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Color change, background choice, and camouflage in a nocturnal treefrog: implications for circadian adaptation

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ABSTRACT

Camouflage through background matching is a widespread antipredator strategy across taxa, enhancing survival by reducing the likelihood of detection or recognition by predators. To achieve this, animals often change color and/or choose appropriate backgrounds to overcome the spatial and temporal variation of substrates. However, how these strategies are modulated by diel variation remains unclear. In this study, we investigated color change and background choice in Hainan frilled treefrogs (*Kurixalus hainanus*), a nocturnal species that exhibits green-brown color patterns. We found that frogs changed brightness, saturation, and hue more rapidly in dark conditions than in light, and exhibited a significantly faster initial response to light during the day than at night. Color change significantly improved background similarity (measured by Euclidean distance) to both green and brown substrates in the light conditions. While frogs did not actively choose backgrounds that matched their coloration when given a choice, they significantly avoided highly contrasting white substrates and were more active during the day. Pattern elements of frogs provided better camouflage than chromatic or achromatic properties when compared with the substrates at their calling sites, as modelled under avian, mammalian, and snake visual systems. Nonetheless, chromatic contrasts varied across predator visual systems, being highest for birds and lowest for mammals. In addition, achromatic contrasts were significantly lower on the observed substrates than on the alternative ones. Our findings provide new insights into the adaptive significance of color change and background choice in nocturnal species, highlighting the importance of diel phase in camouflage strategies.

Keywords: Background matching; Camouflage; Diel variation; Pattern energy difference; Visual modelling

INTRODUCTION

Coloration is a fundamental trait shaped by ecological and evolutionary forces across the animal kingdom, serving diverse ecological functions such as thermoregulation, communication, and preventing predation (Stuart-Fox & Moussalli, 2009). Camouflage through body coloration is a widespread antipredator strategy in nature, which reduces detection or recognition by potential predators and thereby increases individual fitness (Duarte et al., 2017; Stevens & Merilaita, 2009). Natural selection thus favors color polymorphism and phenotypic variability in cryptic species, as such variation enhances concealment across diverse and changing environments (Rojas, 2017; Stevens & Ruxton, 2019).

Among various forms of camouflage, such as self-shadow concealment, disruptive coloration, and masquerade, background matching is the most prevalent across taxa (Mark et al., 2022; Smithers et al., 2018; Stevens et al., 2017). Background matching is the resemblance of an individual to the color, lightness, and/or pattern of its immediate environment (Duarte et al., 2025). Cryptic species may rely on color or pattern polymorphism to blend into heterogeneous environments, thereby reducing detection by visually oriented predators (de Alcantara Viana et al., 2024; Goutte & Boissinot, 2025). However, achieving effective background matching at the individual level is challenging in natural substrates that are temporally and spatially dynamic (Green et al., 2024; Stevens et al., 2015). To overcome this challenge, animals exhibit two forms of phenotypic plasticity (Figon & Casas, 2018; Stevens, 2016; Stevens & Ruxton, 2019): morphological plasticity (e.g., changing color, brightness, or pattern) and behavioral plasticity (e.g., choosing appropriate backgrounds). Physiological color change (i.e., a form of morphological plasticity) involves the rapid dispersion or concentration of

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pigment granules within chromatophores and occurs within seconds to hours (Figon & Casas, 2018; Stevens, 2016). This form of plasticity facilitates swift concealment within changing backgrounds and is commonly employed by taxonomic groups such as cephalopods (Drerup et al., 2024), chameleons (Whiting et al., 2022), and fish (Ueda et al., 2024). In contrast, morphological color change (i.e., the other form of morphological plasticity) involves changes in the number and proportion of chromatophores, which take place over a time scale of days, weeks, or even months (Duarte et al., 2017; Stuart-Fox & Moussalli, 2009). This form of plasticity helps animals cope with predictable or seasonal shifts in habitat composition across time or space (Caro et al., 2016; Zimova et al., 2020). These species often use a combination of color change and background choice to improve camouflage and enhance survival (Green et al., 2019). Therefore, behavioral plasticity provides an alternative strategy for species with slow or limited color-change ability to achieve rapid background matching (Camacho et al., 2020; Twort & Stevens, 2023).

In addition to the temporal and spatial variation of substrates, animals must also cope with dramatic shifts in light conditions associated with the diel cycle (Duarte et al., 2017). Light conditions influence both the movement of pigment granules and behavioral patterns, thereby affecting animals' crypsis (Deng et al., 2019; Dickerson et al., 2023; Shawkey & D'Alba, 2017). In addition, different predators are active at different diel phases (i.e., day and night) and possess distinct visual systems. These contrasting ecological conditions of day and night impose opposing selective pressures on concealment, which potentially shaping divergent camouflage strategies. Many animals exhibit diel color changes (becoming lighter at night and darker during the day, or vice versa) yet whether these shifts are driven by endogenous rhythmic regulation or by direct responses to light cues is still controversial and appears to be species specific (Darnell, 2012; Gamble & Keeble, 1900; Stevens et al., 2013). Despite its ecological significance, the extent to which diel variation modulates the morphological and behavioral plasticity underlying background matching remains poorly understood (Duarte et al., 2025).

Anurans (frogs and toads) provide valuable models for investigating this topic, given their diverse body coloration and patterns and their capacity for active color change (Hoffman & Blouin, 2000; Rudh & Qvarnström, 2013). In anurans, color change serves multiple ecological functions that vary with environmental and social contexts. Many species adjust skin brightness according to ambient temperature and light intensity, becoming darker in cooler or dimmer environments and lighter in warmer or brighter ones to facilitate thermoregulation (King et al., 1994; Tattersall et al., 2006). Some species undergo temporary color changes from dull brown to vibrant hues during the breeding season, which serve as intra- or intersexual signals to enhance mate recognition and pairing efficiency (Rehberg-Besler et al., 2015; Sztatecsny et al., 2012). In addition, color change can enhance background matching and thus improve crypsis, potentially reducing predation risk (Kang et al., 2016; King et al., 1994; Stegen et al., 2004). Since most anurans are nocturnal, these diverse adaptive functions of color change may involve potential trade-offs under varying environmental contexts, particularly between maintaining crypsis to avoid predation and producing conspicuous signals for communication or social interactions (Anderson & Wiens, 2017; Rojas, 2017). However, little empirical attention has been paid to how diel variation influences color change and background choice, and whether anurans employ phenotypic plasticity and matching behavior to maintain effective background matching during nocturnal activity.

Hainan frilled treefrogs (*Kurixalus hainanus*) are a nocturnal anuran species that exhibit a mixed green-brown coloration pattern, with individuals varying in the relative dominance of each color (Figure 1A–C). In this study, we first investigated the ability of frogs to change color in response to different lighting conditions (light vs. dark) under both natural and inverted diel phases, measured by three color metrics: brightness, saturation, and hue. We also investigated whether this ability enhances the similarity of frogs to different backgrounds (green vs. brown) in the light conditions, measured by Euclidean distance in XY-coordinate space. Second, we conducted laboratory experiments to investigate whether frogs show a preference for backgrounds which they match the most using both green-dominated and brown-dominated individuals. Furthermore, we examined whether color change responses and background choice differ between day and night. Since *K. hainanus* are nocturnal, engaging in foraging and mating at night and resting during the day, we hypothesized that an endogenous circadian rhythm underlies their diel patterns, influencing both morphological and behavioral plasticity. We predicted that frogs would exhibit faster color change and stronger preference for matching backgrounds during their active phase than during their resting phase.

Last, we investigated whether background choice helps male frogs maintain crypsis during nocturnal displays. Since frogs are preyed upon by a variety of predators, we quantified the chromatic and achromatic contrasts (i.e., just noticeable differences, JNDs) and the pattern energy difference (PED) between frogs and their substrates, as modelled under bird, mammal, and snake visual systems. Frogs vocalize to access mating opportunities, but this behavior increases predation risk (Wells & Schwartz, 2007), highlighting a trade-off between communication and camouflage. Therefore, we hypothesized that males choose calling sites with smaller chromatic and achromatic JNDs and PED between their dorsum and the substrates. Field observations revealed that startled male *K. hainanus* often cease calling and cling closely to the substrate (Figure 1C). Therefore, we predicted that the substrates at the calling sites would provide better visual camouflage than adjacent substrates. In addition, since vegetation cover can reduce the probability of visual detection by predators, we further predicted that background matching would increase as vegetation cover around the calling site decreases.

MATERIALS AND METHODS

Study site and subjects

The study was conducted at Diaoluo Mountain National Nature Reserve in Hainan, China (N18.72°, E109.87°, elevation 933 m). Color change experiments were performed in April 2022, background choice experiments and background matching in the field were performed between May and June 2021. Only male individuals were collected from the natural population for testing. Before the tests, we placed the male *K. hainanus* in plastic containers (10 cm in diameter×12 cm in height). After each experiment, males were marked by clipping a small piece of the toe pad from the smallest finger to prevent recapture and were released at their original capture location. The wound was cleaned immediately with 75% ethanol to

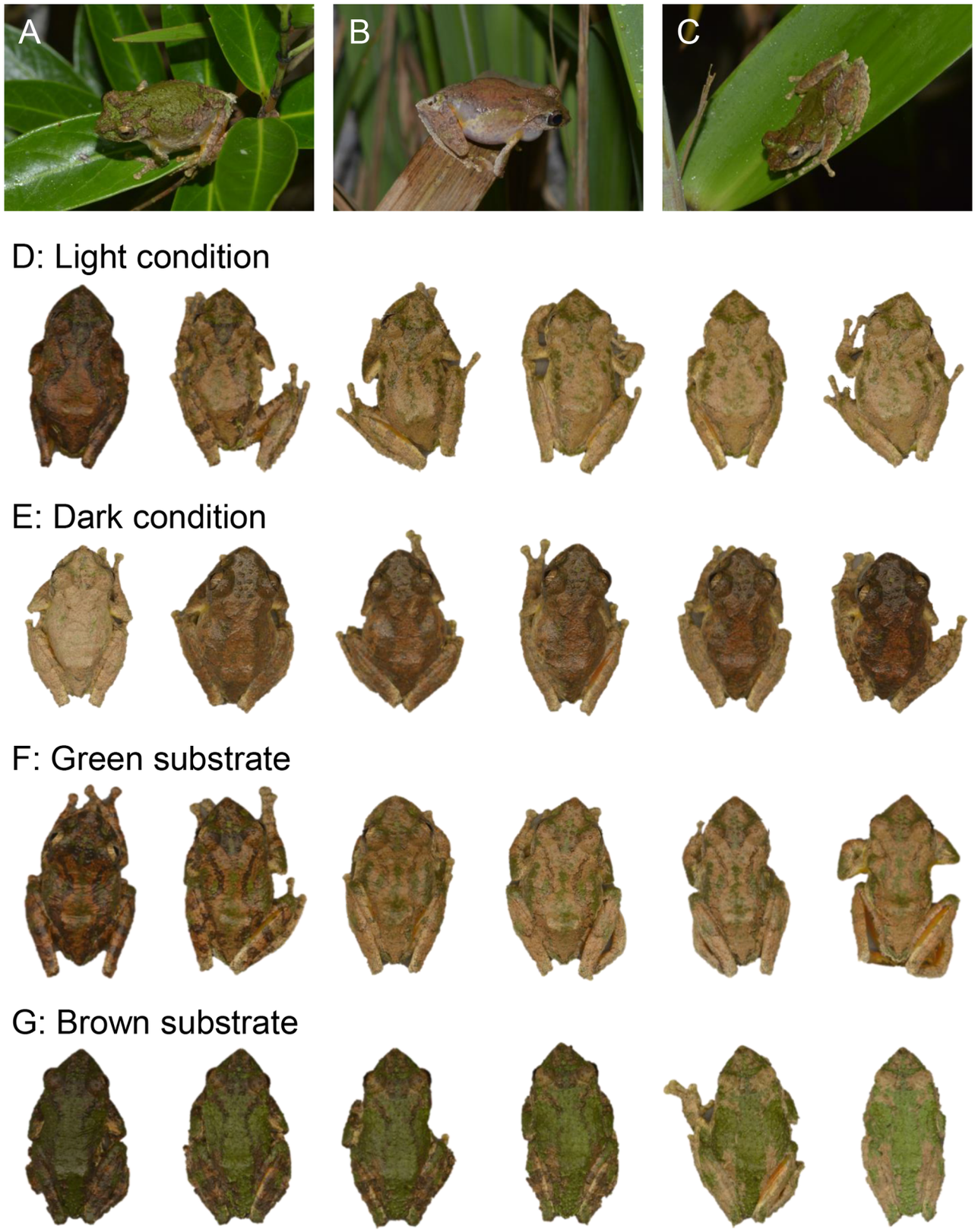

Figure 1 The green-brown coloration pattern and morphological plasticity in *Kurixalus hainanus*

A: A green-dominated frog. B: A brown-dominated frog. C: A frog that clings closely to the leaf when disturbed. D: Color change of a frog in the light condition. E: Color change of a frog in the dark condition. F: Color change of a frog against green substrate. G: Color change of a frog against brown substrate. Photos by Ke Deng.

avoid infection. All experiments were approved by the management office of the Diaoluo Mountain National Nature Reserve and the Animal Care and Use Committee of the Chengdu Institute of Biology, CAS (CIB2016042403).

Photography and image calibration

We used digital image analysis to quantify the chromatic, achromatic, and pattern properties of frogs and the backgrounds, which were photographed in a dark room using

a Nikon D800 digital camera with a Nikkor 105 mm kit lens. The camera was mounted on a stand and all images were taken at a fixed distance of 30 cm. Illumination was provided by two LED lamps (24 W, 5 000 K, Philips HO T5). As ambient spectral composition, including Ultraviolet (UV) radiation, can affect pigment responsiveness as well as the visual detectability of animals against their backgrounds, it is typically an important consideration in studies of color change and camouflage. Although the dorsum of *K. hainanus* showed a UV reflectance (Zhu et al., 2022), this species is nocturnal and mainly active in understory and shrub habitats where direct sunlight is presumably limited. Moreover, the UV reflectance of their natural backgrounds (e.g., tree bark, leaves, or soil) is negligible. Therefore, consistent with other anuran studies (Barnett et al., 2020; Kang et al., 2016), UV light was excluded from the present study. Images were taken in RAW format with manual white balancing and fixed shutter speed and aperture settings to prevent overexposure (Stevens et al., 2007). A black (10%) and white (90%) Spectralon standard with a millimeter ruler was included in each image.

Images were equalized for any changes in light conditions using the black and white standards and converted into 32-bit multispectral images (Troscianko & Stevens, 2015), which contained three bandpass layers corresponding to the long-wavelength (LW), medium-wavelength (MW), and short-wavelength (SW) parts of the spectrum. Image channels were then scaled to reflectance values, where an image value of 255 on an 8-bit scale equals 100% reflectance (Stevens et al., 2007). For each multispectral image, regions of interests (ROIs) were selected from both the frogs and the backgrounds for measurement. On frogs, two circular ROIs (100 pixels in diameter) were placed on the head, six on the middle of the dorsum, and two on the posterior dorsum, with sampling points distributed to ensure an equal number on the left and right sides of the body. For backgrounds (i.e., fresh green leaves and dead brown leaves), ten circular ROIs were randomly selected. The ROIs were chosen carefully to avoid regions with glare. All these routines were performed using the Multispectral Image Calibration and Analysis (MICA) toolbox implemented in ImageJ software (Troscianko & Stevens, 2015).

Color change experiments

The experiments were conducted in a temperature-controlled room, with an average temperature of 23.09±0.05°C and an average humidity of 81.4±0.74% (mean±SE). To investigate whether color change is influenced by diel variation, the experiments were conducted from 2030 to 0500 h and from 0830 to 1700 h.

First, we examined the ability of color change in the light and dark conditions, with each individual exposed to the light condition first, followed by the dark condition. In the light condition, focal individuals were kept in a bowl-shaped container (5.5 cm in bottom diameter, 17 cm in top diameter, and 4 cm in height), with the top covered by a transparent glass (0.55 mm in thickness). The inside of the container was covered with white cloth and kept moist during the experiments. Illumination was provided by an LED lamp (24 W, 5 000 K, Philips HO T5), and the illuminance was 200 lux at the center of each container, measured using Light Meter Pro. TES-1339, TES Electrical Electronic Corp. Photographs were taken at 0, 0.5, 1, 2, 4, and 8 hours after the experiment began. Frogs were gently taken out of their containers for image capture with efforts made to maintain a consistent position across individuals and sessions. Each photography session was usually completed within one minute, after which the frog was immediately returned to its container. After the 8-hour point, frogs remained in their containers with the lights on. At 12 hours, they were photographed again, and this time point was regarded as time 0 of the subsequent dark condition, which was initiated by turning off the lights and inverting the containers. In the dark condition, photographs were taken at the same time intervals as in the light condition. For each session, frogs were briefly exposed to light during the photography and were promptly returned to their dark containers. In total, 48 frogs were used in this experiment: 24 individuals first experienced the light condition at night followed by the dark condition during the day (opposite to the actual diel phase), while the other 24 first experienced the light condition during the day followed by the dark condition at night (aligned with the diel phase). All individuals were kept for less than 36 h and released at their original capture location after photography.

The brightness, saturation, and hue of ROIs in each image were calculated to examine the rate of color change. Brightness was calculated as (LW+MW+SW)/3 and is a measurement of how dark or bright frogs are across the entire spectrum (Stevens et al., 2014b). Saturation was calculated by transforming the normalized LW, MW, and SW reflectance values to two-dimensional XY-color space (Kelber et al., 2003). Saturation describes a color's similarity to a neutral grey or white and is considered as the shortest distance from a given color point to the achromatic center of the space, with larger values representing greater saturation (Kelber et al., 2003). Hue was calculated as the ratio MW/(LW+SW), which is a simple measurement of medium-wavelength versus the two extremes of the light spectrum, broadly analogous to an opponent color channel (Duarte et al., 2021; Nokelainen et al., 2019; Spottiswoode & Stevens, 2011).

Second, we examined whether color change helps to enhance background similarity to green and brown substrates. In this experiment, the inside of the container was covered with fresh green leaves or dead brown leaves (collected from the frogs' native habitat) and kept moist during the experiments. Focal individuals were placed on substrates of contrasting coloration (green-dominated individuals on brown leaves, brown-dominated individuals on green leaves). The experiments were conducted in the light condition, and illuminance was 200 lux at the center of each container. Photographs were taken at 0, 0.5, 1, 2, 4, and 8 hours after the experiment began. In total, 96 frogs were used in this experiment, with 48 tested at night and 48 tested during the day. All individuals were kept for less than 24 h and released at their original capture location after photography. The similarity in coloration between the frogs and their backgrounds was estimated by calculating the Euclidean distance in XY-coordinate space (Nokelainen et al., 2018). It provides a receiver-independent estimate of the degree of background match of the frogs, for which lower distances indicate more similar coloration between the frogs and their backgrounds.

Background choice experiments

This experiment aimed to examine whether frogs show a behavioral preference for backgrounds they match the most, and to determine whether the preference is influenced by diel variation. Therefore, the experiments were conducted from 2030 to 2400 h and from 0830 to 1200 h. Focal individuals

were tested in a circular arena, which was set up in a sound-attenuating chamber (4.9 m long×3 m wide×3.2 m high). The test arena was divided into four areas (Supplementary Figure S1), each covered with a different substrate: fresh green leaves, dead brown leaves, white paper (Azone Perfect Copy A4), and black paper (printed with Canon color laser printer LBP 9100Cdn). The orientation of the substrates was placed randomly to control for potential side biases, but the green and brown leaves (or white and black paper) were always opposite. The green leaves remained fresh during the experiment, and all substrates were covered by a transparent glass film (0.55 mm in thickness). Illumination was provided by an LED lamp (24 W, 5 000 K, Philips HO T5), and the illuminance was 150 lux at the center of the arena, measured using Light Meter Pro (TES-1339, TES Electrical Electronic Corp).

Focal individuals were placed in the arena and allowed to acclimatize to the novel environment for 2 min and were then observed for 10 min. The test arena was covered by a transparent glass lid (30 cm in diameter×5 cm in height) during the tests to prevent the frogs from escaping (Supplementary Figure S1). After testing, frogs were returned to their containers and tested again the next morning (i.e., once at night and once during the day). The glass film was cleaned with 75% ethanol, followed by running water after each test to eliminate any residual chemicals. Experiments were recorded using a video camera (Woshida 84H10P, Shenzhen Woshida Technology Ltd.). The duration that the focal individuals stayed in each area and the number of times frogs crossed an area boundary was recorded from the video. A total of 78 frogs (32 green-dominated and 46 brown-dominated) were tested, and all individuals were kept for less than 24 h and released at their original capture location after the experiments. There was no significant difference in temperature or humidity between the two test phases (temperature (mean±SE): night=23.32±0.18°C, day=23.13±0.18°C, paired *t*-test: t_{15}=–0.74, P=0.47; humidity (mean±SE): night=87.1±2.26%, day=90.31±1.93%, paired *t*-test: t_{15}=1.64, P=0.11).

Background matching in the field

To examine the degree of background matching between the dorsal coloration of male *K. hainanus* and the substrate of their display sites, calling males were collected between 2030 and 2330 h from the natural population (n=84). To examine whether males preferentially vocalize on substrates that provide better camouflage effectiveness, both the substrates where males were observed calling and nearby alternative substrates of contrasting coloration were collected. For example, if a male frog vocalized on a green leaf, then a brown dead leaf was collected as a contrasting substrate. In addition, the density of vegetation around the calling males was recorded and classified into 3 levels: (1) low, there was no vegetation around the calling males, and they could be seen from any direction; (2) middle, there were a few leaves and/or branches around the calling males, and they could be seen from some certain angles; (3) high, there were dense leaves and/or branches around the calling males, and they could barely be seen without putting aside the leaves and/or branches. Frogs and substrates (observed green substrates=52, brown substrates=32) were transported to a dark room, where they were photographed together that night. All frogs were kept for less than 4 h and released at their original capture location after photography.

Visual modelling

The chromatic, achromatic, and pattern properties of calling frogs in conjunction with substrates (both observed and alternative substrates) were measured from calibrated images (Troscianko & Stevens, 2015). Since treefrogs are commonly preyed upon by birds, mammals, and snakes, we analyzed the reflectance data for both frogs and substrates through the receptor noise limited (RNL) model (Vorobyev et al., 2001; Vorobyev & Osorio, 1998), considering the vision of blue tits (*Cyanistes caeruleus*), ferrets (*Mustela putorious furo*), and garter snakes (*Thamnophis sirtalis*). For the avian visual model (i.e., blue tits), we used Weber fractions SW 0.059, MW 0.050, LW 0.050, with a receptor ratio of 1.92:2.68:2.7 (Hart et al., 2000). For the mammalian visual model (i.e., ferret), we used Weber fractions SW 0.187, and LW 0.050, with a receptor ratio of 1:14 (Calderone & Jacobs, 2003). For the snake visual model (i.e., garter snakes), we used Weber fractions SW 0.135, MS 0.106, LW 0.050, with a receptor ratio of 1:1.6:7.3 (Sillman et al., 1997). The avian and snake visual models were used over the 400–700 nm range due to the lack of UV data. All visual models were calculated under a standard D65 illumination.

Chromatic (color) and achromatic (luminance) contrasts were calculated for each visual model using the MICA toolbox (Troscianko & Stevens, 2015). Chromatic contrast was calculated using LW, MW, and SW cones in the avian (603, 541, and 453 nm) and snake (553, 482, and 400 nm) visual model, while LW and SW cones were used in the mammal (558 and 433 nm) visual model. Achromatic contrast was calculated from the response of the double cone in the avian (566 nm) visual model and from the LW cones in the mammalian and snake visual models. For each visual model, the chromatic and achromatic contrasts between frog ROIs and backgrounds are expressed as just noticeable differences (JNDs), representing discrimination thresholds. JND values lower than 1 are considered indistinguishable, values between 1 and 3 are considered difficult to distinguish, and values greater than 3 are increasingly likely to be distinguishable (Nokelainen et al., 2019; Siddiqi et al., 2004).

As frogs exhibit substantial inter-individual variation in dorsal patterns, with green and brown patches differing in shape and size, pattern energy difference (PED) was also calculated for each predator viewer. The pattern energy was estimated using granularity analysis, which is based on the decomposition of an image into a series of different spatial frequencies using Fast Fourier bandpass filtering (Barbosa et al., 2008; Stoddard et al., 2019). The amount of information (i.e., pixel energy) was calculated from markings of different sizes, starting with small markings (2 pixels) and increasing in size to larger markings. An increase in pixel step size was set to multiply each step by 1.414 (i.e., exponential growth), up to a maximum of 128 pixels. No pattern energy was observed beyond this point, as the ROI was 100 pixels in size. Pattern analyses such as PED generally focus on achromatic information, so we conducted all PED calculations using the luminance channel. The setting of the luminance channel differed among predators: it was set to double cones for the avian visual model and to LW cones for the mammalian and snake visual models. The granularity analysis results were used to compare PED between ROIs of the frogs and backgrounds using a calculator within the MICA toolbox (Troscianko & Stevens, 2015). PED is a value of the absolute difference between the pattern spectra of the two ROIs across all spatial scales. Lower PED values indicate greater pattern

similarity and better background matching.

Statistical analysis

All statistical analyses were performed using R software v.4.3.0 (http://cran.r-project.org). To determine the rate of color change and its effectiveness in improving similarity to background, and to examine whether the rate is influenced by diel variation, we ran a two-way repeated measures ANOVA followed by pairwise comparisons between day and night at each time point using the EMmeans post hoc test with Tukey adjustment. The analyses were performed separately for the light and dark conditions in the first experiment, and for the green and brown backgrounds in the second experiment. In each model, brightness, saturation, hue, or Euclidean distance was used as the dependent variable. Time (hours after the trial began) was used as a within-subject factor because each frog was measured repeatedly at multiple time points, whereas diel phase was a between-subject factor, as each individual was assigned to either the day or night condition.

To determine the behavioral preference for backgrounds and to examine whether the choice is influenced by coloration pattern (green-dominated or brown-dominated) or diel variation, a generalized linear mixed model (GLMM) was performed using a negative binomial function. The dependent variable was the duration of frogs spent on each background during the tests. Background, coloration pattern, diel phase and their interactions were treated as fixed effects, and individual ID was treated as a random effect. To examine whether the locomotor activity within the experimental arena varies with diel variation, a Wilcoxon signed rank test was used to detect the difference in the number of times that frogs crossed the backgrounds between day and night.

To examine whether the degree of background matching at the display site varies in visual perception of different predators, a series of linear mixed models (LMMs) were conducted on color JNDs, luminance JNDs, and PED separately using the lme4 package (Bates et al., 2015) and the lmerTest package (Kuznetsova et al., 2017) was used for obtaining *P*-values. Color JNDs, luminance JNDs, and PED were used as dependent variables separately, and predator viewers were used as independent variables. To test whether males preferentially choose substrates that provide better background matching and whether the preference is influenced by vegetation coverage, an LMM was conducted for each predator vision. In these models, color JNDs, luminance JNDs, and PED were used as dependent variables separately, while the calling site and the density of vegetation (e.g., 1, 2, and 3) around calling males were treated as fixed effects, and individual ID was treated as a random effect.

RESULTS

Color change

Brightness, saturation, and hue of frogs changed over time in both light and dark conditions (Figure 1D, E; Figure 2A). In the light conditions, brightness changed from 1.73% to 17.66% ($F_{5\ 230}$=108.070, P<0.001), hue changed from 0.09 to 0.53 ($F_{5\ 230}$=98.215, P<0.001), whereas saturation changed from 0.71 to 0.35 ($F_{5\ 230}$=110.084, P< 0.001) over time (Figure 2A). In addition, there were significant interaction effects between time and diel phase on these metrics (all P-values<0.05). Specifically, the rate of change was faster during the first half hour of the day than at night and then gradually slowed, while significant diel differences in saturation and hue appeared at 4 hours (Figure 2A). In contrast, in the dark conditions, brightness changed from 18.11% to 5.19% ($F_{5\ 230}$=78.039, P<0.001), hue changed from 0.53 to 0.30 ($F_{5\ 230}$=29.947, P<0.001), whereas saturation changed from 0.34 to 0.58 ($F_{5\ 230}$=55.426, P<0.001) over time (Figure 2A). These metrics changed rapidly within half an hour of trial initiation and showed consistent patterns and rates of change between day and night (Figure 2A).

The Euclidean distance between frogs and substrates changed over time on both green and brown substrates (Figure 1F, G; Figure 2B). Specifically, the Euclidean distance decreased significantly from 0.65 to 0.29 on green substrates ($F_{5\ 230}$=67.478, P<0.001, Figure 2B) and from 0.36 to 0.12 on brown substrates ($F_{5\ 230}$=36.896, P<0.001, Figure 2B). There were no significant interaction effects between time and diel phase on Euclidean distance (all P-values>0.05), although significant diel differences were observed at specific time points (Figure 2B).

Background choice

The initial model revealed no significant interaction effects between background, coloration pattern, and diel phase, and neither coloration pattern nor diel phase had significant effects on background choice (GLMM: all P-values>0.1). Consequently, the final model included only the background as the fixed effect. Frogs spent significantly less time on the white background than on the green (GLMM: z=2.119, P=0.034), brown (GLMM: z=2.238, P=0.025), and black (GLMM: z=3.943, P<0.001) backgrounds during the tests (Figure 2C). There was no significant difference in the time that frogs spent on green, brown, and black backgrounds (GLMM: all P-values>0.05, Figure 2C). The number of times frogs crossed the boundary of areas at night was significantly fewer than that during the day (Wilcoxon signed rank test: V=2580.5, P<0.001, Figure 2C).

Background matching in the field

The color and luminance JNDs between dorsal coloration and the observed substrate showed high values (mostly greater than 3), and the PED showed low values (mostly lower than 0.03) for avian, mammalian, and snake visual models (Figure 3A). There were significant differences in color JNDs and PED among visual models, with the highest values for the avian visual model (LMM: all P-values<0.05, Table 1; Figure 3A). For all visual models, there were no significant effects of substrate or vegetation density on the color JNDs or PED (LMM: all P-values>0.1, Table 2; Figure 3B). In contrast, the luminance JNDs on the observed substrates were significantly lower than those on the alternative substrates (LMM: all P-values<0.05, Table 2; Figure 3B).

DISCUSSION

In the present study, we investigated the ability of color change in the nocturnal anuran species *Kurixalus hainanus* and examined whether and how body coloration contributes to individual camouflage. First, we assessed the rate of color change in light and dark conditions, and our results revealed that the brightness, saturation, and hue changed rapidly during the tests in both conditions. The rate of color change was faster in the dark than in the light, with brightness, saturation, and hue showing larger changes within the first 30 minutes (e.g., brightness changed by 12.2% vs. 4.7%, Figure 2A) and maintaining similar levels for the next 7.5 hours. This is likely associated with their nocturnal lifestyle, as

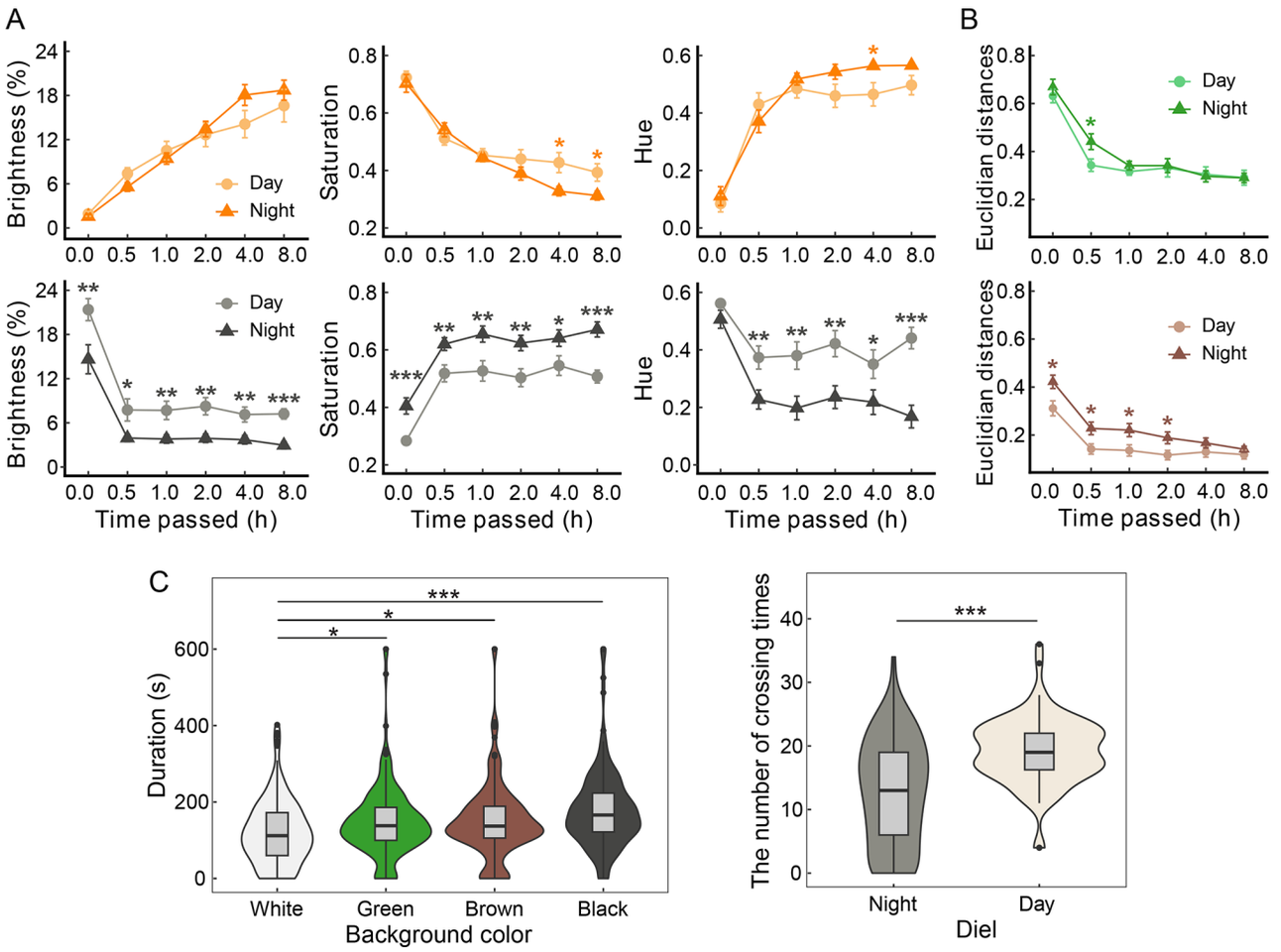

Figure 2 Results of color change and background choice experiments of *Kurixalus hainanus*

A: The change of brightness (%), saturation, and hue of frogs in the light (top) and dark conditions (bottom, *n*=48). B: The change of Euclidean distance between frogs and green (top) and brown (bottom) substrates since the initiation of each trial (*n*=96). Lighter lines indicate that the experiments were conducted during the day, while darker lines indicate that the experiments were conducted at night. Statistical differences between day and night at each corresponding time point were calculated based on EMmeans post hoc test. C: The duration (s) of focal individuals spent on each area during the 10-min choice tests (*n*=78). D: The number of times focal individuals crossed the boundary of areas during the 10-min choice tests (*n*=78). *: P<0.05, **: P<0.01, ***: P<0.001.

individuals are primarily active at night and may have evolved a greater capacity for rapid responses to dark conditions. A similar finding has been reported in the American bullfrog (*Rana catesbeiana*), where skin darkening occurred more rapidly than lightening (Camargo et al., 1999). Camargo et al. (1999) reported that the dispersal of pigment granules is mediated by melanophore-stimulating hormone (α-MSH), and elevated serum levels of this hormone under constant darkness accelerate darkening responses. In contrast, the reversal of α-MSH-induced darkening was only partially achieved by melatonin, and the melanophores showed limited responsiveness to adrenergic signaling due to the lack of active β- and α-adrenoceptors, reflecting a physiological constraint in pigment control mechanisms (Camargo et al., 1999).

Our results also revealed that in the light condition, the rate of change in these metrics was influenced by diel phase, with frogs exhibiting a faster initial response during the day than at night. Such rapid color change in response to light during the day might be beneficial for enhancing survival during crepuscular activity or daytime resting periods. A study with fiddler crab (*Uca panacea*) showed that individuals became darker during the day and lighter at night, even under constant darkness, indicating an endogenous circadian rhythm in color change (Darnell, 2012). We speculate that the faster daytime response observed in *K. hainanus* occurred because the light conditions were aligned with their natural diel phase, potentially synchronizing with the frogs' endogenous rhythms of color change (Filadelfi et al., 2005).

We further evaluated whether color change facilitates the rapid matching of individuals to specific backgrounds. We found that the similarity to background, measured as the Euclidean distance between frogs and substrates, decreased rapidly within half an hour of trial initiation in both green and brown background treatments. This result suggests that *K. hainanus* can enhance their crypsis in heterogeneous habitats in the light conditions by adjusting their coloration to better match the background. A study with Japanese tree frogs (*Hyla japonica*) also demonstrated that individuals changed their coloration within one hour to match the background on which they were placed (Kang et al., 2016). A recent study with Neotropical tree frog (*Pithecopus hypochondrialis*) showed that individuals underwent rapid background-induced color changes under dim conditions, thereby reducing their conspicuousness against green or brown substrates (de Alcantara Viana et al., 2025). Background matching through rapid color change is crucial for daily survival, especially for animals that frequently move between different substrates. For

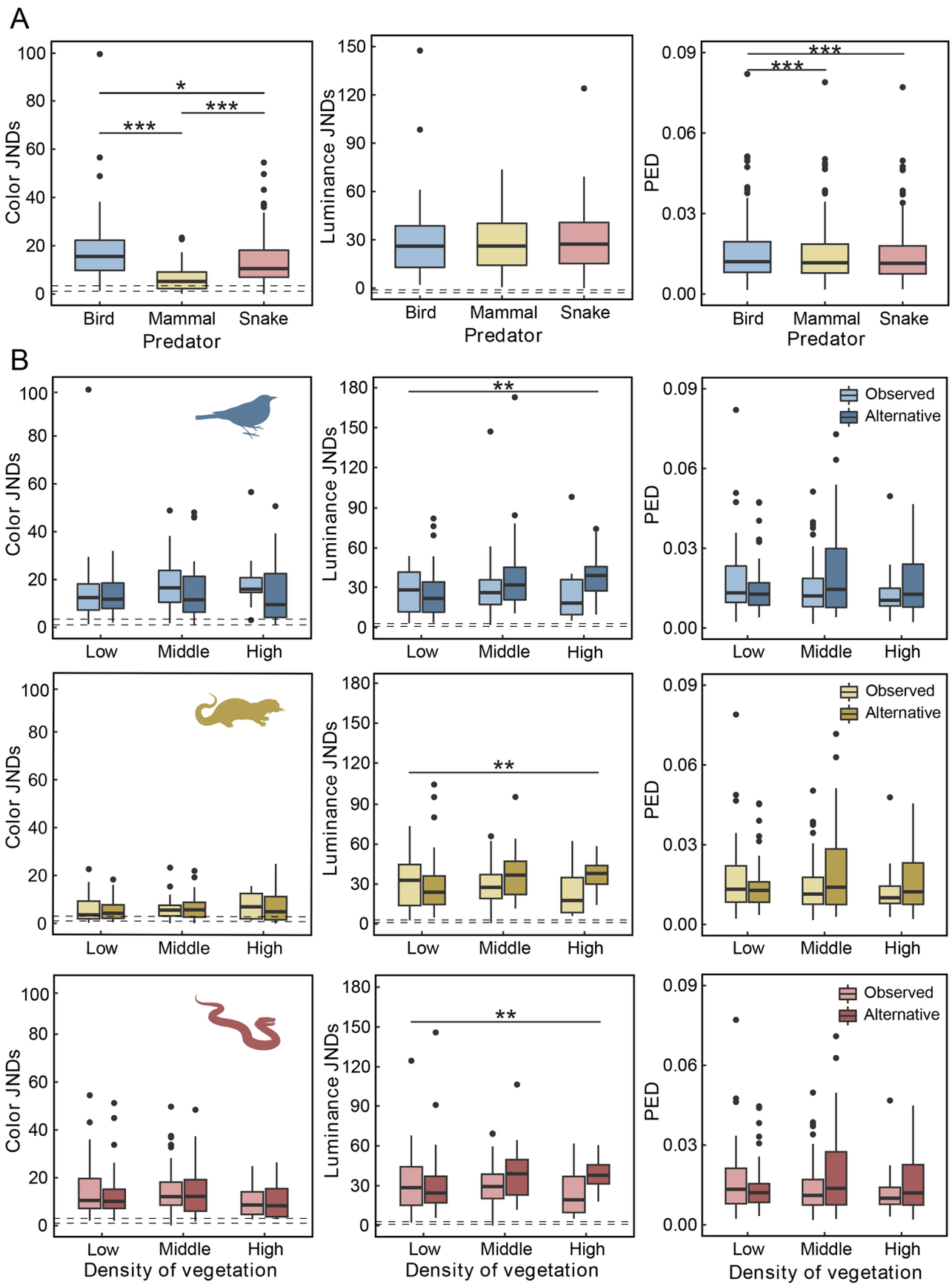

Figure 3 Just noticeable differences (JNDs) and pattern energy difference (PED) for calling *Kurixalus hainanus* on the substrates as modelled under avian, mammalian, and snake visual models (*n*=84)

A: JNDs and PED on the observed substrates. B: JNDs and PED on the observed and alternative substrates. The density of vegetation around calling males is shown on the x-axis. The dashed lines represent the 1-JND and 3-JND discrimination thresholds, respectively. Boxplots show medians, inter-quartile ranges (IQRs), 1.5×IQRs, and black dots represent outliers. *: P<0.05, **: P<0.01, ***: P<0.001.

Table 1 Linear mixed model analysis of the difference in color and luminance just noticeable differences (JNDs) and pattern energy difference (PED) among predator visual models (*n*=84).

Measurements	Factors	Estimate	SE	*t*	*P*
Color JNDs	Intercept	17.454	1.147	15.220	**<0.001**
	Predator | mammal	–10.928	1.519	–7.196	**<0.001**
	Predator | snake	–3.276	1.519	–2.158	**0.032**
Luminance JNDs	Intercept	27.913	2.133	13.081	**<0.001**
	Predator | mammal	0.261	1.486	0.176	0.861
	Predator | snake	2.100	1.486	1.413	0.160
PED	Intercept	0.0164	0.0014	11.370	**<0.001**
	Predator | mammal	–0.0005	0.0001	–6.078	**<0.001**
	Predator | snake	–0.0007	0.0001	–8.426	**<0.001**

The intercept refers to the bird visual model. Significant effects (P<0.05) are shown in bold.

Table 2 Linear mixed model analysis of the effects of substrate and vegetation density on the color and luminance just noticeable differences (JNDs) and pattern energy difference (PED) for avian, mammalian, and snake visual models (*n*=84).

Predator	Measurements	Factors	Estimate	SE	*T*	*P*
Bird	Color JNDs	Intercept	16.553	1.889	8.763	**<0.001**
		Substrate | alternative	–2.700	1.914	–1.411	0.160
		Density | middle	1.162	2.188	0.531	0.596
		Density | high	1.783	2.589	0.689	0.492
	Luminance JNDs	Intercept	24.318	3.879	6.269	**<0.001**
		Substrate | alternative	7.120	2.257	3.155	**0.002**
		Density | middle	6.120	4.987	1.227	0.223
		Density | high	4.301	5.899	0.729	0.467
	PED	Intercept	0.0168	0.0021	7.806	**<0.001**
		Substrate | alternative	0.0022	0.0021	1.012	0.313
		Density | middle	0.0006	0.0025	0.252	0.801
		Density | high	0.0030	0.0029	–1.029	0.305
Mammal	Color JNDs	Intercept	6.208	0.895	6.935	**<0.001**
		Substrate | alternative	–0.121	0.629	–0.193	0.848
		Density | middle	0.238	1.126	0.212	0.833
		Density | high	0.954	1.331	0.717	0.475
	Luminance JNDs	Intercept	27.904	3.054	9.134	**<0.001**
		Substrate | alternative	7.070	2.219	3.186	**0.002**
		Density | middle	1.127	3.824	0.295	0.768
		Density | high	–0.939	4.523	–0.208	0.836
	PED	Intercept	0.0162	0.0020	7.762	**<0.001**
		Substrate | alternative	0.0022	0.0021	1.041	0.299
		Density | middle	0.0007	0.0024	0.288	0.774
		Density | high	–0.0029	0.0028	–1.035	0.302
Snake	Color JNDs	Intercept	14.809	1.854	7.984	**<0.001**
		Substrate | alternative	–0.812	1.089	–0.746	0.458
		Density | middle	0.653	2.382	0.274	0.785
		Density | high	–4.029	2.818	–1.430	0.156
	Luminance JNDs	Intercept	29.793	3.528	8.445	**<0.001**
		Substrate | alternative	6.982	2.176	3.209	**0.001**
		Density | middle	1.310	4.509	0.290	0.772
		Density | high	–1.503	5.334	–0.282	0.778
	PED	Intercept	0.0161	0.0020	7.807	**<0.001**
		Substrate | alternative	0.0021	0.0020	1.008	0.315
		Density | middle	0.0006	0.0023	0.290	0.772
		Density | high	–0.0030	0.0028	–1.070	0.286

The intercept refers to the observed substrate with low vegetation density. Significant effects (P<0.05) are shown in bold.

example, shore crabs (*Carcinus maenas*) can change their brightness within two hours, becoming darker on black and lighter on white backgrounds, which may improve camouflage efficiency and reduce detection by predators (Stevens et al., 2014c). Similarly, rock gobies (*Gobius paganellus*) can adjust their luminance or color within one minute in response to specific backgrounds, leading to significant improvements in the level of background matching (Stevens et al., 2014a).

Although the Euclidean distance between frogs and substrates significantly decreased, we did not observe a

complete change from green to brown or vice versa during the tests. Unlike changes in brightness, color changes (e.g., from green to brown) are more complex and may depend on the combined changes in iridophores, xanthophores, and melanophores (Hoffman & Blouin, 2000). As a result, a change from green to brown in many anuran species typically takes several days or weeks (Choi & Jang, 2014; Wente & Phillips, 2003). In the present study, we focused on color change over a diel cycle, so each frog was kept in an experimental treatment for no more than 12 hours. A complete transition between green and brown in *K. hainanus* may also take several days or even weeks, and its extent and underlying mechanism require further investigation.

Second, we examined whether frogs prefer backgrounds that match their coloration pattern using behavioral choice tests. Contrary to our prediction, neither green-dominated nor brown-dominated individuals prefer backgrounds that matched their coloration patterns in the light conditions. Instead, they spent the least amount of time on the white background, with no significant difference in the time spent on the other three backgrounds, regardless of their color pattern or diel phase. Background preferences at a morph-specific level have been reported in a range of taxa, which enable increased levels of camouflage (Camacho et al., 2020; Isaac & Gregory, 2013). For example, chameleon prawns (*Hippolyte varians*) could accurately choose between green and red seaweed that match their current coloration (Green et al., 2019). Interestingly, there is often asymmetry in background preference for morph-specific choices. Heinze et al. (2022) found that meadow grasshoppers (*Pseudochorthippus parallelus*) in uniform green morphs spent significantly more time on green than on brown patches, but brown morphs did not significantly prefer any background color. Similarly, brown filefish (*Monacanthus chinensis*) significantly preferred brown seagrass to green marine macroalga, while green morphs showed no preference (Gilby et al., 2015). A study with Pacific tree frogs (*Hyla regilla*) showed that both fixed green and brown frogs preferred matching substrates, but the latter was only observed in the presence of predator cues (Wente & Phillips, 2005). These findings suggest that morph-specific choices could be context-dependent or inconsistent among morphs, even in species that change color relatively slowly. In the present study, frogs did not show a preference for either green or brown backgrounds, possibly because the tested individuals had mixed green-brown coloration rather than purely green or brown dorsum. Furthermore, since the rate of achromatic changes is faster than that of chromatic changes, and *K. hainanus* darken more rapidly than they lighten, choosing darker backgrounds facilitates faster crypsis. A similar finding was reported for shore crabs (*Carcinus maenas*), which preferred substrates matching their brightness rather than their color (Twort & Stevens, 2023). In addition, we found that tested frogs crossed area boundaries more often during the day than at night, possibly because they are more sensitive to external disturbance during their resting phase.

Lastly, we evaluated whether the coloration of calling males provides effective camouflage against natural substrates under different predator visual systems. We found that the chromatic and achromatic contrasts between the dorsal coloration of calling males and the observed substrates showed high JND values for avian, mammalian, and snake visual models, indicating poor camouflage in terms of color and luminance at display sites. On one hand, vegetation cover may help reduce the likelihood of detection by predators. On the other hand, male frogs often call from sites that enhance signal transmission or facilitate detection by females (Halfwerk et al., 2017; Lardner & Lakim, 2002), thereby offsetting the cost of poor background matching through potential reproductive benefits (Duarte et al., 2025). In addition, eavesdropping predators may primarily rely on acoustic or chemical cues to detect and locate frog prey (Gomes et al., 2016; He et al., 2023), thereby reducing the selective pressure for visual background matching at night. Although the results revealed that color did not provide effective camouflage for frogs, chromatic contrasts varied across predator visual systems, with the highest values for birds and the lowest for mammals. This pattern may be related to differences in visual physiology among predators. For dichromatic mammals (e.g., ferret), lacking medium-wavelength (green-sensitive) photoreceptors makes it challenging to discriminate frogs from green or brown backgrounds (Calderone & Jacobs, 2003). For birds and snakes possessing these receptors, however, they can perceive stronger chromatic contrasts between frogs and foliage (Troscianko et al., 2017). Conversely, the pattern contrast showed low PED values for all predator models, suggesting that the pattern elements of *K. hainanus* play an important role in visual concealment at night. Similar findings were reported in a study with lichen moth (*Declana atronivea*), which found that only the pattern elements closely matched those of lichen substrates, whereas color or luminance alone does not predict background matching well (Mark et al., 2022).

The achromatic contrasts on the observed substrates were significantly lower than those on the alternative substrates, suggesting that male *K. hainanus* tend to display at sites with better luminance matching, even though predators can still distinguish frogs from backgrounds via the achromatic channel. Some studies have shown that luminance is important for the detection of small objects over long distances and in dim illumination (de Alcantara Viana et al., 2022; Olsson et al., 2018; Potier et al., 2018; Walton & Stevens, 2018). Therefore, minimizing achromatic contrast may be beneficial for species inhabiting open areas such as treefrogs, especially during their nocturnal activities. However, increasing anthropogenic disturbances have substantially altered the natural visual environment, potentially undermining such adaptive strategies (Barnett et al., 2021; Briolat et al., 2021; Duarte et al., 2024). For example, artificial light at night (ALAN) disrupts natural diel cycles of illumination and spectral composition (Knop et al., 2017; Van Doren et al., 2017), which may interfere with circadian regulation of color change and cryptic behavior. In addition, this anthropogenic disturbance may benefit some nocturnal predators while simultaneously increasing the exposure and predation risk of other species, thereby creating novel selective pressures on visual concealment in nocturnal animals (Briolat et al., 2021; Sanders et al., 2021). Consequently, understanding how ALAN reshapes nocturnal visual ecology is essential for interpreting the maintenance of color and pattern diversity and for assessing the adaptive significance of phenotypic plasticity in the Anthropocene.

In contrast, chromatic or pattern contrasts on the observed substrates did not differ significantly from those on the alternative substrates. The natural habitats of *K. hainanus* primarily consist of tree barks, leaves, shrubs, and soil, with backgrounds mostly comprising green and brown tones. The green-brown coloration of *K. hainanus* may reflect a long-term adaptive evolutionary result at the species level, facilitating camouflage in the macrohabitat. Since most individuals exhibit

a mixed green-brown dorsum rather than purely green or brown, future studies could use behavioral tests and visual modelling to investigate whether these pattern elements function as an alternative form of camouflage, such as disruptive coloration. In addition, there were no significant differences in chromatic, achromatic, or pattern contrasts among frogs at sites with varying vegetation densities. Both the dorsum and the grey-white vocal sac of *K. hainanus* reflect a certain amount of UV light, with the vocal sac showing higher overall reflectance than the dorsum (Zhu et al., 2022), making calling males particularly conspicuous to predators. Consequently, male frogs may rely more on vegetation cover rather than on camouflage to reduce the predation risks associated with calling.

CONCLUSIONS

We demonstrate that *K. hainanus* can rapidly adjust the brightness, saturation, and hue of their dorsum in response to varying light conditions. This plasticity allows the frogs to quickly enhance background similarity to green and brown substrates, as measured by Euclidean distance. The rate of darkening was faster than that of lightening, likely associated with their nocturnal lifestyle and physiological constraints in pigment control mechanisms. Frogs did not show a preference for background color but tended to avoid backgrounds with high reflectance. Both color change and locomotor activity in the light condition were influenced by diel variation, suggesting that frogs possess an endogenous circadian rhythm. The calling sites chosen by male frogs did not provide better camouflage in terms of color or luminance; however, males still tended to call from substrates that more closely matched their own luminance. In contrast, pattern elements might play a more crucial role in nocturnal crypsis. The potential alternative camouflage function of the mixed green-brown dorsum requires further investigation.

DATA AVAILABILITY

Data used in this study are available in the electronic supplementary material.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

K.D. and J.G.C. conceived and designed the study. K.D., T.L.W., and J.C.W. arranged the technical equipment. K.D. and Q.L.H. performed the experiments. K.D. analyzed the data, drafted and revised the manuscript. All authors read and approved the final version of the manuscript.

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