



## **Variation in Display Behavior, Ornament Morphology, Sexual Size Dimorphism, and Habitat Structure in the Fan-Throated Lizard (Sitana, Agamidae)**

Author: Kamath, Ambika

Source: Journal of Herpetology, 50(3) : 394-403

Published By: Society for the Study of Amphibians and Reptiles

URL: <https://doi.org/10.1670/15-040>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## Variation in Display Behavior, Ornament Morphology, Sexual Size Dimorphism, and Habitat Structure in the Fan-Throated Lizard (*Sitana*, Agamidae)

AMBIKA KAMATH

Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts USA; E-mail: ambikamath@gmail.com

**ABSTRACT.**—Fan-Throated Lizards (*Sitana*; Agamidae) are a widespread yet little-studied genus of lizards found in dry habitats throughout South Asia. Male lizards in this genus bear a fan-like structure under their throats that is displayed by rapid extension and retraction during the breeding season, particularly during courtship and male–male interactions. Throat-fans vary dramatically in both size and coloration across the genus, ranging from small and white to large and blue, black, and orange. In this paper, I investigate variation in throat-fan morphology and display behavior in eight populations of Fan-Throated Lizards. Displays of these lizards included partial and complete throat-fan extensions, changes in body position, rapid head-turning behavior, and occasional bipedality. Part of the variation in display behavior across these lizards was associated with throat-fan elaboration, and increased throat-fan size and coloration were associated with male-biased sexual size dimorphism but not with changes in habitat. These results suggest that sexual selection may underlie increases in both throat-fan size and coloration in the genus *Sitana*. Therefore, Fan-Throated Lizards are a promising system in which to further investigate the coevolution of different display components of a striking visual signal.

The evolution of colorful ornaments displayed by animals during courtship and agonistic interactions has long been of interest to behavioral ecologists. Indeed, the theory of sexual selection was proposed to explain the presence of conspicuous and costly ornaments that are almost certainly detrimental to survival (Darwin, 1871; Andersson, 1994). Many factors other than sexual selection, however, also can play a role in shaping ornament morphology, including the environmental contexts in which ornaments are displayed (Endler, 1992; Seehausen et al., 1997; Bro-Jørgensen, 2009) and the physiological and biomechanical constraints that limit or direct ornament elaboration (Podos, 2001; Irschick et al., 2007; Rosenthal, 2007). Ornaments also are often deployed as part of complex multicomponent and multimodal displays, and all of the above factors can influence the relationships between different display components and modalities (Hebets and Papaj, 2005; Bradbury and Vehrencamp, 2011). This multitude of interacting forces that drive ornament evolution offers a number of starting points from which to begin investigating the origin and maintenance of ornament variation in understudied taxa. In this paper I explore some behavioral, environmental, and morphological correlates of ornament variation in Fan-Throated Lizards (*Sitana*, Agamidae), a widespread yet little-studied genus from South Asia.

Showy ornaments, including fans, frills, and horns, are often central to lizard displays, though many species also incorporate movement, changes in body coloration, chemical cues, and even sound (e.g., Marcellini, 1977; Duvall, 1979; Cooper and Greenberg, 1992; Fleishman, 1992). Each of the factors that drive display evolution has played an important role in shaping the evolution of lizard ornamentation. For example, sexual selection, especially male–male competition, is thought to have driven the evolution of male ornaments and colors in both agamid and lacertid lizards such that species with more intense sexual selection show more elaborate ornamentation (Stuart-Fox and Ord, 2004; Chen et al., 2012; Perez i de Lanuza et al., 2013). Habitat structure and the visual environment affect both color and motion signals in *Anolis* lizards, as well as ultraviolet color signals in *Bradypodion* chameleons, with signals varying such that they are maximally conspicuous in the habitat in which

they occur (Leal and Fleishman, 2002, 2004; Ord et al., 2007; Stuart-Fox et al., 2007; Ng et al., 2013). Conversely, conspicuousness also may be selected against in habitats where lizards suffer high rates of predation (e.g., in *Ctenophorus* lizards [Stuart-Fox et al., 2003] and *Crotaphytus* lizards [Husak et al., 2008]), leading to geographic variation in coloration that corresponds to variation in predation risk (McLean et al., 2014). Finally, anatomical and biomechanical constraints affect variation in motion signaling between closely related species of anoles (Ord et al., 2013). Variation across lizard taxa, in not only the ornaments themselves but also in the proximate and ultimate causes for ornament diversification, makes lizards an interesting group in which to examine ornament evolution.

Fan-Throated Lizards, belonging to the South Asian agamid genus *Sitana*, are a promising taxon in which to investigate the patterns and processes of visual display diversification. These lizards are named for fan-like structures, also known as “dewlaps,” that are borne under the throats of males. The throat-fan is displayed by rapid extension and retraction during the breeding season, particularly during courtship and male–male interactions (Kratzer, 1980; Kästle, 1998; Patankar et al., 2013). These lizards’ ornamentation drew the attention of Darwin who, in his treatise on the evolution of secondary sexual characters, described them thus: “the males alone are furnished with a large throat-pouch, which can be folded up like a fan, and is colored blue, black, and red. . . The female does not possess even a rudiment of this appendage” (Darwin, 1871:33). Though Darwin was correct about the sexual dimorphism of their ornamentation (Kratzer, 1980; Pal et al., 2011), he appeared unaware that male *Sitana* vary substantially in the size and coloration of their throat-fan (Fig. 1). While males with the large blue, black, and orange throat-fans described by Darwin (“colored-fan variant”) are found predominantly in western peninsular India, males in most of the remainder of the range of this genus have smaller white throat-fans with blue margins (“white-fan variant”), except for southern peninsular India and Sri Lanka where males have intermediately colored throat-fans (“intermediate-fan variant”).

Despite their ubiquity in dry grassland, thorn-scrub, and coastal habitats across South Asia, Fan-Throated Lizards remain very poorly studied—species delimitations and phylogenetic

DOI: 10.1670/15-040

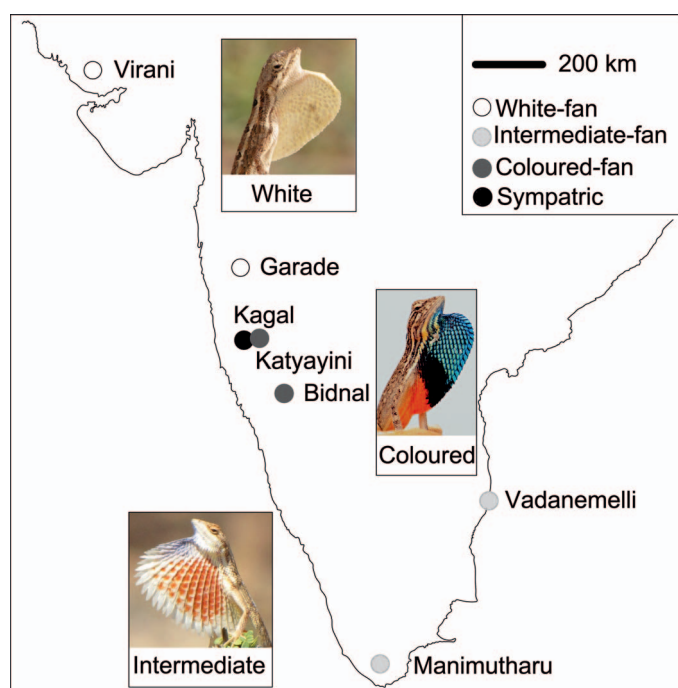


FIG. 1. Locations of sites sampled in this study in India with representative photographs of male throat-fans from a white-fan population (Virani), colored-fan population (Katyayini; photograph by Varad Giri), and intermediate-fan population (Manimutharu). The sympatric site included lizards of both the white-fan and the colored-fan variants.

relationships of species within the genus are currently being determined (Amarasinghe et al. 2015; Deepak and Karanth, pers. comm.), and their ornamentation and display behavior has received very little attention (but see Kästle, 1998; Patankar et al., 2013). In this paper, I first investigate variation in ornament morphology and display behavior in Fan-Throated Lizards, asking if lizards with morphologically different throat-fans deploy these ornaments using different display behaviors. Next, I examine variation in male body size, sexual size dimorphism (SSD), and habitat openness across populations of Fan-Throated Lizards with morphologically different throat-fans. These comparisons provide a starting point for future investigations into the role of sexual selection and environmental context in the origin and maintenance of variation in ornament morphology in these lizards.

#### MATERIALS AND METHODS

**Study Sites.**—I determined localities for the three throat-fan variants by contacting ecologists and naturalists across India through the Young Ecologists Talk and Interact listserv as well as from georeferenced photographs of Fan-Throated Lizards on the India Nature Watch website ([www.indianaturewatch.net](http://www.indianaturewatch.net)). I sampled from seven sites, two each of the white-fan, intermediate-fan, and colored-fan variants, as well as one site, Kagal, in which the white-fan and colored-fan variants were sympatric (Fig. 1). Preliminary data on the phylogenetics of *Sitana* suggest that the throat-fan variants belong to different clades (Deepak and Karanth, pers. comm.) and do not interbreed, though species demarcations have yet to be determined. Moreover, both males and females of the white-fan and colored-fan variants can be distinguished from one another on the basis of head shape and

patterning (AK, pers. obs.; Fig. S1). Therefore, the sympatric white-fan and colored-fan variants at Kagal were considered distinct populations (KagW and KagC), amounting to a total of eight sampled populations. Also, throat-fan size and coloration differed substantially between the two intermediate-fan populations (Vadanemelli [Vad] in northern Tamil Nadu, and Manimutharu [Man] in southern Tamil Nadu), despite their geographic proximity (see Fig. 1 and Results; see also Amarasinghe et al. [2015], who documented substantially different throat-fan coloration in the intermediate-fan variant in Sri Lanka). Therefore, I completed pairwise comparisons for behavioral and morphological variables of these two intermediate-fan populations. Sites were outside of protected areas, in habitats ranging from fallow agricultural fields and grazing fields to thorn scrub vegetation. I sampled sites during the lizards' breeding season in 2012 and 2013, prior to the arrival of the monsoon rains (i.e., between April and June before the south-west monsoon in white-fan and colored-fan populations in Karnataka, Maharashtra, and Gujarat and between September and October before the north-east monsoon in the intermediate-fan populations in Tamil Nadu).

**Display Behavior.**—Using a Canon Vixia HF S21HD Camcorder, I recorded display behavior of individual lizards I opportunistically encountered while walking slowly through the environment (Rand, 1964). Individuals were identified as males by the presence of 1) a throat-fan, 2) blue coloration on the first diamond below the head on the dorsum, or 3) blue coloration on the throat, depending on the population. Undisturbed males were observed from a distance of approximately 10 m for up to 30 min or as long as the lizard remained in sight (mean  $\pm$  SD length of observation per individual:  $20.8 \pm 12.4$  min).

Video observations of displays in the field were analyzed frame-by-frame to quantify display behavior. Each display included one or more extensions of the throat-fan; extensions separated by 10 sec or more were counted as separate displays whereas extensions separated by less than 10 sec were counted as part of the same display. For each individual, I measured the proportion of time the individual spent displaying and the number of displays performed per unit time observed. The following variables were measured and averaged by individual for each display: 1) total duration in seconds of the display from the beginning of the first throat-fan extension to the end of the last throat-fan extension, 2) number of partial and complete throat-fan extensions, 3) number of linked throat-fan extensions (i.e., an extension of the throat-fan following an incomplete retraction of an already extended throat-fan comprised two linked extensions), 4) number of turns to the left or right, and 5) number of changes in body position (i.e., up or down movements) or changes in the angle between the lizard's body and the substrate (Table 1). Additionally, I scored as a 1 or 0 the presence or absence of the following display modifiers (Jenssen, 1977) for each display: raised nuchal crest, raised dorsal crest, bipedality, and raised tail (Fig. 2); scores were averaged by individual.

**Morphology.**—After concluding the observation, I attempted to capture the lizard using standard noosing techniques; males disturbed by my presence and all females were caught immediately after they were spotted; I captured 86% of these spotted lizards. I recorded snout-vent length (SVL) of all individuals as a measure of body-size; additionally, for males I assessed throat-fan area by photographing the extended throat-fan. A metric scale was included in each photograph, and the outline of the throat-fan was traced in the program ImageJ (Schneider et al., 2012) to measure throat-fan area. For males from all populations except Vadanemelli, I used an Ocean Optics

TABLE 1. Loadings of 12 behavioral variables on principal component 1.

Variable	Variable description	PC1 loading
Mean display duration (sec)	The duration of a display was defined as the length in seconds from the beginning of the first throat-fan extension to the end of the last extension. Throat-fan extensions separated by >10 sec were considered to belong to separate displays	-0.47
Proportion of time spent displaying	Sum of all display durations divided by the total time the individual was observed	0.32
Number of displays per unit time observed	Total number of displays (as defined above) divided by the total time the individual was observed	0.25
Number of partial throat-fan extensions	Partial throat-fan extensions were defined as extensions in which the angle between the top margin of the throat-fan and the bottom of the lizard's jaw was >90°; see Figure 2	-0.37
Number of complete throat-fan extensions	Complete throat-fan extensions were defined as extensions in which the angle between the top margin of the throat-fan and the bottom of the lizard's jaw was ≤90°; see Figure 2	-0.40
Number of linked throat-fan extensions	Throat-fan extensions in which a second extension was begun before a previous extension was completed (i.e., before the throat-fan was completely retracted) were considered linked	0.03
Number of turns	Number of side-to-side changes in the position of the head and upper body of the lizard conducted during a display	-0.38
Changes in body position	A change in the angle between the ventral surface of the lizard's body and the substrate between the following angle intervals: 0–30°; 30–60°; 60–90°; >90°; see Figure 2	0.16
Presence of raised nuchal crest	Coded as a binary variable; see Figure 2, Figure S5 E,F	-0.19
Presence of raised dorsal crest	Coded as a binary variable; see Figure 2, Figure S5 E,F	-0.11
Presence of bipedality	Coded as a binary variable (whether or not the lizard's front legs did not touch the substrate at any point during the display)	-0.28
Presence of tail raises	Coded as a binary variable (whether or not the tail was raised off the substrate at any point during the display); see Figure 2	-0.13

USB2000 spectrophotometer with a pulsed-xenon light source to measure the reflectance spectra of different color patches on the throat-fan: blue and orange patches were measured on colored-fan and intermediate-fan males, black areas were measured in colored-fan males, and white areas were measured on white-fan and intermediate-fan males. Two readings were taken per color per individual. To avoid resampling individuals, I marked lizards on the flanks and ventrally with nontoxic sharpie markers and dorsally with temporary colored cardboard queen-bee tags (Johnson, 2005) or white paint before releasing.

**Environmental Variables.**—For eight randomly located transects per site, I assessed the presence of vegetation and rocks on the transect every 30 cm for 15 m. Ground cover was calculated as the proportion of points at which vegetation or rocks were present on the transect. For four of the eight transects, I measured the height in centimeters of every plant and rock directly on the transect to calculate the average height of the ground cover at the site. These variables were chosen as simple measures of visual environment—more open environments are expected to have a lower proportion of ground cover or shorter ground cover than are more closed environments. Further, I measured perch height at which lizards were first seen perching, to the nearest centimeter, to assess if the throat-fan variants occupy distinct microhabitats, which may also contribute to differences in the visual environment in which their throat-fans are deployed.

**Statistical Analysis.**—I completed all statistical analyses in R v.3.0.2 (R Core Team, 2013). Throat-fan area and SVL were log-transformed prior to analysis. I used a linear mixed effects model ('nlme' package; Pinheiro et al., 2013) with a fixed effect of throat-fan variant and a random effect of population to compare SVL among males of different throat-fan variants. Variance was allowed to vary with population to improve the normality and homoscedasticity of model residuals. Similarly, I compared throat-fan area across throat-fan variants, both with and without

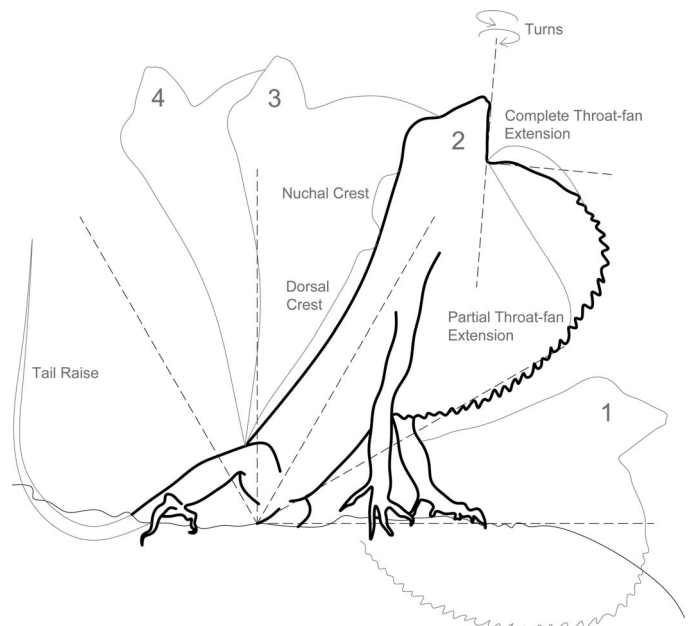


FIG. 2. Measurements of display behavior. Throat-fan extensions were considered complete if the minimum angle between ventral surface of the head and the front margin of the throat-fan was estimated as 90° or less; for angles estimated as >90°, throat-fan extensions were considered partial. Body position was categorized based on the estimated angle between the substrate and the ventral surface of the body: 1: 0–30°, 2: 30–60°, 3: 60–90°, and 4: >90°, and the number of changes between these four body positions was counted for each display. The number of head turns as well as the presence of four display modifiers—raised nuchal crest, raised dorsal crest, raised tail, and bipedality (not depicted here)—were assessed.

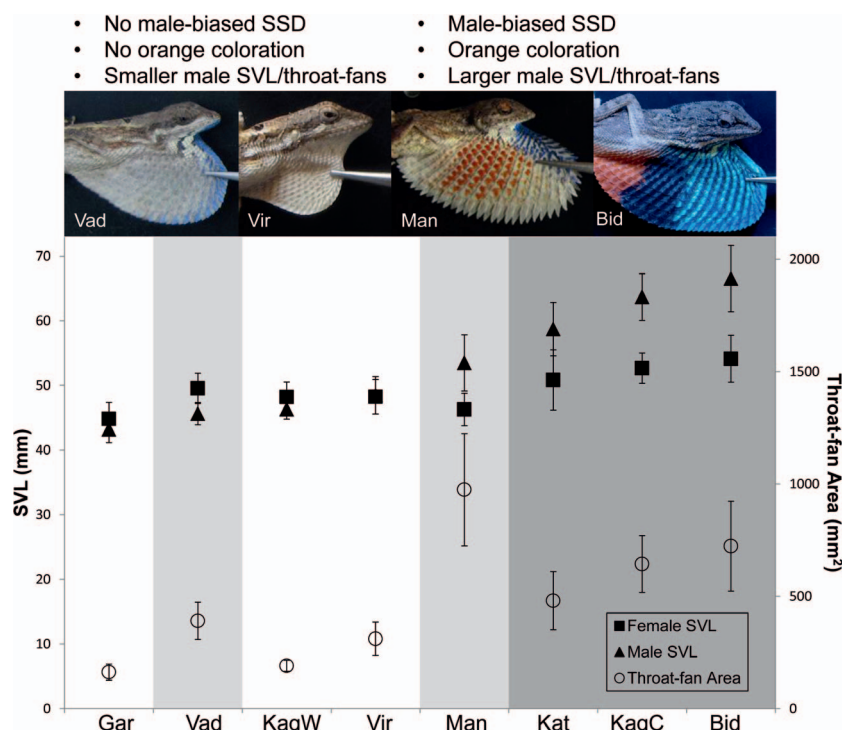


FIG. 3. Sexual size dimorphism (SSD) in the snout-vent length (SVL) and variation in throat-fan area in sampled populations of Fan-Throated Lizards, including photographs of representative individuals from the white-fan variant (Vir), colored-fan variant (Bid), and the northern (Vad) and southern (Man) intermediate-fan populations, depicting variation in throat-fan coloration. Populations are arranged in order of increasing male SVL.

SVL included as a covariate. Additionally, I compared both SVL and throat-fan area between the two intermediate-fan populations using *t*-tests because preliminary observations revealed unexpectedly large differences in throat-fan morphology between these two populations. Finally, I assessed the direction of SSD using *t*-tests in each population, with a sequential Bonferroni correction to account for multiple comparisons. I used an analysis of variance (ANOVA) on SVL with main effects of population and sex, and a population  $\times$  sex interaction to test if the degree of SSD differed across populations.

Spectral data were smoothed and condensed to 1-nm intervals from 300 to 700-nm wavelengths using CLR v1.05 (Montgomerie, 2008) and averaged by individual. I calculated and plotted mean and 95% confidence intervals of reflectance at 1-nm intervals for each color in each population.

I conducted a principal components analysis on 12 behavioral variables and used the first principal component axis (PC1) as a measure of display behavior (it explained 31% of the variation in the behavioral variables). Subsequent PC axes each explained less than 15% of the total variation in display behavior and were not readily biologically interpretable in conjunction with PC1 and were, therefore, not analyzed further. Though this approach does not analyze all of the behavioral variation (including among-individual and among-population variation as well as differences between throat-fan variants), PC1 by definition represents the largest independent axis of variation in display behavior.

I used a linear mixed effects model with a fixed effect of throat-fan variant and a random effect of population to evaluate the difference in display behavior (PC1) between the three throat-fan variants. Variance was allowed to vary with population to improve the normality and homoscedasticity of model residuals. I used a *t*-test to investigate if the two intermediate-fan populations, which differ substantially in throat-fan morphology, had different display behavior (PC1).

Additionally, I compared patterns of variation across populations in two movement components—changes in body position (up-and-down movements) and head turns (side-to-side movements) and examined the relationship between throat-fan area and body position changes across populations. I did not perform hypothesis-testing for these comparisons, however, because these specific patterns were not predicted and were instead observed a posteriori.

The proportion of ground cover was compared across throat-fan variants using a generalized linear mixed effects model (GLMM, 'lme4' package; Bates et al., 2014) with a binomial distribution, and with a fixed effect of variant and a random effect of site. I used a GLMM with a negative binomial distribution, with a fixed effect of variant and a random effect of site, to compare the height of ground cover across throat-fan variants. I treated the site at which the white-fan and colored-fan variants were sympatric as a separate variant category for these two comparisons. A GLMM with a negative binomial distribution, a fixed effect of throat-fan variant, and a random effect of population was used to compare perch height at lizards' initial positions across the eight sampled populations. For all models I assessed overall significance of the fixed effect of throat-fan variant by comparison with a null model in which the term was dropped.

## RESULTS

*Morphology.*—Morphology was measured from an average of 23.4 males (range: 17–26) and 20.0 females (range: 16–24) per population (see Tables S1, S2 for sample sizes and summary statistics). Fan-Throated Lizards were small, with a mean ( $\pm$ SD) SVL of  $53 \pm 9$  mm for males and  $49 \pm 4$  mm for females across all populations; however, both size and the degree of SSD varied substantially across populations (Fig. 3).

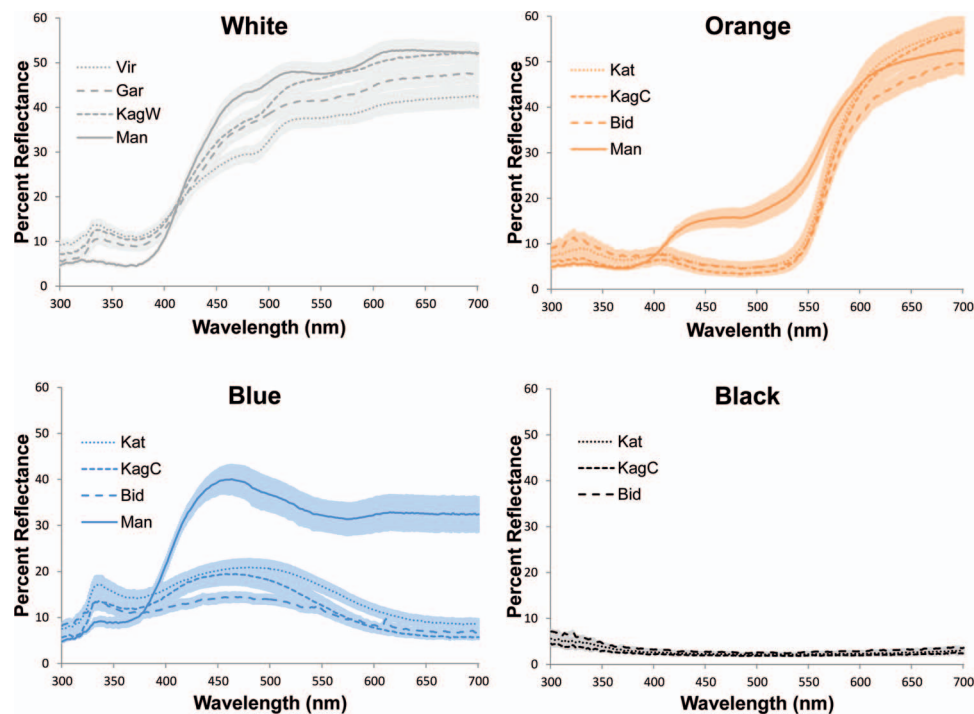


FIG. 4. Mean and 95% confidence intervals of reflectance spectra from all populations except the northern intermediate-fan population (Vad). Solid lines indicate mean reflectance spectra from the southern intermediate-fan population (Man; for the white, blue, and orange spectra) while broken lines indicate mean reflectance spectra for the white-fan populations (for the white spectra) populations or the colored-fan populations (for the blue, black, and orange spectra).

Males of the colored-fan variant were larger than males of the intermediate-fan variant ( $\beta = 0.24 \pm 0.05$ ,  $t_5 = 4.56$ ,  $P = 0.006$ ) and the white-fan variant ( $\beta = 0.31 \pm 0.05$ ,  $t_5 = 6.58$ ,  $P = 0.001$ ), but SVL did not differ between white-fan and intermediate-fan variant males ( $t_5 = 1.30$ ,  $P = 0.25$ ). Comparing the two intermediate-fan populations, males were larger in the southern population (Man) than in the northern population (Vad;  $t_{32.5} = 8.33$ ,  $P < 0.001$ ).

Body size differed between males and females in seven of the eight populations, ranging from males being 4% smaller to 23% larger than females (Fig. 3). Male-biased SSD was observed in all three colored-fan populations (Bid:  $\alpha = 0.007$ ,  $t_{42.4} = -9.49$ ,  $P < 0.001$ ; Kat:  $\alpha = 0.006$ ,  $t_{35.0} = -10.54$ ,  $P < 0.001$ ; KagC:  $\alpha = 0.008$ ,  $t_{27.7} = -10.48$ ,  $P < 0.001$ ) and the southern intermediate-fan population (Man:  $\alpha = 0.01$ ,  $t_{39.6} = -6.98$ ,  $P < 0.001$ ). Sexual size dimorphism was female-biased in two white-fan populations (Gar:  $\alpha = 0.025$ ,  $t_{42.4} = 2.44$ ,  $P = 0.019$ ; KagW:  $\alpha = 0.017$ ,  $t_{27.9} = 2.85$ ,  $P = 0.008$ ) and in the northern intermediate-fan population (Vad:  $\alpha = 0.013$ ,  $t_{24.9} = 5.79$ ,  $P < 0.001$ ). Male and female body size did not differ from one another in the remaining white-fan population (Vir:  $\alpha = 0.05$ ,  $t_{48} = -0.30$ ,  $P = 0.76$ ). The degree of SSD differed significantly across populations (population  $\times$  sex interaction:  $F_7 = 43.8$ ,  $P < 0.001$ ).

Throat-fans varied substantially across populations in both size and coloration (Fig. 3). Throat-fan area was smaller in males of the white-fan variant than in males of the colored-fan variant ( $\beta = 1.04 \pm 0.24$ ,  $t_5 = 4.26$ ,  $P = 0.008$ ) and the intermediate-fan variant ( $\beta = 1.05 \pm 0.27$ ,  $t_5 = 3.81$ ,  $P = 0.01$ ), though throat-fan area did not differ between the colored-fan and intermediate-fan variants ( $t_5 = 0.04$ ,  $P = 0.97$ ). Comparing the two intermediate-fan populations, throat-fan area was larger in males in the southern population (Man) than in the northern population (Vad;  $t_{32.5} = 8.33$ ,  $P < 0.001$ ). On including SVL as a covariate, and relative to

white-fan populations, I determined that the increase in throat-fan area in colored-fan populations was proportionate to the increase in SVL (i.e., there was no difference in the intercepts of the linear relationship between the two variants:  $\beta = 0.10 \pm 0.10$ ,  $t_5 = 0.94$ ,  $P = 0.39$ ). In contrast, the increase in throat-fan area in intermediate-fan populations was disproportionate relative to the increase in SVL ( $\beta = 0.80 \pm 0.10$ ,  $t_5 = 7.66$ ,  $P = 0.0006$ ; Fig. S2).

In colored-fan populations, throat-fans included blue, black, and orange sections in the front, middle, and rear of the throat-fan; these sections comprised  $60 \pm 5\%$ ,  $28 \pm 5\%$ , and  $12 \pm 4\%$  of the throat-fan area, respectively (see Table S2 for population averages). Males in white-fan populations could induce a thin margin of blue coloration along the front edge of their throat-fans, but this coloration was not always expressed (area not measured; see also Kästle, 1998; Patankar et al., 2013). The change in color from white to blue in white-fan populations was observed to take place within seconds, often in the presence of other lizards (AK, pers. obs.); in contrast, throat-fan colors in colored-fan populations were not observed to change. The coloration of the throat-fan differed in the two intermediate-fan populations (Fig. 3). In Vadanemelli in northern Tamil Nadu, throat-fans were white with an inducible blue patch ( $26 \pm 6\%$  of the throat-fan area) toward the front of the throat-fan. In Manimutharu in southern Tamil Nadu, throat-fans were large and white with an inducible blue patch at the front of the throat-fan and an orange patch toward the center and rear of the throat-fan ( $13 \pm 3\%$  and  $44 \pm 10\%$  of the throat-fan area, respectively; see Fig. S3 for an example of color change on the throat-fan from this population). Lizards in Manimutharu also had enlarged lanceolate scales along the edge of the throat-fan (see also Kratzer, 1980; Kästle, 1998). Reflectance spectra of throat-fan colors were similar in all colored-fan populations (for blue, black, and orange patches) and in all white-fan populations (for white areas; Fig. 4). Both blue and

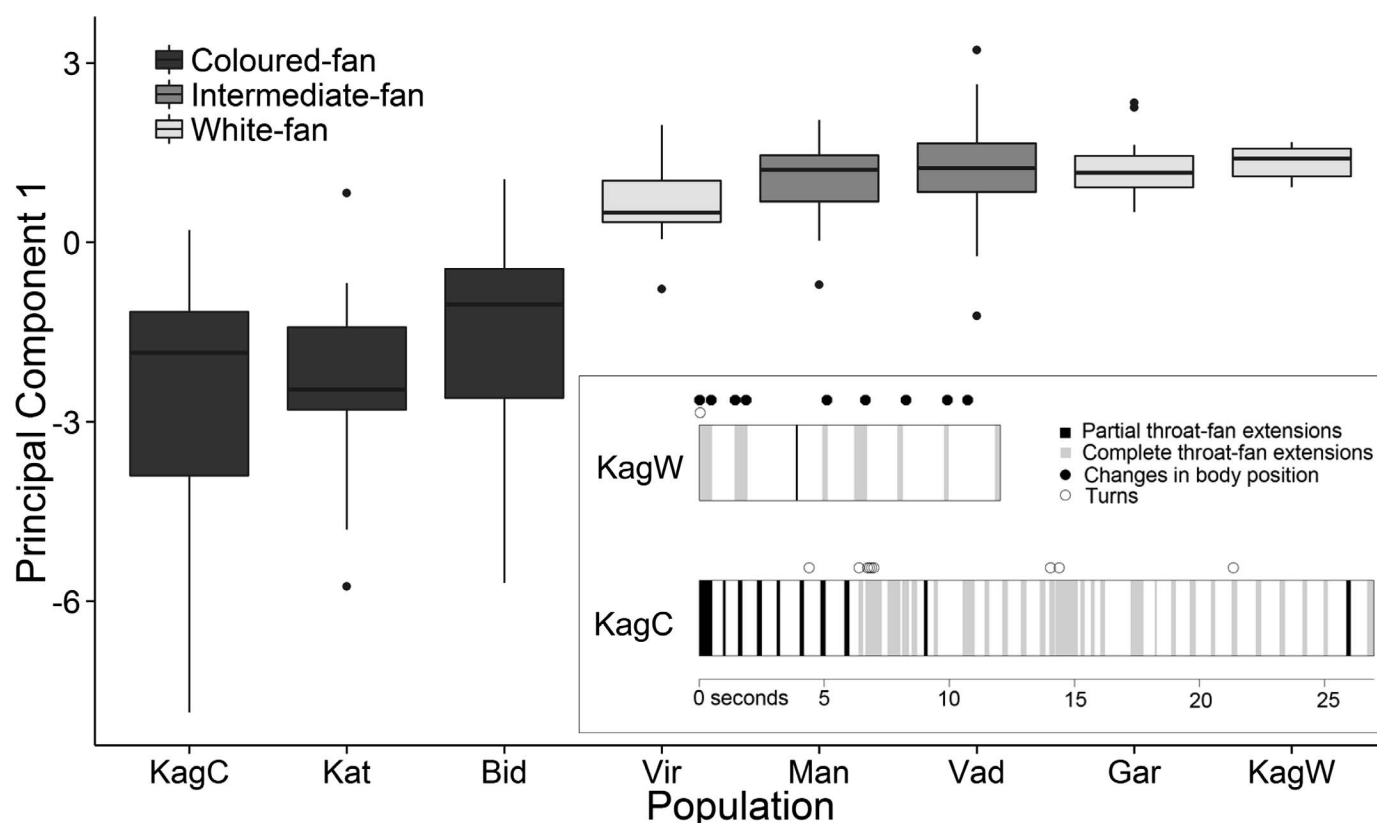


FIG. 5. Variation in display behavior, as measured by the first axis in a principal components analysis on 12 behavioral variables (see Table 1 for loadings) among the three throat-fan variants. Inset: representative displays from the populations with the greatest difference in mean PC1. The individuals from the white-fan and colored-fan populations in Kagal whose displays are depicted here have PC1 values of 1.57 and  $-1.54$ , respectively.

orange reflectance spectra, however, differed substantially between colored-fan populations and the southern intermediate-fan population (Man), and white reflectance spectra differed slightly between white-fan populations and the southern intermediate fan population, particularly in the ultraviolet region (Fig. 4; recall that reflectance data were not collected from the northern intermediate-fan population, Vad). This is at least partially a consequence of the difference in scale margin coloration between the throat-fan variants (note the white scale margins in the Man population; Fig. 3).

In summary, male-biased SSD, large throat-fan size, and the presence of orange coloration on the throat-fan were found in all three colored-fan populations as well as the southern intermediate-fan population (Man). However, the southern intermediate-fan population differed from the colored-fan populations in both reflectance spectra and the relationship between SVL and throat-fan area. In the remaining populations (white-fan and the northern intermediate-fan), males were smaller in size and bore smaller dewlaps lacking orange coloration, and male-biased SSD was not observed.

**Display Behavior.**—Display behavior was observed for an average of 20.1 males per population (range: 14–25). Displays comprised 1–112 throat-fan extensions and ranged from 0.04 sec to over 2 min in duration. Principal component 1 had absolute values of loadings  $>0.10$  for most variables (Table 1; see Table S3 for loadings of subsequent principal component axes) and differed significantly between the throat fan variants ( $\chi^2_2 = 25.6$ ,  $P < 0.001$ ). In particular, PC1 differed between the colored-

fan variant and the white-fan and intermediate-fan variants (colored-fan vs. white-fan:  $\beta = 3.21 \pm 0.32$ ,  $t_5 = 10.1$ ,  $P < 0.001$ ; colored-fan vs. intermediate-fan:  $\beta = 3.22 \pm 0.35$ ,  $t_5 = 9.20$ ,  $P < 0.001$ ; Fig. 5); however, the white-fan and intermediate-fan displays did not differ from one another ( $t_5 = 0.06$ ,  $P = 0.95$ ). Display behavior did not differ between the two intermediate-fan populations ( $t_{35.1} = 0.85$ ,  $P = 0.40$ ). Loadings of the behavioral variables on PC1 indicated that displays in colored-fan populations included more partial and complete throat-fan extensions, as well as more turns and modifiers, but fewer changes in body position. Moreover, though individual displays in colored-fan populations were longer, the number of displays per unit time and the proportion of time spent displaying were lower compared with white-fan and intermediate-fan populations. Examples of displays of each throat-fan variant (including both northern and southern populations of the intermediate-fan variant) are included as supplementary material (videos S1a–d).

Fan-Throated Lizards' displays include two striking movement components: changes in body position (up-and-down movements) and head turns (side-to-side movements; Fig. 2). Populations varied in the frequency at which these two movement components are deployed (Fig. 6), and this variation can be linked to among-population variation in dewlap size and coloration. In particular, displays by individuals in populations with larger throat-fans include fewer changes in body position than displays by individuals in populations with smaller throat-fans (estimated slope in linear regression between population

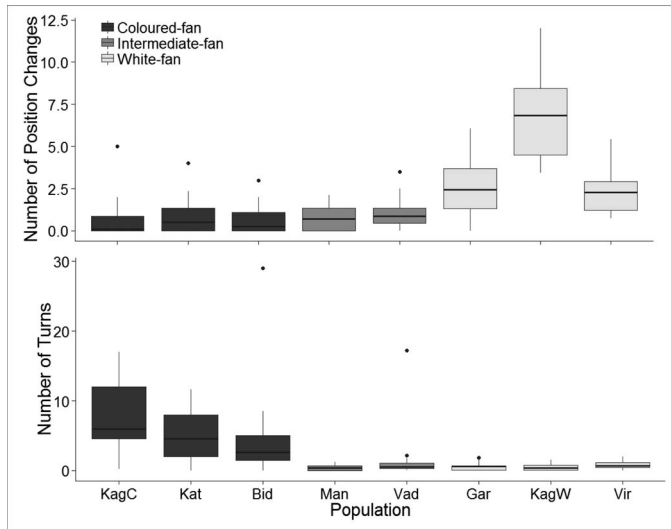


FIG. 6. Variation among the sampled populations in the number of body position changes (up and down movements) and turns (side to side movements) observed in displays.

means of body position changes against throat-fan area:  $-0.47 \pm 0.23$ , adjusted  $r^2 = 0.32$ ).

**Environmental Variables.**—The proportion and height of ground cover did not differ among the sites in which the different throat-fan variants were found (proportion of ground cover:  $\chi^2_3 = 4.40$ ,  $P = 0.22$ ; height of ground cover:  $\chi^2_3 = 3.05$ ,  $P = 0.38$ ; Fig. S4). Fan-Throated Lizards perch low (mean initial perch height across all populations =  $18.9 \pm 17.5$  cm), usually on the ground (modal initial perch height = 0 cm), but also on rocks, vegetation, and piles of mud. Perch height did not differ among throat-fan variants ( $\chi^2_2 = 1.94$ ,  $P = 0.38$ ).

#### DISCUSSION

Fan-Throated Lizard displays include not only extensions and retractions of the throat-fan but also other movements such as head turns and changes in body position as well as modifiers such as raised nuchal and dorsal crests, raised tails, and bipedality. The display behavior of colored-fan males differs from the display behavior of white-fan and intermediate-fan males, suggesting that at least part of the variation in the display behavior of the fan-throated lizard is related to the morphological elaboration of the throat-fan. Increased throat-fan size and coloration in the colored-fan populations and one of the intermediate-fan populations is associated with male-biased SSD, but the habitats in which the different throat-fan variants are found today do not differ from each other in ground cover, vegetation height, or the lizards' perch height.

On one hand, the displays of colored-fan variants are distinct from the displays of white-fan and intermediate-fan variants. On the other hand, displays are similar in all white-fan and intermediate-fan populations despite large variation across these populations in throat-fan size and coloration. Therefore, the association between ornament elaboration and variation in display behavior is not straightforward. The reasons for such a complex association can include the structural constraints imposed and opportunities afforded by changes in throat-fan size and color. In particular, Fan-Throated Lizards' displays include two striking movement components, changes in body position (up-and-down movements) and head turns (side-to-

side movements), which vary in frequency among populations (Fig. 6). This variation points to possible structural constraints that may shape display behavior. For example, the ability of a lizard with a large throat-fan to adopt a body position that is nearly horizontal (body position 1; Fig. 2) with a fully extended throat-fan must be limited. Indeed, we observed a pattern that males in populations with larger throat-fans showed fewer changes in body position than males in populations with smaller throat-fans. The higher prevalence of head turns in colored-fan populations also is potentially explained by throat-fan morphology, specifically iridescent coloration. Unlike white-fan and intermediate-fan populations, colored-fan variant males express what appears to be iridescent blue coloration on their throat-fans throughout the breeding season (AK, pers. obs; see video S1a). Because the perceived coloration of iridescent surfaces depends on the angles between incident light, the surface, and the viewer (Prum, 2006; Meadows et al., 2011), rapid turning can ensure that most receivers will observe the iridescence, irrespective of viewing geometry, and may increase the conspicuousness of the signal. Research on the biomechanics of displays and the visual anatomy of signal recipients (Hebets and Papaj, 2005; Rosenthal, 2007) may reveal proximate explanations for the relationship between display behavior and ornament morphology in Fan-Throated Lizards.

Intricate interactions between multiple types of cells known as chromatophores are responsible for the diversity of colors seen in reptile ornaments and displays (reviewed in Grether et al., 2004). The presence of structural color (iridescent blue), melanin-based color (black), and pteridine- or carotenoid-based color (orange) on their throat-fans, as well as variation in throat-fan size and the size of each color-patch, suggests that many potentially honest signals of male quality may be contained within the Fan-Throated Lizards' display (Grether et al., 2004; Hill and McGraw, 2006), each of which may convey different information to the recipient or act to amplify one another (Hebets and Papaj, 2005). Moreover, in addition to rapid changes in blue coloration on the throat-fan in some populations, *Sitana* can change color on many different parts of the body including the nuchal crest, dorsum, tail, lips, eyelids, and hind legs (see Fig. S5 for examples; Kästle, 1998). In light of recent research on the complex physiologies underlying color production and change in lizards (Saenko et al., 2014; Teyssier et al., 2015), and comprehensive frameworks for the analysis of coloration in natural populations (Kemp et al., 2015), Fan-Throated Lizards offer a veritable cornucopia to biologists interested in the physiological basis of coloration.

The association across populations of increased throat-fan size and coloration with increased male body size and male-biased SSD strongly suggests that sexual selection has played a role in shaping ornament variation in Fan-Throated Lizards. Male-male competition often is suggested as the mechanism of sexual selection in lizards, and both increased body size and increased ornamentation are expected under stronger male-male competition (Stamps, 1977; Tokarz, 1995). Larger individuals frequently win agonistic interactions against smaller individuals (Stamps, 1977, 1983; Cox et al., 2007), and ornamentation is thought to signal fighting ability to potential competitors (Ord et al., 2001; Vanhooydonck et al., 2005; Whiting et al., 2006; Irschick et al., 2007). The co-elaboration of both male body size and ornamentation is therefore interpreted as evidence for sexual selection via male-male competition (Ord et al., 2001; Stuart-Fox and Ord, 2004; Perez i de Lanuza et al., 2013). Explicit measurements of the correla-



tions between reproductive success and male body size and ornamentation within populations will be necessary, however, to confirm whether and how sexual selection acts in this system. Also, the correlation between signal components and performance metrics such as bite force (Vanhooydonck et al., 2005; Irschick et al., 2007) will need to be examined in different environmental and social conditions to understand their role in signaling during male–male competition (Bro-Jørgenson, 2009; Lailvaux and Kasumovic, 2011) and other social interactions. More fundamentally, the mating systems of these lizards remain unknown, so we cannot know the precise mechanisms by which sexual selection acts upon them. Learning if mating systems vary across these different throat-fan variants, possibly as a consequence of variation in ecological factors such as densities and resource distributions (Emlen and Oring, 1977), will be fascinating.

The importance of environmental context in driving ornament diversification in Fan-Throated Lizards is difficult to ascertain because these lizards persist today in highly anthropogenically modified environments. Modified habitats, such as the sites sampled in this study, are likely very different from the environments in which these lizards diversified. Nevertheless, the present-day habitats of all three throat-fan variants are similar, and the colored-fan and white-fan variants co-occur in at least one site, suggesting that throat-fan variants are not restricted to different environmental conditions. Therefore, environmental context likely does not play a role in maintaining variation in ornament morphology in Fan-Throated Lizards, similar to other agamid lizards (e.g. Chen et al., 2012); however, this is in contrast with *Anolis* lizards which bear a throat-fan that is functionally similar to that of *Sitana* (Ord et al., 2015). Changes in visual environment from xeric to mesic forests are correlated with variation in throat-fan coloration within *Anolis* species in a manner that is consistent with selection for maximum conspicuousness of the throat-fan in each habitat (Leal and Fleishman, 2004; Ng et al., 2013). Precise measurements of both the visual environment and throat-fan coloration across a larger sample of populations may reveal similar relationships in Fan-Throated Lizards but, at present, there is little evidence for the importance of environmental context in ornament elaboration in this genus.

Of course, environmental factors other than light environment also may drive ornament elaboration. In particular, variation in predation pressure across populations is expected not only to influence ornament morphology (Stuart-Fox et al., 2003; Husak et al., 2008; McLean et al., 2014) but also may affect how ornaments are deployed in displays. Quantifying the role of a dynamically displayed ornament in attracting the attention of predators will be challenging, however. Also, given the extensive presence of Fan-Throated Lizards in human-modified environments, discerning how variation in predation pressure has historically influenced throat-fan evolution in *Sitana* may prove tricky, though contemporary effects of predation on conspicuousness and crypsis in these lizards certainly warrant attention.

Although the potential for the throat-fan to function in interspecific communication was not explicitly explored in this study, Fan-Throated Lizards may provide an opportunity for such studies in the future. In populations where closely related taxa are sympatric, signals often are crucial for species recognition (Ryan and Rand, 1993; Panhuis et al., 2001). For example, both throat-fan morphology and patterns of head-bobbing differ among sympatric *Anolis* species, likely to

facilitate species recognition (Rand and Williams, 1970; Jenssen, 1977; Ord and Martins, 2006). The throat-fan variants of *Sitana*, which belong to different clades (Deepak and Karanth, pers. comm.) and likely are different species (Amarasinghe et al. 2015), are rarely sympatric. The site sampled in this study in which colored-fan and white-fan variants coexist is, to my knowledge, the only recorded occurrence of sympatry between throat-fan variants. The white-fan and colored-fan populations in this sympatric site showed a greater difference in display behavior than any two allopatric throat-fan variant populations (Fig. 5), suggesting that displays might play a role in species recognition where different *Sitana* species coexist. Species delimitations within *Sitana*, as well as fine-scale mapping of the ranges of these species and the locations at which they are sympatric, will determine the utility of this genus in understanding the co-option of a signal used in intraspecific communication for species recognition.

Understanding the systematics of *Sitana* and the phylogenetic relationships among the different throat-fan variants also will shed light on how often the throat-fan has changed in size and color across this genus, as well as for its close relatives in the genus *Otocryptis*, some of which also bear throat-fans (Das, 2002; Bahir and Silva 2005). That the colored-fan and intermediate-fan variants of *Sitana* differ not only in the spectral reflectance of blue and orange patches of the throat-fan, but also in allometric relationships between body size and throat-fan size, suggests the intriguing possibility that ornament elaboration has evolved by different mechanisms, perhaps multiple times, in these lizards.

Very few previous studies have examined the behavioral ecology of Fan-Throated Lizards, despite their ubiquity across drier areas in South Asia (Daniel, 2002; Das, 2002), their high local densities (Shanbhag et al., 2003; Subramanean and Reddy, 2010), and their readily observable display behavior. In this paper, I document an association between throat-fan morphology and display behavior in Fan-Throated Lizards and show that both sexual selection and structural constraints and opportunities may have shaped the dramatic diversity in the size and coloration of their throat-fans. These results suggest that Fan-Throated Lizards are a promising system in which to further investigate the coevolution of different display components of a striking visual signal.

*Acknowledgments.*—All research was conducted in accordance with Harvard University Institutional Animal Care and Use Committee protocol 26-11. Because study sites did not fall within Protected Areas, and *Sitana* is not mentioned as a scheduled species in the Wildlife (Protection) Act (1972) and subsequent amendments, conducting this study did not require government permits. C. Kokatnur and A. Lokhande assisted with field work. The following people helped with locating field sites and logistical organization (in alphabetical order): I. Agarwal, A. Chaudhry, K. V. Dheeraj, A. Dutta, M. Gala, T. Ganesh, V. Giri, H. Kulkarni, R. Kulkarni, P. Kumar, G. Mallapur, M. Mathivanan, S. Masur, J. Pai, G. Patil, K. S. Seshadri, A. Shankar, R. Sharma, D. Shelar, Y. Shipchandler, R. Sreekar, S. Subramanean, S. Tamizhazhagan, J. C. Tiwari, S. Varma, D. Veerappan, S. Waingankar, and A. Zambre. In particular, the site of sympatry between the white-fan and colored-fan variants was located by H. Kulkarni. I also thank the organizers of the Young Ecologists Talk and Interact listserv, and contributors to the India Nature Watch website, for facilitating the identification of field sites and the Agasthyama-

lai Community-based Conservation Centre and the Madras Crocodile Bank Trust for logistical support. This project was funded by a Graduate Research Award from the South Asia Institute and a Miyata Award from the Museum of Comparative Zoology, both at Harvard University, as well as a Rosemary Grant Student Research Award from the Society for the Study of Evolution. J. Losos, A. S. Harrison, R. G. Reynolds, O. Lapiedra, and two anonymous reviewers provided helpful feedback on the manuscript.

## LITERATURE CITED

- AMARASINGHE, A. T., I. INEICH, D. M. S. S. KARUNARATHNA, W. M. S. BOTEJUE, AND P. D. CAMPBELL. 2015. Two new species of the genus *Sitana* Cuvier, 1829 (Reptilia: Agamidae) from Sri Lanka, including a taxonomic revision of the Indian *Sitana* species. *Zootaxa* 3915:67–98.
- ANDERSSON, M. 1994. *Sexual Selection*. Princeton University Press, USA.
- BAHIR, M. M., AND A. SILVA. 2005. *Otocryptis nigrissima*, a new species of agamid lizard from Sri Lanka. *Raffles Bulletin of Zoology* 12:393–406.
- BATES, D., M. MAECHLER, B. BOLKER, AND S. WALKER. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>
- BRADBURY, J. W., AND S. L. VEHRENCAMP. 2011. *Principles of Animal Communication*. Sinauer Associates, USA.
- BRO-JØRGENSEN, J. 2009. Dynamics of multiple signaling systems: animal communication in a world in flux. *Trends in Ecology and Evolution* 25:292–300.
- CHEN, I., D. STUART-FOX, A. F. HUGALL, AND M. R. E. SYMONDS. 2012. Sexual selection and the evolution of complex color patterns in dragon lizards. *Evolution* 66:3605–3614.
- COOPER, W. E., JR., AND N. GREENBERG. 1992. Color and behavior. Pp. 298–422 in C. Gans and D. Crews (eds.), *Hormones, Brain, and Behavior, Biology of the Reptilia*. Volume 18. University of Chicago Press, USA.
- COX, R. M., M. A. BUTLER, AND H. B. JOHN-ALDER. 2007. The evolution of sexual size dimorphism in reptiles. Pp. 38–49 in D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely (eds.), *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*. Oxford University Press, UK.
- DANIEL, J. C. 2002. *The Book of Indian Reptiles and Amphibians*. Bombay Natural History Society, India.
- DAS, I. 2002. *Photographic Guide to Snakes and Other Reptiles of India*. Om Books, India.
- DARWIN, C. 1871. *Sexual Selection and the Descent of Man*. Volume 2. Murray Books, UK.
- DUVALL, D. 1979. Western fence lizard (*Sceloporus occidentalis*) chemical signals. I. Conspecific discriminations and release of a species-typical visual display. *Journal of Experimental Zoology* 210:321–325.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- ENDLER, J. A. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist* 139:S125–S153.
- FLEISHMAN, L. J. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *American Naturalist* 139:S36–S61.
- GRETHER, G. F., G. R. KOLLURU, AND K. NERSISSIAN. 2004. Individual colour patches as multicomponent signals. *Biological Reviews* 79:583–610.
- HEBETS, E. A., AND D. R. PAPA. 2005. Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology* 57:197–214.
- HILL, G. E., AND K. J. MCGRAW. 2006. *Bird Coloration: Function and Evolution*. Harvard University Press, USA.
- HUSAK, J. F., J. M. MACEDONIA, S. F. FOX, AND R. C. SAUCEDA. 2008. Predation cost of conspicuous male coloration in collared lizards (*Crotaphytus collaris*): an experimental test using clay-covered model lizards. *Ethology* 112:572–580.
- IRSCHICK, D. J., A. HERREL, B. VANHOYDONCK, AND R. VAN DAMME. 2007. A functional approach to sexual selection. *Functional Ecology* 21:621–626.
- JENSSEN, T. A. 1977. Evolution of anoline display. *American Zoology* 17: 203–215.
- JOHNSON, M. A. 2005. A new method of temporarily marking lizards. *Herpetological Review* 36:277–279.
- KÄSTLE, W. 1998. Studies on the ecology and behavior of *Sitana sivalensis*. Pp. 121–206 in Schleich, H.H., and W. Kästle (eds.), *Contributions to the Herpetology of South Asia (Nepal, India)*. Veröffentlichungen aus dem Fuhlrott-Museum, Germany.
- KEMP, D. J., M. E. HEBERSTEIN, L. J. FLEISHMAN, J. A. ENDLER, A. T. D. BENNETT, A. G. DYER, N. S. HART, J. MARSHALL, AND M. J. WHITING. 2015. An integrative framework for the appraisal of coloration in nature. *American Naturalist* 185:705–724.
- KRATZER, W. 1980. On the territorial behavior of the agamid lizard (*Sitana ponticeriana ponticeriana*). *Loris* 15:162–163.
- LAILVAUX, S. P., AND M. M. KASUMOVIC. 2011. Defining individual quality over lifetimes and selective contexts. *Proceedings of the Royal Society of London B* 278:321–328.
- LEAL, M., AND L. J. FLEISHMAN. 2002. Evidence for habitat partitioning based on adaptation to environmental light in a pair of sympatric lizard species. *Proceedings of the Royal Society of London B* 269:351–359.
- . 2004. Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. *American Naturalist* 163:26–39.
- MARCELLINI, D. 1977. Acoustic and visual display behavior of gekkonid lizards. *American Zoologist* 17:251–260.
- MCLEAN, C. A., A. MOUSSALLI, AND D. STUART-FOX. 2014. Local adaptation and divergence in colour signal, conspicuousness between monomorphic and polymorphic lineages in a lizard. *Journal of Evolutionary Biology* 27:2654–2664.
- MEADOWS, M. G., N. I. MOREHOUSE, R. L. RUTOWSKI, J. M. DOUGLAS, AND K. J. MCGRAW. 2011. Quantifying iridescent coloration in animals: a method for improving repeatability. *Behavioral Ecology and Sociobiology* 65:1317–1327.
- MONTGOMERIE, R. 2008. CLR, version 1.05. Queen's University, Canada.
- NG, J., E. L. LANDEEN, R. M. LOGSDON, AND R. E. GLOR. 2013. Correlation between *Anolis* lizard dewlap phenotype and environmental variation indicates adaptive divergence of a signal important to sexual selection and species recognition. *Evolution* 67:573–582.
- ORD, T. J., AND E. P. MARTINS. 2006. Tracing the origins of signal diversity in anole lizards: phylogenetic approach to inferring the evolution of complex behavior. *Animal Behavior* 71:1411–1429.
- ORD, T. J., D. T. BLUMSTEIN, AND C. S. EVANS. 2001. Intrasexual selection predicts the evolution of signal complexity in lizards. *Proceedings of the Royal Society of London B* 268:737–744.
- ORD, T. J., R. A. PETERS, B. CLUCAS, AND J. A. STAMPS. 2007. Lizards speed up visual displays in noisy motion habitats. *Proceedings of the Royal Society of London B* 274:1057–1062.
- ORD, T. J., D. C. COLLAR, AND T. J. SANGER. 2013. The biomechanical basis of evolutionary change in a territorial display. *Functional Ecology* 27: 1186–1200.
- ORD, T. J., D. A. KLOMP, J. GARCIA-PORTA, AND M. HAGMAN. 2015. Repeated evolution of exaggerated dewlaps and other throat morphology in lizards. *Journal of Evolutionary Biology* 28:1948–1964.
- PAL, A., M. M. SWAIN, AND S. RATH. 2011. Reproduction and sexual dichromatism in *Sitana ponticeriana* (Reptilia: Draconinae: Agamidae). *Taprobanica* 3:31–37.
- PANHUIS, T. M., R. BUTLIN, M. ZUK, AND T. TREGENZA. 2001. Sexual selection and speciation. *Trends in Ecology and Evolution* 16:364–371.
- PATANKAR, P., I. DESAI, J. N., TRIVEDI, AND S. Balakrishnan. 2013. Ethogram of courtship and mating behavior of *Sitana cf. ponticeriana* (Reptilia: Draconinae: Agamidae) in India. *Taprobanica* 5:44–49.
- PÉREZ DE LANUZA, G., E. FONT, AND J. L. MONTERDE. 2013. Using visual modelling to study the evolution of lizard coloration: sexual selection drives the evolution of sexual dichromatism in lacertids. *Journal of Evolutionary Biology* 26:1826–1835.
- PINHEIRO, J., D. BATES, S. DEBROY, D. SARKAR, AND THE R DEVELOPMENT CORE TEAM. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-113. R Foundation for Statistical Computing, Vienna, Austria.
- PODOS, J. 2001. Correlation evolution of morphology and vocal signal structure in Darwin's finches. *Nature* 409:185–188.
- PRUM, R. O. 2006. *Anatomy, Physics, and Evolution of Avian Structural Colors*. Pp. 295–353 in Hill, G. E. and K. J. McGraw (eds.), *Bird Coloration*. Volume 1. Mechanisms and Measurements. Harvard University Press, USA.
- R CORE TEAM. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>

- RAND, A. S. 1964. Ecological distribution in anoline lizards of Puerto Rico. *Ecology* 45:745–752.
- RAND, A. S., AND E. E. WILLIAMS. 1970. An estimation of redundancy and information content of anole dewlaps. *American Naturalist* 104:99–103.
- ROSENTHAL, G. G. 2007. Spatiotemporal dimensions of visual signals in animal communication. *Annual Review of Ecology, Evolution, and Systematics* 38:155–178.
- RYAN, M. J., AND A. S. RAND. 1993. Species recognition and sexual selection as a unitary problem in animal communication. *Evolution* 47:647–657.
- SAENKO, S. V., J. TEYSSIER, D. VAN DER MAREL, AND M. C. MILINKOVITCH. 2014. Precise colocalization of interacting structural and pigmentary elements generates extensive color pattern variation in *Phelsuma* lizards. *BMC Biology* 11: 105.
- SCHNEIDER, C. A., W. S. RASBAND, AND K. W. ELICEIRI. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9:671–675.
- SHANBHAG, B. A., R. S. RADDER, N. P. GRAMAPUROHIT, K. V. DHEERAJ, V. H. AMMANNA, B. N. PANDAV, AND S. K. SAIDAPUR. 2003. Demography of fan-throated lizard, *Sitana ponticeriana* (Cuvier) in a cotton field in Dharwad District of Karnataka State, India. *Current Science* 85:1363–1367.
- SEEHAUSEN, O., J. J. M. VAN ALPHEN, AND F. WITTE. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277:1808–1811.
- STAMPS, J. A. 1977. Social behavior and spacing patterns in lizards. Pp. 265–334 in C. Gans and D. Crews (eds.), *Hormones, Brain, and Behavior, Biology of the Reptilia, Volume 7*. University of Chicago Press, USA.
- . 1983. Sexual selection, sexual dimorphism, and territoriality. Pp. 169–204 in R. R. Huey, E. R. Pianka, and T. W. Schoener (eds.), *Lizard Ecology: Studies of a Model Organism*. Harvard University Press, USA.
- STUART-FOX, D. M., AND T. J. ORD. 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society of London B* 271: 2249–2255.
- STUART-FOX, D. M., A. MOUSSALLI, N. J. MARSHALL, AND I. P. F. OWENS. 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Animal Behaviour* 66:541–550.
- STUART-FOX, D., A. MOUSSALLI, AND M. J. WHITING. 2007. Natural selection on social signals: signal efficacy and the evolution of chameleon display coloration. *American Naturalist* 170:916–930.
- SUBRAMANEAN, J., AND M. V. REDDY. 2010. Seasonal variations in population densities of three lizard species along the Coromandel Coast, India. *Hamadryad* 35:37–45.
- TEYSSIER, J., S. V. SAENKO, D. VAN DER MAREL, AND M. C. MILINKOVITCH. 2015. Photonic crystals cause active colour change in chameleons. *Nature Communications* 6:6368.
- TOKARZ, R. R. 1995. Mate choice in lizards: a review. *Herpetological Monographs* 9:17–40.
- VANHOODYDONCK, B., F. B. CRUZ, C. S. ABDALA, D. L. MORENO AZOCAR, M. F. BONINO, AND A. HERREL. 2005. Sex-specific evolution of bite performance in *Liolaemus* lizards (Iguania: Liolaemidae): the battle of the sexes. *Biological Journal of the Linnean Society* 101:461–475.
- WHITING, M. J., D. M. STUART-FOX, D. O'CONNOR, D. FIRTH, N. C. BENNETT, AND S. P. BLOMBERG. 2006. Ultraviolet signals ultra-aggression in a lizard. *Animal Behaviour* 72:353–363.

Accepted: 24 December 2015.

#### SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at <http://dx.doi.org/10.1670/15-040.s1>.