, a landlocked arid region in eastern Central Asia. In this study, we used *P. helioscopus* and *P. grumgrzimailoi* to investigate the effects of light intensity and substrate color on their body color. We hypothesized that when they are exposed to an external stimulus, they use the same factor as a cue to change their body color. To confirm or reject this hypothesis, we aimed to establish the functional meaning of color change and quantify dorsal coloration by measuring the gray gradient during manipulating experiments with different light and substrate conditions.

2. Materials and methods

2.1. Ethics statement

All animals in this study were maintained under animal research protocol IOZ-2015 that was approved by the Animal Welfare Ethics Review Committee of the Institute of Zoology, Chinese Academy of Sciences and animals were cared for in accordance with the principles and guidelines of the Animal Welfare Ethics Review Committee of the Institute of Zoology, Chinese Academy of Sciences, and the Chinese Wildlife Management Authority.

2.2. Study area and animals

We conducted our experiment in a monitoring station in the Kalamaili Nature Reserve (KNR) (88°30′–90°03′E, 44°36′–46°00′N), which is located in the northeastern Junggar Basin in Xinjiang, China. Altitude ranges from 600 to 1200 m above sea level and an arid continental climate is prevalent in this area. The mean annual temperature is 4°C–6°C (average of 20.5°C in July and –18°C in January), which is lower compared with the deserts in Central Asia but higher than that in the northern Mongolia Plateau (Xu et al., 2012a,b). Given the arid conditions of the area, water in KNR is extremely limited, and while the average annual precipitation is 159.1 mm, the average annual evaporation is 2090 mm (Chu, 2008). *Phrynocephalus helioscopus* and *P. grumgrzimailoi* were caught in sand dunes with plant communities dominated by *Allium polyrhizum*, *Anabasis salsa*, *Artemisia desertorum*, *Atraphaxis frutescens*, *Calligonum mongolicum*, *Ceratocarpus arenarius*, *Ceratoides latens*, *Haloxylon ammodendron*, *Reaumuria songarica*, and *Stipa glareosa* (Xu et al., 2012a,b).

Phrynocephalus helioscopus inhabits open arid regions of moderate elevation in Central and Western Asia. This species typically inhabits open areas with scattered rocks and bushes, and it relies largely on crypticity to escape detection (Clark and Clark, 1973; Clark et al., 1966). They feed on small invertebrates such as beetles and ants (Clark et al., 1966). *Phrynocephalus grumgrzimailoi* is another dominant species in eastern Central Asia (Ananjeva et al., 2011; Zhao et al., 1999) where it inhabits desert, farm, and salty soil regions (Zhao et al., 1999). As there is no difference in dorsal color in male and female *P. helioscopus* and *P. grumgrzimailoi* (Fu et al., 2013), we did not differentiate between females and males when we collected them.

2.3. Experimental procedure

The experiment was carried out in a test cage (100 × 50 × 50 cm) with two compartments and light could shine through the cage (Fig. 1). Five cages were set up as the treatment groups with different substrates: (1) white paper (represents a very bright substrate), (2) yellow sand (represents a natural substrate), (3) gray rock (represents occasional conditions), and (4) rock and sand (represents a natural substrate).

Before the experiment, 10 *P. helioscopus* were placed in one compartment and 10 *P. grumgrzimailoi* were placed in the other one. Cages were then carried to a fixed position exposed to sunlight. A photograph

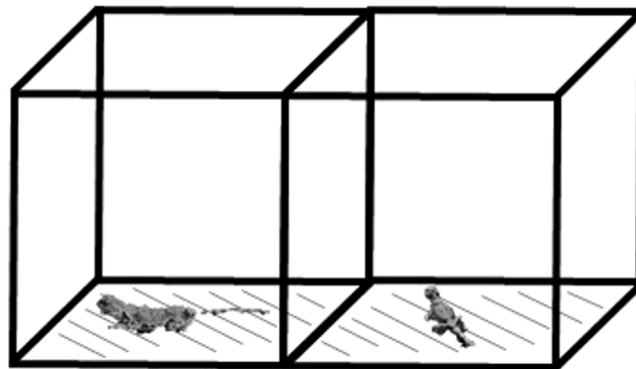


Fig. 1. Schematic diagram of the test cage used to determine the influence of light intensity and substrate color on dorsal gray change in *Phrynocephalus helioscopus* and *Phrynocephalus grumgrzimailoi*. The transparent surface indicates light exposure and the gray diagonal zone is the background (substrates are the same in both compartments during every experiment.) See text for details.

was taken every hour with an OLYMPUS SP-565UZ camera (resolution 2560 × 1920 pixels). Photographs were taken from a distance of about 0.5 m and focused on the dorsum to provide a grayness standard index (Fig. 2). We took a photo three times to minimize variation. Some individuals escaped from the cage due to strong winds, and specimens were caught and the experiment was restarted. Escape data are still included as these data are valid.

Many other methods are used to measure the dorsal color of a lizard. Compared with other color correction methods, the gray gradient has various advantages. First, many color samples with information of different intensity values can be obtained. This helps to improve the accuracy of the color correction. Second, we can acquire a whole range of intensity from 0 to 255. Captured images of the bar function as a basis of the color sensitivity properties (Jung and Ho, 2009). A dorsal gray gradient of *P. helioscopus* and *P. grumgrzimailoi* and the substrate were determined using a gray gradient bar and Photoshop Cs4 (©1990–2008, Adobe Systems Incorporated). We converted the photo from RGB to grayscale mode in Photoshop. The value of dorsal color (R_1), background color (R_2), region 25 standard index (S_{25}), and region 100 standard index (S_{100}) were then read. Light intensity was measured with a portable light meter (TES-1330A), and grayness was calculated using the following formula.

$$\text{Grayness value} = 100 - (100 - 25) * (R_i - S_{100}) / (S_{25} - S_{100}) \quad (i = 1, 2)$$

Successive tests ran from 09:00 to 23:00 when the light intensity was close to zero. Each experiment with a different background treatment lasted about 2–3 d, and each experiment was separated by an interval of at least one night roosting to return to the normal state.

2.4. Data analysis

Data analyses were performed using SPSS v. 20 (Armonk, NY: IBM Corp.). Because all data were not normally distributed (one sample Kolmogorov–Smirnov test, $P < 0.05$), we used nonparametric tests (Kruskal–Wallis test and Spearman correlation) to assess the variables. For our main analysis of differences in dorsal gray coloration of *P. helioscopus* and *P. grumgrzimailoi* by light intensity, the light intensity value was divided into six groups: Group A, 0; Group B, 0–10; Group C, 10–100; Group D, 100–1000; Group E, 1000–10000; and Group F, > 10000. The gray value in the range 0–100 was divided into 10 groups: Group I, 0–10; Group II, 10–20; Group III, 20–30; Group IV, 30–40; Group V, 40–50; Group VI, 50–60; Group VII, 60–70; Group VIII, 70–80; Group IX, 80–90; and Group X, 90–100. We also assessed the relationship between dorsal gray and substrate gray by a Spearman correlation. The dorsal: substrate gray ratio was analyzed with



Fig. 2. Grayness standard determining the gray index of dorsal patches of Agamidae. Numbers are the values of relative grayness.

descriptive statistics to define whether the mean ratio of dorsal gray was correlated to substrate gray. The chi-square test was used to examine ratio frequencies. The Mann–Whitney *U* test was used to determine whether the general trend of dorsal change had the same distribution. Moreover, data that indicated an abnormal white or black dorsal color (< 0 or > 100) were excluded prior to the analysis. Values are means ± standard error. *P* < 0.05 was considered statistically significant for all tests.

3. Results

We examined 132 individuals and acquired 515 valid data points, 266 for *P. helioscopus* and 249 for *P. grumgrzmailoi*.

3.1. *Phrynocephalus grumgrzmailoi*

3.1.1. Light intensity

The dorsal color differed significantly among the six light intensity groups (Kruskal–Wallis test, *df* = 4, $\chi^2 = 71.375$, *P* < 0.01). *Phrynocephalus grumgrzmailoi* changed their dorsal color due to light intensity; the peak in dorsal gray was observed in Group A (83.22 ± 0.74 ; Fig. 3a), and it decreased monotonically with increasing light intensity (Fig. 3a). Dorsal gray was moderately correlated to light intensity (Spearman's correlation, *r* = −0.436, *P* < 0.01; Table 1).

3.1.2. Substrate

Phrynocephalus grumgrzmailoi changed their dorsal color based on differences in the gray substrate (Kruskal–Wallis test, *df* = 9, $\chi^2 = 92.307$, *P* < 0.01). The dorsal gray trend was highest in Group II (74.89 ± 8.42 ; Fig. 3b) and Group IX (84.78 ± 5.24 ; Fig. 3b) and was moderately correlated to substrate gray (Spearman's correlation, *r* = 0.590, *P* < 0.01; Table 1). Moreover, the dorsal:substrate gray ratio was equal in each group (chi-square test, $\chi^2 = 30.904$, *P* = 1.00). The descriptive statistics indicated that the mean value of the ratio was

Table 1

Correlation coefficient for substrates and light intensity tests.

Species and factors	<i>r</i> value of correlation between factor and gray	<i>P</i> value
<i>Phrynocephalus grumgrzmailoi</i>		
Light intensity	−0.436	< 0.01**
substrate	0.590	< 0.01**
<i>Phrynocephalus helioscopus</i>		
Light intensity	−0.438	< 0.01**
substrate	0.201	< 0.01**

**Correlation is significant at the *P* < 0.01 (two tailed).

1.34 ± 0.06.

3.2. *Phrynocephalus helioscopus*

3.2.1. Light intensity

The dorsal color differed significantly among the six light intensity groups (Kruskal–Wallis test, *df* = 5, $\chi^2 = 63.219$, *P* < 0.01). *Phrynocephalus helioscopus* dorsal color change was more complicated compared with that of *P. grumgrzmailoi*. The peak in dorsal gray was observed in Group A (83.22 ± 0.74 ; Fig. 3a); it decreased with increasing light intensity, fluctuated in Group E (75.82 ± 1.16 ; Fig. 3a) and then fell gradually in the last group (72.73 ± 0.79 ; Fig. 3a). Dorsal gray was moderately correlated to light intensity (Spearman's correlation, *r* = −0.438, *P* < 0.01; Table 1).

3.2.2. Substrate

In the substrate experiment, *P. grumgrzmailoi* changed their dorsal color dependent on the treatment (Kruskal–Wallis test, *df* = 8, $\chi^2 = 56.294$, *P* < 0.01) and change was highest in Group III (82.87 ± 6.84 ; Fig. 3b) and Group IX (81.08 ± 6.45 ; Fig. 3b). However, the degree of dorsal gray change in *P. helioscopus* was weak (Spearman's correlation, *r* = 0.201, *P* < 0.01; Table 1). The dorsal:substrate gray ratio of *P. helioscopus* was equal in each group ($\chi^2 = 46.78$, *P* = 1.00). The descriptive statistics indicated that the

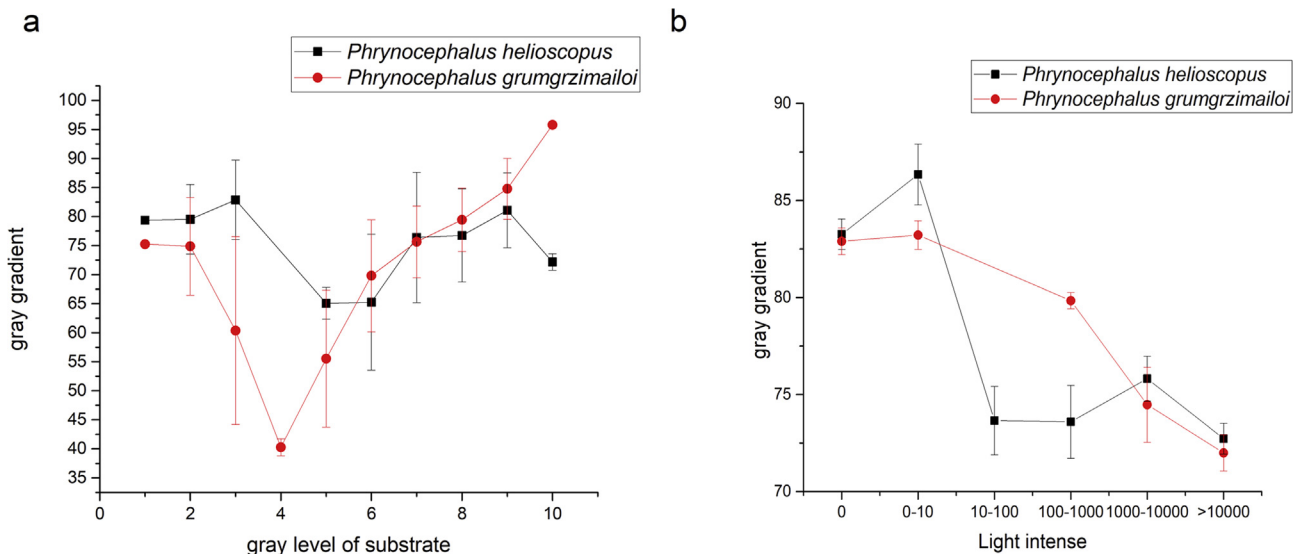


Fig. 3. Dorsal gray gradient by different substrate (a) and light intensity (b). Error bars indicate 95% confidence intervals.

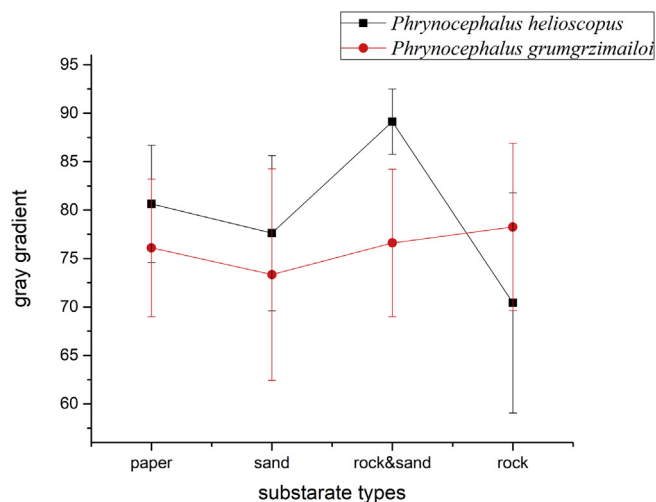


Fig. 4. Dorsal gray gradient on different types of substrates. Error bars indicate 95% confidence intervals.

mean ratio of *P. helioscopus* was 1.33 ± 0.06 .

3.3. Species comparison

The general trend of dorsal change in response to light intensity and substrate differed significantly between two species (two samples Kolmogorov–Smirnov test, $P < 0.05$) and the strength varied between species in each substrate (two samples Kolmogorov–Smirnov test, $P < 0.05$). On a rock substrate, *P. helioscopus* was significantly brighter than *P. grumgrzimailoi* (Fig. 4).

The correlation coefficient for substrate and light intensity (Table 1) showed that they used different environmental factors as their main cues. The results suggested that light intensity played a more important role than substrate in *P. helioscopus* dorsal color change. By contrast, *P. grumgrzimailoi* used substrate as the main cue.

4. Discussion

Our study clearly rejected the hypothesis that *P. helioscopus* and *P. grumgrzimailoi*, when exposed to an external stimuli, shared the same cue to change their body color. Two congeneric species had different reactions to environmental conditions, *P. grumgrzimailoi* became brighter than *P. helioscopus* with increasing light intensity but became darker as the substrate darkened. *Phrynocephalus grumgrzimailoi* used the substrate as a main cue and *P. helioscopus* used light intensity.

Our results show a negative relationship between light intensity and color change and the correlation coefficients (-0.436 and -0.438) were similar ($P = 0.98$, Fisher's exact test). It shows that the two species had approximately the same reaction under natural light conditions. Further work is needed to understand whether these phenomena would also occur under non-natural light conditions.

We observed an abnormal level of gray among the light substrates investigated. Very white substrates may be scarce naturally, and they are probably actively avoided. Hence, *P. helioscopus* and *P. grumgrzimailoi* may not discriminate among super light substrates or adjust their dorsal color according to them. In other words, there may be a physical limit to the aggregation of melanosomes that constrain skin lightening (Vroonen et al., 2012).

Our data indicated that *P. helioscopus* and *P. grumgrzimailoi* maintained on a dark background significantly raised their dorsal color. This suggests that color change in *P. helioscopus* and *P. grumgrzimailoi* may be a predator avoidance strategy. Substantial evidence suggests that the degree of background matching is correlated with the risk of predator detection in animals that have the ability to change color, such as fish,

chameleons, and cephalopods (Stevens and Merilaita, 2009). In lizards, color change in the ornate tree lizard *Urosaurus ornatus* is possibly related to crypsis (Hamilton et al., 2008) and dwarf chameleons *Bradypodion transvaalense* exhibit facultative crypsis. The degree to which their body color matches the background depends not only on the risk of predation but also on the type of predator (Stuart-Fox et al., 2006b, 2008).

Given the diurnal activities of *P. helioscopus* and *P. grumgrzimailoi*, the rare rock substrate, and the high intensity of uninterrupted sunlight in the dry KNR suggests that *P. helioscopus* is darker than *P. grumgrzimailoi* most of time (Fig. 3b). However, given the confined distribution of *P. helioscopus* together with the previous study, we can assume that crypsis plays an important role in color change.

Previous studies have successfully manipulated the dorsal color in response to background and light intensity (Fleishman and Persons, 2001; Hamilton et al., 2008; Stuart-Fox et al., 2006b), but seldom did they quantify the background factor. Our study of color change in *P. helioscopus* and *P. grumgrzimailoi* used a gray gradient to describe the substrate and dorsal color. Thus, the relationship between background and dorsal color is more explicit. Further study will be required.

Congeneric species vary in the strength of their dorsal color response to an external stimulus. *Phrynocephalus helioscopus* used light as a main cue and *P. grumgrzimailoi* used substrate to initiate color change. These phenomena may have been derived from different natural selection pressures in arid habitats. *Phrynocephalus helioscopus* inhabit a gravel sand substrate so they have a lower predation risk being surrounded by scattered gravels and bushes than *P. grumgrzimailoi*. Biophysical theory predicts that darker colored animals heat faster and achieve a higher body temperature than lighter colored one (Bakken and Gates, 1975). This may explain the darker gray in *P. helioscopus* than *P. grumgrzimailoi* with increasing light intensity. It suggests that thermoregulation may be a prominent function in *P. helioscopus* although predator avoidance is an essential trigger. By contrast, *P. grumgrzimailoi* is usually found on sand substrates and their color change may be mainly a predator avoidance strategy.

As for the mechanisms of color change, there are two main different types: (1) morphological color change, which involves changes in the number and quality of chromatophores in the dermis and usually takes place over a time scale of days or months, and (2) physiological color change, which involves movement (dispersion and aggregation) of pigment granules within chromatophores and is much more rapid, taking milliseconds to hours (Thurman, 1988). Rapid responses to changes in the animal's visual environment is generally rely on physiological color change (Nery and Castrucci, 1997). For many species, visual feedback is important when color change occurs in the short term. In some animals, chromatophore state is under direct nerve control from the visual system (Duarte et al., 2017). It was noted that some animals change color in response to light, even their eyes were covered or removed, the brightness were perceived by skin receptors (Frisch, 1911; Sumner, 1935; Mähger et al., 2010; Fulgione et al., 2014). The behavior of the lizards, which they used different environmental factors as main cues may prove that the eye is determinant in *P. grumgrzimailoi* color change, and dermal photosensitivity in *P. helioscopus* play a more important role than in *P. grumgrzimailoi*.

Although *P. helioscopus* and *P. grumgrzimailoi* adjusted their body coloration in response to external factors, they exhibited different responses based on different cues, as such, we are cautious about generalizing our results to all Agamid species. Because we performed our color measurements every hour, the average speed of dorsal coloration changes was difficult to quantify. Thus, we cannot compare their speed by different gray intervals. This may be important for their social interactions.

Acknowledgements

We acknowledged the financial support of the Key Basic Science and

Technology Project of the Ministry of Science and Technology, China (2013FY110300), the National Key Research and Development Program of China (2016YFC0503304), the National Natural Science Foundation of China (31472021, 31572260), and the Knowledge Innovation Project of the Chinese Academy of Sciences (KSCX2-EW-J-2). We are grateful to Heqing Huang, Shanhui Liu and Kehao Wang for their assistance in the Kalamaili Nature Reserve.

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