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Source: Herpetologica, 71(1) : 1-7

Published By: The Herpetologists' League

URL: https://doi.org/10.1655/HERPETOLOGICA-D-14-00014

HERPETOLOGICA

VOL. 71 MARCH 2015 NO. 1

Herpetologica, 71(1), 2015, 1–7

Ontogenetic Change of Signal Brightness in the Foot-Flagging Frog Species *Staurois parvus* and *Staurois guttatus*

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Abstract: Adult individuals of several anuran species exhibit conspicuous visual displays during intraspecific communication. While signal properties in adults have been subject to an increasing number of studies, little is known about the variation of visual signals in juveniles and during ontogenetic changes. Foot-flagging signals of the Bornean frogs *Staurois guttatus* and *S. parvus* were observed in juveniles a few days after metamorphosis. We investigated color parameters of foot webbings and body coloration of individuals bred at the Vienna Zoo, and their relation to age and body size using spectrophotometry. Our results indicate that the brightness of foot webbings of *S. guttatus* and *S. parvus* increased with increasing age. Additionally, we compared the results with measurements of adult individuals from a population in Brunei and discuss possible differences related to diet and age as well as the habitat use of juveniles and adults. We suggest that the ontogenetic increase in foot-webbing brightness enhances visual conspicuousness and the signal-to-noise ratio of the visual signal with sexual maturity and potentially functions as cue to the age of the signaler.

Key words: Body coloration; Color change; Color signal; Foot webbing; Ranidae; Visual signals

Conspicuous colors, patterns, and patches are common in numerous animal taxa (Bradbury and Vehrencamp 2011). In addition to fixed color patterns, some animals undergo color changes during their lifetime. Ontogenetic change of coloration is generally unidirectional and usually occurs at the onset of sexual maturation of an individual (Hoffman and Blouin 2000; Wente and Phillips 2003; Galan 2008). Hormonal changes are suggested to affect ontogenetic variations in coloration (Richards 1982; Hayes and Menendez 1999; Hoffman and Blouin 2000). In Bocage's Wall Lizards (*Podarcis bocagei*), the onset of maturity can implement an abrupt, nonreversible change of dorsal and ventral coloration in males (Galan 2008). The bright yellow, orange, or blue dewlaps of male Tree Lizards (*Urosaurus ornatus*) are reliable status signals that can develop prior to sexual maturity (Thompson and Moore 1991).

Conspicuous and bright color displays are known to influence female mate choice (Andersson 1982; Milinski and Bakker 1990; Hill 1991) and male–male competition (Krebs and Davies 1993; Hebets and Uetz 2000; Cummings et al. 2008). Hence, visual signals play a prominent role in sexual selection in several animal species. Visual displays are most conspicuous when the contrast of brightness, color, pattern, and movement is enhanced relative to the background (Endler 1992; Hödl and Amézquita 2001; Bradbury and Vehrencamp 2011). Environmental conditions such as ambient light incidence or the structuring of habitats such as the presence or absence of vegetation have a strong impact on the conspicuousness, thus on the transmission and detectability of a visual signal (Endler 1992; Peters 2008). To avoid predator detection, colorful signals of short duration, simple form, and/or signaling during favorable light periods maximize intraspecific communication (Endler 1991, 1992; Harper 1991). For example, male Blue-black Grassquits (*Volatinia jacarina*) adjust their timing of their acoustic and plumage displays to sunlight incidence to maximize detectability and minimize energetic costs (Sicsú et al. 2013).

Although anuran signals are primarily associated with acoustic cues for intraspecific communication (Gerhardt and Huber 2002), several species also use visual or multimodal displays for communication (Hödl and Amézquita 2001; Narins et al. 2003; Rosenthal et al. 2004; Hirschmann and Hödl 2006; Grafe and Wanger 2007; Preininger et al. 2009; Starnberger et al. 2014a). Detection and discrimination of a sender is enhanced by conspicuous visual display such as an inflated vocal sac in anurans (Narins et al. 2003; Rosenthal et al. 2004; Hirschmann and Hödl 2006; Taylor et al. 2011; Starnberger et al., 2014b).

Many anuran species exhibit striking body patterns and colorations. Variations among hue and patterns are represented within species and/or across sexes (reviewed in Hoffman and Blouin 2000; Bell and Zamudio 2012). Several studies have focused on the conspicuously colored family of dendrobatids and provided valuable information on the collective evolution of coloration and toxicity (Summers and Clough 2001; Summers et al. 2003). Apart from aposematism, however, little is known about the function of color signals in other frog species. Numerous anurans undergo distinct changes in body coloration from juvenile to the adult morph (Hoffman and Blouin 2000). Transformation from a green to a brown body coloration seems to be a common transition in anurans (Duellman and Ruiz-Carranza 1986; Hoffman and Blouin 2000), while some anuran species show a striking reversible dichromatism during the mating season

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(Bell and Zamudio 2012). In Moor Frogs (*Rana arvalis*), the dynamic nuptial blue coloration in males is suggested to be a visual signal that promotes mate recognition (Ries et al. 2008; Sztatecsny et al. 2010, 2012). Reports of visual displays that incorporate color signals in anurans have increased during the last decade (Hödl and Amézquita 2001; Bell and Zamudio 2012). Investigations of ontogenetic and dynamic color variation broaden our understanding of visual and multimodal communication systems.

The Bornean foot-flagging frogs *Staurois parvus* and *S. guttatus* are model organisms to analyze differences in color change of foot webbings and body coloration. Investigations of the closely related species allow for a more general prediction regarding signal design. The diurnal and predominantly stream-dwelling species exhibit foot-flagging behavior in which legs are extended and rotated, and brightly colored foot-webbings are displayed for a short period during male–male agonistic interactions (Grafe and Wanger 2007; Grafe et al. 2012). The interdigital webbings of adult individuals of *S. parvus* and *S. guttatus* are colored bright white and bluish, respectively, and pose a strong contrast to the dark coloration of the bodies. Males of *S. parvus* perch on black shale rocks close to the waterline, whereas males of *S. guttatus* display on branches and vegetation along waterfalls (Grafe and Wanger 2007; Grafe et al. 2012) and are well camouflaged in their respective habitat. Foot-flagging behavior occurs in male and female individuals of both species (Grafe and Wanger 2007; Preininger et al. 2012).

The visual display can be performed by juvenile *S. parvus*, even though the foot webbings at this life stage do not exhibit the coloration typical of adults. (Instead, the plantar surface is light gray.) Only a few observations exist of juvenile individuals in the field, and detailed investigations on the behavior of foot-flagging frogs at this life stage are lacking. The first-ever successful breeding of *Staurois* spp. in captivity at the Vienna Zoo (Preininger et al. 2012) has provided the opportunity to describe visual signaling behavior in juvenile frogs. Breeding efforts at the Vienna Zoo also allow us to investigate the differences in web and body coloration at different age classes, starting immediately after metamorphosis.

In the course of this study, we quantified the variation of color parameters of foot webbings and body coloration of different age classes in *S. parvus* and *S. guttatus* by the means of spectrophotometry. Additionally, we compared previous color measurements of an adult wild population from Brunei and discuss color variation in relation to diet, signaling behavior, and habitat.

Materials and Methods

Study Site and Species

The study was conducted in a bio-secure container facility of the Vienna Zoo from November 2012 to February 2013. The Vienna Zoo has successfully established a breeding program for the species *S. guttatus* and *S. parvus* from individuals collected in the Ulu Temburong National Park, Brunei Darussalam in Borneo, in 2010. Several generations of juveniles are housed in separate aquaria equipped with plants, tree branches, and a water pump. Juveniles of both study species were supplied with *Drosophila* sp. and *Collembola* sp. Prior to metamorphosis, larvae were fed algae tablets, fish food flakes, and fish slices (for details see Preininger et al. 2012).

In nature, *S. parvus* and *S. guttatus* live in sympatry along fast-flowing streams, where males display during agonistic encounters (Grafe and Wanger 2007; Grafe et al. 2012). Foot-web coloration of adult *S. parvus* and *S. guttatus* appears bright white and light blue, respectively, and poses a contrast to the darker body coloration in both species, as well as to the surrounding darker background. We observed foot-flagging displays in freshly metamorphosed juveniles. Foot-webbing coloration at early life stages appears translucent gray.

Frog Sampling and Reflectance Measurements

At the beginning of the study, we separated 30 recently metamorphosed individuals of each study species from their breeding terraria and housed them in smaller enclosures (50 × 60 × 70 cm). Older age classes were obtained from previously separated individuals—the species were first bred successfully in October 2011 (*S. parvus*) and March 2012 (*S. guttatus*). We performed monthly reflection measurements of recently metamorphosed juveniles and additional measurements of individuals of older age classes to obtain reflectance data over a period of 12 mo for *S. parvus* and 7 mo for *S. guttatus*. Metamorphosis was taken as reference point for classification of age.

Reflectance spectra of foot webbings and the dorsal surfaces of juveniles of both study species were obtained with a spectrometer (JAZ series; Ocean Optics, Dunedin, FL, USA) between 300 and 700 nm, the spectral range of ultraviolet (UV) and visible light (Zuk and Deruyenaere 1994; Cuthill et al. 1999; Grill and Rush 2000; Ries et al. 2008). The spectrometer had an integrated pulsed xenon light source (Jaz-PX) with a spectral response of 190–1100 nm. The reflectance data were collected for 300–700 nm and expressed in percentage of reflectance relative to a white standard (WS-1 Diffuse Reflectance Standard, Ocean Optics). We used a custom-made probe holder to keep the reflection probe at a distance of 5 mm and an angle of 45° to the frog's skin surface in order to reduce specular reflection. The probe holder touched the frog skin, preventing stray light from entering. Three reflectance measurements per individual were averaged.

All reflection measurements were taken on handheld, nonanesthetized frogs immediately after taking them out of the terraria to shorten handling time and disturbance. We took reflectance scans on two body parts: the skin on the frog's dorsum as a proxy of the frog's general body coloration and the foot webbing of the right hind foot. As foot webbings at early life stages appeared translucent, black rubber gloves were worn to avoid light reflection from the human skin. We measured snout–vent length (SVL; ±0.1 mm) and body mass (±0.1 g) of each individual.

We also compared our measurements with previous data collected in January to March 2010 from the adult wild population living along the Sungai Mata Ikan, a small freshwater stream that merges into the Belalong River close to the Kuala Belalong Field Studies Centre (4°33′N, 115°09′E; datum = WGS84) in the Ulu Temburong National Park (Preininger et al. 2013). Reflectance measurements of the wild population were conducted in the

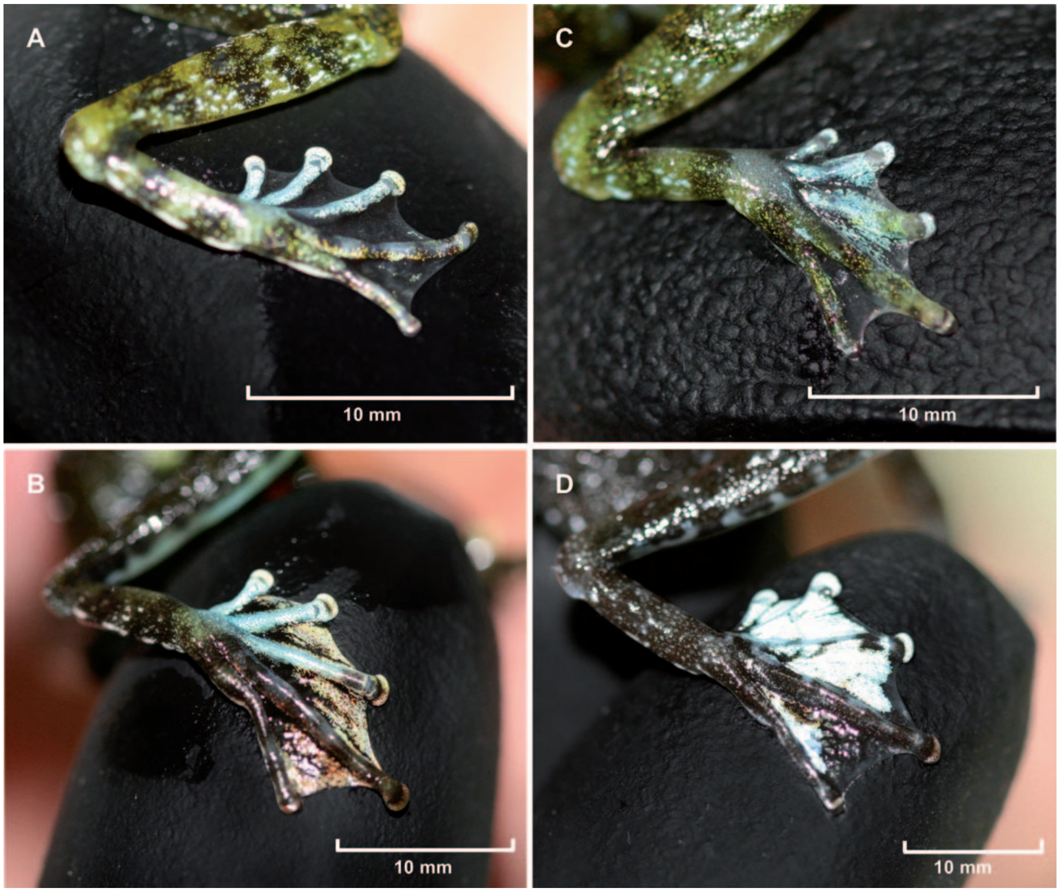

FIG. 1.—Foot webbings of *Staurois guttatus* (A,B) and *S. parvus* (C,D) at an age of 1 mo (A,C), 7 mo (B), and 12 mo (D).

same manner as measurements carried out in the zoo. Given that no correct age classification could be obtained from the Brunei cohort, only basic comparisons were analyzed.

Spectral Data and Statistical Analysis

For each frog, three parameters of coloration were extracted from the reflectance spectra using Avicol software v6 (Gomez 2006): brightness, hue, and UV blue chroma. Brightness corresponds to the total reflectance, calculated as the surface area under the spectral curve. Hue corresponds to the notion of color and we calculated it as the wavelength of the maximum slope (Endler 1990) because the reflectance spectra of our study species lacked distinct peaks at specific wavelengths. UV blue chroma corresponds to color saturation, calculated as the proportion of the total reflectance located between 300 and 450 nm: (R300 nm − R450 nm)/(R300 nm − R700 nm).

To test for ontogenetic differences in color parameters we compared the first measurements (age cohort 1 mo) with the last measured age class (*S. guttatus*: 7 mo; *S. parvus*: 12 mo) using Mann–Whitney *U* tests. The parameter brightness was chosen for further statistical analyses to characterize coloration.

Total brightness of different age classes, body sizes, and body masses were compared, using linear mixed models (LMM). The LMM allows repeated measurements of the same individual to be fitted in the model as random variables, thus controlling for measurements of the same individuals in differing age classes. The statistical assumptions for LMM analysis were met (Kolmogorov–Smirnov test) and nonnormal data were square-root transformed to meet the criteria. To test if foot and back brightness are dependent on age, body size, or body mass of *S. parvus* and *S. guttatus,* six models were run. Square-root transformed brightness values of foot or back of the respective species were entered as dependent variables, with age, body size, or body weight as predictor variables. The identity of individuals was entered as a random variable.

To test for differences of body size and body mass between individuals of an adult wild cohort and the oldest measured age class of the zoo cohort (*S. guttatus* = 7 mo, *S. parvus* = 12 mo) we used Mann–Whitney *U* tests. All analyses were run using SPSS v19 (SPSS Inc., Chicago, IL, USA).

RESULTS

Foot coloration of *S. guttatus* and *S. parvus* changed during ontogeny (Fig. 1). Measurements of color variables at 1 mo in both species compared to 7 mo later in *S. guttatus*, and 12 mo later in *S. parvus*, show that foot colorations differ in intensity or brightness (Table 1; Figs. 2A,B). We found no differences in hue or UV blue chroma for foot colorations (Table 1). The body coloration of both species was green after metamorphosis and changed to a light brown dorsal coloration in *S. guttatus*, and overall dark gray coloration in *S. parvus* (Figs. 2C,D).

In *S. guttatus*, the total brightness of foot webbings and back coloration increased with age (Foot: LMM pairwise

TABLE 1.—Median values ± SE of color variables of foot and back measurements in captive-bred *Staurois guttatus* and *S. parvus*.[a]

Species / Age (mo)	Total brightness (300–700 nm)	Z / *P*	Hue (nm)	Z / *P*	UV blue chroma ($300–450^{-1}$)	Z / *P*
Staurois guttatus						
Foot						
1 (*n* = 20)	913 ± 76	400	414 ± 9.2	163	0.21 ± 0.02	204
7 (*n* = 20)	3353 ± 300	**<0.001**	411 ± 4.6	0.314	0.23 ± 0.01	0.914
Back						
1 (*n* = 20)	401 ± 53	359	513 ± 0.7	146	0.00 ± 0.02	397
7 (*n* = 20)	854 ± 74	**<0.001**	504.5 ± 31.4	0.143	0.25 ± 0.01	**<0.001**
Staurois parvus						
Foot						
1 (*n* = 20)	580 ± 96	280	414 ± 15.8	91	0.20 ± 0.03	189
12 (*n* = 14)	6227 ± 794	**<0.001**	331.5 ± 10.6	0.086	0.26 ± 0.01	0.086
Back						
1 (*n* = 20)	350 ± 4	107	513 ± 10.1	110	0.00 ± 0.01	187
12 (*n* = 14)	88 ± 74	0.248	494.5 ± 26.6	0.292	0.03 ± 0.04	0.065

[a] Z, Mann–Whitney *U*-statistic for comparison between age classes; *P*, significance level; *n*, sample size; values in bold indicate significant differences at $P \leq 0.05$.

comparison, ß = 5.16, SE = 0.47, t = 11.00, $P \leq 0.001$; Back: LMM pairwise comparison, ß = 1.17, SE = 0.33, t = 3.57, $P \leq 0.001$; Fig. 3).

In *S. parvus*, webbing brightness increased with age (LMM pairwise comparison: ß = 4.88, SE = 0.33, t = 14.70, $P \leq 0.001$), whereas no differences in back brightness between age classes were found (LMM pairwise comparison, ß = −0.23, SE = 0.15, t = −1.478, P = 0.14; Fig. 3). Additionally, in both species, foot brightness increased with SVL (LMM pairwise comparison: *S. guttatus,* ß = 114.33, SE = 11.50, t = 9.94, $P \leq 0.001$; *S. parvus,* ß = 190.44, SE = 14.40, t = 13.23, $P \leq 0.001$; Fig. 4) and mass (LMM pairwise comparison: *S. guttatus*, ß = 32.29, SE = 3.90, t = 8.27, $P \leq 0.001$; *S. parvus,* ß = 59.87, SE = 4.84, t = 12.36, $P \leq 0.001$).

The mean reflectance of foot webbings of adult individuals of a wild cohort (26.6 ± 1.7%, n = 13) compared to the oldest individuals of *S. guttatus* (7 mo: 9.5 ± 0.8%, n = 14) measured in the zoo was three times higher (Fig. 5A). Body size (Z = 0.000, $P \leq 0.001$) and body mass (Z = 0.000, $P \leq 0.001$) of the 7-mo-old age class were both smaller than in the wild cohort of frogs.

The foot webbings of an adult cohort of *S. parvus* (31.3% ± 1.9, n = 13) reflected twice as much light than those of 12-mo-old individuals (14.9 ± 2.0, n = 20) of the study cohort (Fig. 5B). No differences in body size (Z = 119.5, P = 0.15) and body mass (Z = 90, P = 0.96) were found among the wild and the captive individuals of *S. parvus*.

DISCUSSION

Our results show that the coloration of foot webbings of *S. guttatus* and *S. parvus* changes with age. We found that brightness is the parameter that most impacts the change of coloration of foot webbings of both study species.

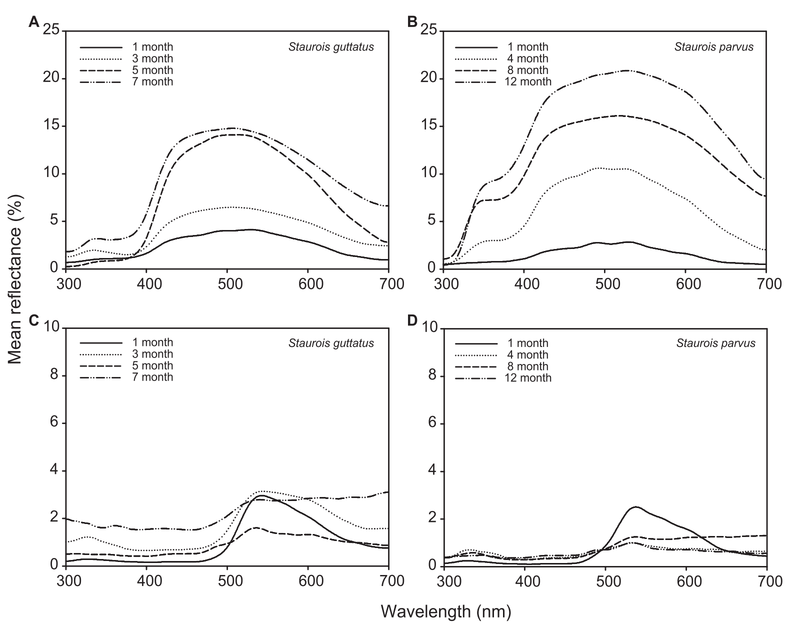

FIG. 2.—Mean reflectance of *Staurois guttatus* (A,C) and *S. parvus* (B,D) at different age classes. Foot reflectance (A,B); back reflectance (C,D; note different scales of y-axis). *Staurois guttatus*: (n = 20) for all age classes; *S. parvus*: 1 mo (n = 20), 4 mo (n = 12), 8 mo (n = 19), 12 mo (n = 14).

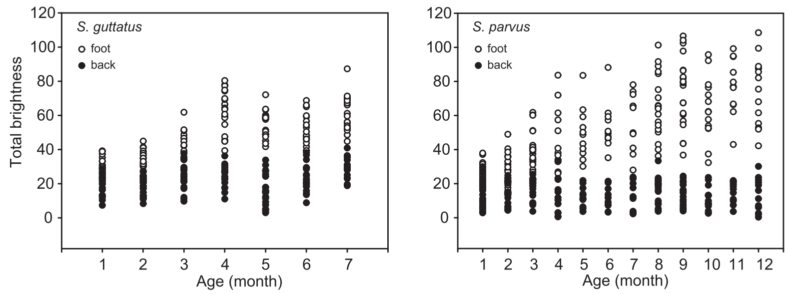

FIG. 3.—Scatterplots of foot and back brightness of measured age classes of *Staurois guttatus* and *S. parvus*. Plotted values are raw data from each individual and do not correspond directly with the statistical results.

The interdigital webbings of recently metamorphosed frogs are colored translucent gray. The body coloration of both species at early life stages is bright green. Juveniles were observed in mossy areas close to the stream (T. Wampula, personal observation). Considering that individuals already display foot-flagging signals at early life stages, we suggest that the green body coloration and inconspicuous web coloration could camouflage juveniles and reduce predation risk in mossy habitats. Similarly, Green Tree Pythons (*Morelia viridis*) undergo an ontogenetic change from a yellow or red morph to a green phenotype to camouflage in different habitats used by juveniles and adults (Wilson et al. 2007).

Directional ontogenetic color change of body coloration has been observed in at least 39 anuran species (Hoffman and Blouin 2000). In most species, hormonal changes were suggested to control age-related color variation (Richards 1982; Hayes and Menendez 1999; Hoffman and Blouin 2000). We suggest that the ontogenetic increase in foot-webbing brightness enhances signal conspicuousness at sexual maturity, and most likely reflects increased androgen levels. During the mating season, males of both species signal the readiness to defend perching sites via visual displays. We propose that foot-flagging displays signal the motivation to defend a signaling site, especially in an agonistic male–male interaction (Preininger et al. 2013). The increase in signal brightness of foot webbings from juvenile to adult leads to an enhanced visual signal-to-noise ratio in the ambient habitat. Additionally, increased signal brightness suggests the following visibility-enhancing strategies in both of the studied species: (1) maximizing contrast to the overall body coloration, (2) maximizing contrast to the environmental background, and (3) increasing conspicuousness, as a movement contrast through the dynamic foot-flagging display appears to increase conspicuousness (sensu Endler 1992; Bradbury and Vehrencamp 2011).

The differences of web brightness between the oldest individuals measured in the Vienna Zoo and the wild cohort could derive from differences of diet or food availability of the respective populations. In some anurans, a diet fortified with carotenoids seems to have a strong impact on development and growth, but also on reproductive success and coloration of adult individuals (Ogilvy et al. 2012). For instance, the coloration of the red ventral patch of *Bombina orientalis* is dependent on the supply of pigments in food and a lack of these carotenes under rearing conditions leads to a yellowish coloration (Steinicke 1976; Frost and Robinson 1984). Likewise, the Japanese newt *Cynops pyrrhogaster* shows yellow ventral skin when lab-reared and undersupplied with pigment substances (Matsui et al. 2002). *Staurois parvus* and *S. guttatus* were offered a diet that is similar to that observed in the adult wild cohort (Preininger et al. 2012); direct observations of food intake were rare, however, and no reports on the diet of tadpoles are available.

The signal intensity might be a cue to the age and/or mating activity of the signaler, thus indicating the hormonal status of an individual and thereby influencing conspecific receivers during agonistic interaction. Because brightness not only increased with age, but also with body size and mass in this study, we suggest that morphometric changes could be a byproduct of the simultaneous ontogenetic changes. The comparisons of body size and mass between 12-mo-old individuals of *S. parvus* and the wild cohort showed no differences, whereas foot brightness doubled. We have no record of the actual age of the wild cohort, however, and the proposed relationship between age and brightness in individuals older than 12 mo remains speculative.

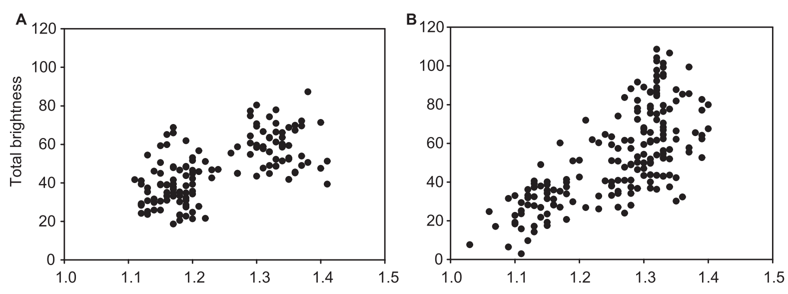

FIG. 4.—Scatterplots of foot brightness and log snout–vent length of *Staurois guttatus* (A) and *S. parvus* (B). Plotted values are raw data from each individual and do not correspond directly with the statistical results.

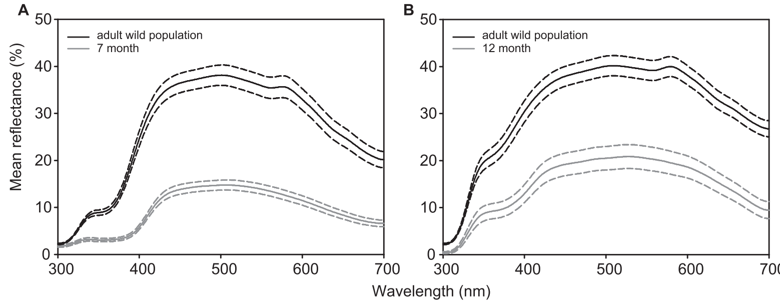

Fig. 5.—Mean reflectance of foot webbings of *Staurois guttatus* (A) and *S. parvus* (B) of the last age class measured in the Vienna Zoo, and of adults measured in their natural habitat (Ulu Temburong National Park, Borneo). Dashed lines below and above solid lines indicate ±1 SE. *Staurois guttatus*: 7 mo ($n = 20$), adult ($n = 13$); *S. parvus*: 12 mo ($n = 14$), adult ($n = 13$).

Future investigations on age-related color change in *Staurois* spp. should clarify if foot-webbing brightness is further enhanced with increasing age, or differs between individuals held in breeding arenas with regular mating activity and other enclosures where no breeding takes place. Investigations of signal behavior and structure of foot-flagging displays at different life stages will further contribute to understanding the function and development of visual signals and multimodal communication. Zoo-based research and conservation breeding programs focusing on amphibians have resulted in increased conservation efforts for many threatened species (Browne et al. 2011). Several frog species in Southeast Asia are restricted to riparian habitats and show morphological and behavioral adaptations to torrential streams and waterfalls (Arch et al. 2008; Haas and Das 2012). Few stream-dwelling Bornean species are able to survive in habitats modified for human use (Inger and Stuebing 2005). Information on natural history, reproduction modes, behavior and habitat-specific adaptations of anurans is important to identify and protect key habitats in the wild.

Acknowledgments.—We thank the Vienna Zoo and director D. Schratter for the productive cooperation. We are grateful for the dedication and support of A. Weissenbacher, T. Wampula, R. Riegler, E. Karell, and all zookeepers that were involved in this project. We thank two anonymous reviewers for their valuable suggestions on this article. The study was supported by the Austrian Science Fund (FWF): P22069 and P25612, the Society of Friends of the Vienna Zoo, and the University of Vienna.

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Accepted on 24 September 2014
Associate Editor: Ryan Taylor