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COMPLEX SIGNAL USAGE BY ADVERTISING MALE GREEN ANOLES (*ANOLIS CAROLINENSIS*): A TEST OF ASSUMPTIONS

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ABSTRACT: The Green Anole (*Anolis carolinensis*) has three stereotyped head bob displays (labeled A, B, and C) which it differentially uses during directed hetero- and conspecific exchanges. We found free-ranging males advertise (i.e., nondirected signaling) with the same three displays in a complex but consistent manner. From videotapes of 10 adult males recorded across breeding and postbreeding seasons, we analyzed 2308 nondirected displays from two functional subsets of the advertisement context—"monitor" (stationary males signaling from monitoring sites) and "travel" (males signaling while moving between monitoring sites). Using five hypotheses to guide the analysis, we found breeding males (1) used all three display types during both monitor and travel; (2) averaged mostly C displays during monitor (ratio of C:A + B = 4:1); (3) increased A and B displays four-fold during travel (C:A + B = 1:1); (4) averaged a four-fold lower display rate during monitor than during travel (displays/min = 0.8 vs. 3.5, respectively); (5) averaged three-fold more volleys of displays (i.e., a rapid succession of displays) during monitor than during travel (ratio of volleys:singly performed displays = 1.7:1 vs. 0.5:1, respectively); (6) averaged longer volleys during monitor than during travel (displays/volley = 3.3 vs. 2.5, respectively); and (7) appended the "shudderbobbing" modifier (rapid, shallow bobs) to a third of all displays. Males maintained these seven tendencies into the postbreeding, but with much reduced frequencies. The nondirected signaling during monitor and travel are respectively similar to that of long- and short-range aggressive signaling used by contesting males, and bears little similarity to the signaling males use toward females. From our data and those of other studies, we argue that males intend their nondirected signaling for an unidentified male audience (i.e., intrasexually selected), and not for an unidentified female audience (i.e., intersexually selected).

Key words: Advertisement; *Anolis carolinensis*; Communication; Display function; Field study; Lizard; Reptile; Seasonal effects; Sexual selection; Social behavior

WE DESCRIBE here the display dynamics of free-ranging Green Anoles (*Anolis carolinensis*) during the advertisement context. This signaling behavior, however, is best understood from the perspective of the species' mating system and its display profile during directed social exchanges. From field studies, we know that the Green Anole exhibits: (1) a polygynous, female-defense mating system (e.g.; Ruby, 1984; Jenssen et al., 1995; Nunez et al., 1997; Jenssen and Nunez, 1998; Orrell and Jenssen, 2002); (2) a 4-mo breeding season (about April through July) with no pronounced protandry (Jenssen et al., 2001); and (3) iteroparous females that ovulate single-egg clutches at 5–7 d intervals throughout the breeding season (Licht, 1973; Smith et al., 1973; Andrews, 1985; Jenssen and Nunez, 1998). As a consequence of this spatial and

temporal distribution of reproductive females, males defend territories throughout the breeding season with frequent displays as they monitor and patrol their territories (Jenssen et al., 1995).

The displays and their usage are also well documented for *A. carolinensis* during adult male–male and female–female contests (DeCourcy and Jenssen, 1994; Jenssen et al. 2000), adult male and female interactions (Orrell and Jenssen, 2003), and juvenile–juvenile interactions (Lovern and Jenssen, 2001, 2003). From the preceding studies, we know the following: (1) the species' display repertoire consists of three highly stereotyped head-bob patterns (labeled display types A, B, and C; Fig. 1A); (2) both sexes share the three display types; (3) the three displays are performed in all directed conspecific exchanges, only their frequencies vary with social context (Table 1); (4) the extended dewlap (i.e., throat fan; Font and Rome, 1990) is

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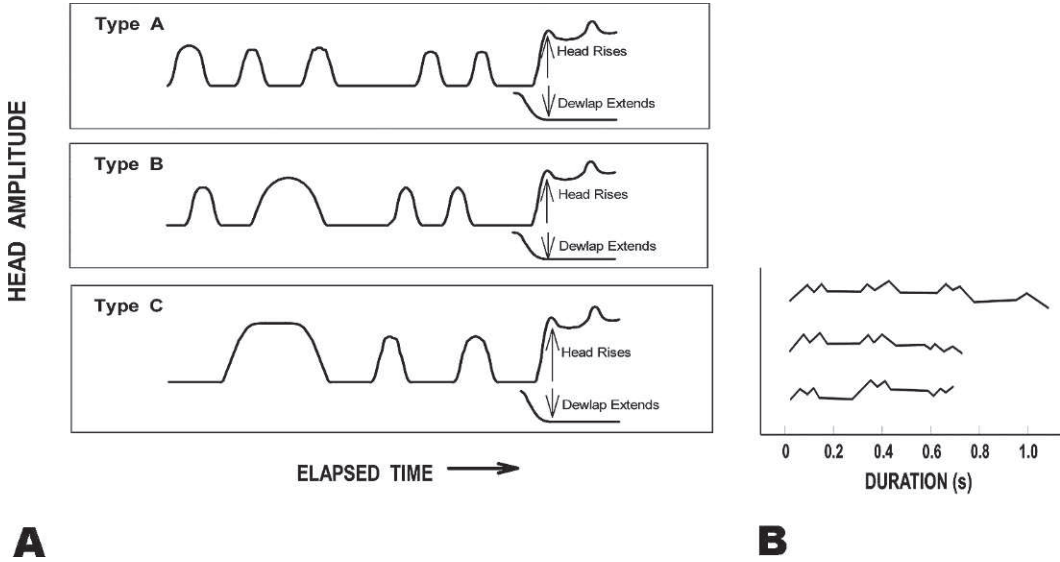


FIG. 1.—(A) The A, B, and C display types of *Anolis carolinensis* (see DeCourcy and Jenssen, 1994, or Lovren et al., 1999, for descriptive statistics). Y-axis depicts relative vertical movements of the head plotted against elapsed time on the x-axis. Dewlap extension is plotted below the x-axis. (B) Three examples of the shudderbob modifier by a male of *Anolis carolinensis* (modified from Orrell and Jenssen, 2003).

predictably integrated into the head-bob patterns (Fig. 1A), but can be withheld at the discretion of both sexes and is correlated with social context (DeCourcy and Jenssen, 1994; Jenssen et al., 2000; Orrell and Jenssen,

2003; Table 1); (5) if the dewlap is extended, signal detection increases for potential recipients (e.g., Fleishman, 2000; Fleishman et al., 2009), especially for male displays where the extended dewlap averages a seven-fold greater

TABLE 1.—Comparative signal profiles of *Anolis carolinensis* during adult male advertising (nondirected) from monitoring sites and when traveling between sites, consensual interactions (male–male, female–female) at long (>60 cm) and short (<20 cm) intersubject separation distances, heterosexual interactions (male–female, female–male), and juvenile interactions.

Signal traits	Male nondirected ¹ (breeding season)		Consensual interactions				Heterosexual interactions ^{3,5}		Juvenile interactions ⁶
	Monitor	Travel	Male–male ²		Female–female ^{3,4}		Males	Females	
			>60 cm	<20 cm	>60 cm	<20 cm			
Display type ratios									
A:B:C	1:3:16	1:1:2	1:1:18	5:7:8	1:3:16	2:3:15	1:1:16	24:25:1	1:1:9 ^o
A + B:C	1:4	1:1	1:9	1:0.7	1:4	1:3	1:8	50:1	1:4
Display rate (avg./h)	46	209	84	228	18	12	19	22	3–14 ^o
% of displays within volleys	86	55	80	8	73	47	80	12	Not examined
% displays with dewlap	97	89	86	7	49	41	99	<2	97–56 ^o
Displays per volley (avg.)	3.3	2.5	4.2	3	3.0	2.8	2.5	2.3	Not examined
Displays with static modifiers ⁷	No	No	Yes	Yes	Yes	Yes	No	No	Yes
% Displays with shudderbobs	33	42	Not examined	None	None	None	22	None	Not examined
Neck-bending	No	No	No	No	No	No	No	Yes	No

¹ Present study.
² DeCourcy and Jenssen, 1994.
³ Nunez et al., 1997.
⁴ Jenssen et al., 2000.
⁵ Orrell and Jenssen, 2003.
⁶ Lovren, 2000.
⁷ Static display modifiers: sagittal compression, gular expansion, raised crest, mouth gape (descriptions in Jenssen, 1979).
^o Ontogenetic shifts in signal use.

area than that of adult females (Jenssen et al., 2000); (6) the sexual size dimorphism of the extended dewlap is an honest sex identification signal; and (7) male dewlap area, which increases nonlinearly with body size, correlates positively with performance traits (Lailvaux et al., 2004; Vanhooydonck et al., 2005a,b; Husak et al., 2007)

Advertisement Function and Assumptions

In our study, we view advertisement signaling as adaptive, whereby a signaler reveals and localizes itself to conspecific neighbors who are as yet undetected or unspecified by the signaler (i.e., nondirected signaling). Nondirected signaling by males is a prominent feature in mating systems in which territorial behavior by males provides access to critical resources and mates (e.g., Emlen and Oring, 1977; Davies, 1991; Shuster and Wade, 2003). In these mating systems, nondirected displaying carries two basic functions—mate attraction and territorial warning to other males; both of these functions are frequently combined into a single, species-specific display (e.g., Bradbury and Vehrencamp, 1998:597–598; McFarland, 2006).

The above paradigm for advertisement signaling (i.e., a single display that carries a dual function) has long been applied to the nondirected displaying of territorial male lizards (e.g., reviews of Carpenter, 1967; Stamps, 1977). Terminology specific to lizard display studies was introduced early on (e.g., Carpenter, 1962a), where the “assertion display” referred to a species’ nondirected displaying (also designated the “signature” display; Stamps and Barlow, 1973). Subsequent studies expanded the general concepts as applied to *Anolis* displays (e.g., reviews of Jenssen, 1977a,b) and contributed to the following generalizations for anoline species: (1) lizards have a repertoire of one to several species-specific display patterns (i.e., display types); (2) only one display type, however, is performed in the assertion context (i.e., nondirected); (3) the nondirected displaying (including dewlap extension) is presumed to attract mates (but see Tokarz, 1995, 2002) and warn rivals; (4) the nondirected display type can also be employed in aggressive and courtship contexts (e.g., *A. garmani*, *A.*

grahami, *A. limifrons*, *A. townsendi* [Jenssen, 1977a,b]; *A. brevirostris*, *A. caudalis*, *A. Webster* [Jenssen and Gladson, 1984]; *A. aeneus* [Stamps and Barlow, 1973]); and (5) during directed displaying, optional postures or movements occur (e.g., Carpenter 1962a,b, 1963) that modify the appearance of the displayer and its display (i.e., “modifiers” such as raised crest, lateral abdominal compression, exaggerated bob amplitude, and appended rapid head-bobs; sensu Jenssen and Hover, 1976; Jenssen, 1979). These five generalizations likely have many exceptions, such that preexisting assumptions may adversely influence experimental designs and data interpretation.

Problems with Advertisement Signals

The “single display” assumption becomes a problem when, without verification, a single display pattern is assumed to carry a species’ advertisement function and is incorporated into laboratory studies (e.g., review of Hebets and Papaj, 2004). What if the assumption is unfounded? Then laboratory protocols, which by their nature test a fixed stimulus on confined subjects in compressed and unnatural environments, risk eliciting distorted signaling behavior and recipient responses from a test subject. Data resulting from a misinformed or naïve protocol can lead to significant misinterpretation.

The “dual function” assumption has its own downside. Where investigators attempt to discriminate between inter- and intrasexual selected attributes of an advertisement signal, both female-choice and male-intimidation attributes are expected to follow similar design rules (e.g., Bradbury and Vehrencamp, 1998: 592–98). Thus, convergence can confound attempts to use physical features of a signal to diagnostically discriminate between those for female attraction and those for intermale aggression. As an experimental approach, recipient responses may be used. Here, the investigator compares the intensity of attraction to that of intimidation to determine relative inter- and intrasexual selected influences. This approach, however, carries intrinsic problems as well (e.g., reviews of Greenfield, 1997; Searcy and Nowicki, 2000). If a recipient has visual contact with the

signaler during testing (a requirement for vision-oriented lizard displays) and if the signaler is aware of the recipient, then the investigator is now observing directed interactions. To counter this last problem, the signal can be separated from the signaler by using playback techniques (not easily done for visual signals, but see Ord and Stamps, 2008; Partan et al., 2011); however, the playback technique carries problems too. First, any resulting qualitative differences between the responses of male and female recipients to the playback stimulus are not usually amenable to quantified intersexual comparisons. Second, playback protocol may simplify complex signaling sequences; the results will likely reflect the same problems arising from the “single display” assumption (e.g., Kroodsma and Byers, 1991).

Guiding Hypotheses

In our study of nondirected signaling by male *A. carolinensis*, we address the “single display” and “dual function” assumptions by avoiding the experimental issues raised above; our data come from (1) wild subjects free of manipulation, (2) continuous video recordings to capture the full expression and normal flow of advertisement signals within a natural habitat, (3) a large data set of associated social behavior, and (4) a large number of corroborative studies and models. To structure our analysis and discussion, we use broad generalizations for advertisement signals and specific generalizations for *Anolis* lizards with multiple display repertoires to propose the following five hypotheses.

Hypothesis 1.—Nondirected displaying should be carried out by only one of the three display types known for the Green Anole (see above citations for assertion context).

Hypothesis 2.—The type C display should serve as the optimal advertisement signal because it is stereotyped, species-specific, sex-specific with the dewlap extended, and because it features an initial large, sustained head-bob (Fig. 1A). The latter would best enhance signal detection at a distance (e.g., Fleishman, 2000; Fleishman and Pallus, 2010).

Hypothesis 3.—Most nondirected displays should occur at high-visibility monitoring

perches and at high duty cycles to facilitate broadcast distance and detection by conspecifics (e.g., Bradbury and Vehrencamp, 1998).

Hypothesis 4.—Nondirected displaying should not be accompanied by optional postures or movements (e.g., Carpenter 1962a,b, 1963).

Hypothesis 5.—Nondirected displaying should serve a dual function—as a female attractant and a male deterrent (e.g., Bradbury and Vehrencamp, 1998; Searcy and Nowicki, 2000; and *Anolis* overview, Losos, 2009: 163–187).

MATERIALS AND METHODS

Our data came from a 63-h (41-h May–July breeding season; 22-h August–September postbreeding season) videotape record with which Jenssen et al. (1995) described the daily activities of free-ranging *A. carolinensis*. Extended, uninterrupted on-camera intervals (mean = 28 min), interspersed by short off-camera intervals (mean = 3.6 min), captured the basic activity events of *A. carolinensis* subjects. These events are defined as follows: (1) monitor—a block of time during which the subject (a) maintains a stationary perch for ≥ 60 s; (b) displays toward no specific individual (i.e., nondirected displays); and (c) shows no evidence of another event, such as moving within the habitat, interacting with specific individuals, or attempting to feed; (2) travel—a block of time during which the subject (a) makes a perch shift by walking or running, including pauses of < 59 s; (b) displays toward no specific individuals (i.e., nondirected displays); and (c) shows no evidence of another event, such as remaining at the same perch locality for a significant length of time (≥ 60 s), interacting with specific individuals, or stalking a food item and attempting to feed; (3) alert—a block of time during which the subject (a) directs his attention toward another male; (b) moves and displays in response to another male; and (c) concludes with the resumption of another event; (4) female—a block of time when the subject (a) directs his attention toward a female; (b) moves and displays in response to a female; and (c) concludes with the resumption of another event; (5) coitus—a block of time when the subject is in copula;

and (6) foraging—a block of time when the subject (a) directs his attention toward a prey item; (b) moves, strikes, and consumes the food item; and (c) continues foraging until the resumption of another event.

The study site, located 12 km northwest of Augusta, Georgia, USA (elev. 130 m; 33.3°N, 82°W; datum = WGS84), was in a bottomland hardwood habitat (Workman and McLeod, 1990) between the Savannah River and the Augusta Canal. A towpath along the canal provided an elevated platform from which lizards were videotaped as they moved in the trees and shrubs on the berm of the canal. We minimized observer effect by using subjects that had not yet been noosed and by recording their behavior at long working distances using a 168-mm zoom lens (equivalent to a 1200-mm lens on a 35-mm camera) fitted to a Panasonic AG 460 camera on a heavy tripod. After the video session, subjects were noosed and paint-marked; snout-vent length (SVL) was measured and individual markings were noted before subjects were released onto their territories. Later, when we videotaped during the postbreeding season, we used site fidelity and paint marks to relocate the same individuals; if they had shed, unique body spotting, scars, and relative body size confirmed their identification.

Each of 10 males was videotaped for approximately 3 h/season by a two-member team. One observer tracked the subject with the camera; the other monitored the broad scope of immediate habitat to provide off-camera data that included presence of other conspecifics (distance and locality) and subject's activities when vegetation blocked the camera image. The observations of the second observer were recorded onto the audio track of the videotape and preprinted data sheets.

We used the above definitions for events to identify the two contexts for nondirected displaying, monitor, and travel. These two events were not pooled because logically they represent different contingencies. For example, in comparison with traveling through habitat, males at monitoring sites should have longer lines of sight (on average) for advertising to a large potential audience, and thus gaining the most response time should potential mates, rival males, or predators be

detected. We also distinguished between breeding and postbreeding periods to compare the rate and manner of nondirected signaling with seasonal shifts in social behavior, physiological state, and presumed selection pressures.

Identifying the two advertisement events was facilitated by our videotape record and the second observer's narrative. As opposed to data that are keyed into handheld devices during real-time activities (i.e., nonreviewable data), the videotapes permitted us to characterize, quantify, and reevaluate events and their display variables through time (nearest 0.03 s) at our playback equipment (Panasonic AG 7350) in the laboratory. We used a conservative filter by eliminating displays from our data set if (1) the audio input from the second observer indicated the near proximity of an off-camera conspecific, (2) the behavior of the videotaped male carried cues he had targeted a recipient (e.g., male intent on a point in the habitat and/or moved toward that point), and/or (3) the video record subsequently revealed a nearby conspecific or food item.

We attempted to classify each display by its type for all six events across both season. From 3838 videotaped displays (3066 in breeding season, 772 in nonbreeding season), 698 (18.2%) could not be typed because the displayer went off-camera or was partially obscured by vegetation; these displays were tagged "U" for unknown. An additional 110 displays (2.8%) were a retrograde version of the A and B patterns that reflected an early stage of display ontogeny (see Lovern and Jenssen, 2003); they were tagged as "X" displays for regressive. The remaining 3030 displays were sorted by event. There were a total of 2308 displays during monitor and travel events that comprised our sample of nondirected and typed displays.

The record for each display included (1) signaler identity, (2) signaler SVL, (3) date (day/mo), (4) season (breeding/post-breeding), (5) time of occurrence (h:m:s), (6) event (monitor/travel), (7) display type, (8) absence or kind of any modifier present, (9) performance as a single display (≥ 2 s before or after another display), and (10) performance within a volley (< 2 s before or after another display),

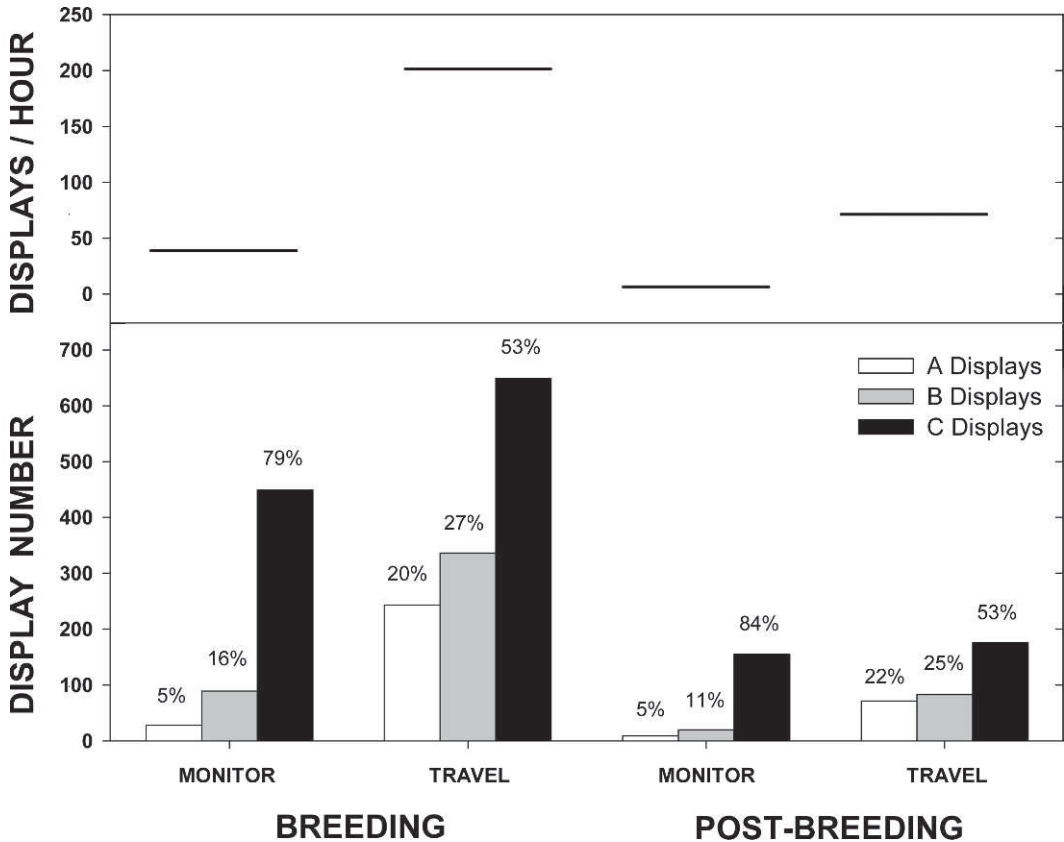


FIG. 2.—Number of displays performed by type (A, B, and C) within monitor and travel events during the breeding and nonbreeding season (present study), including the mean display rate for combined A, B, and C displays for each seasonal event (from Jenssen et al., 1995), as performed by 10 free-ranging males of *Anolis carolinensis*. Proportion of each display type within a seasonal event is given over each respective bar.

and if in a volley, its numeric position in the volley. Central tendencies of these data were calculated as grand means and standard errors from the means of individual lizards. Non-parametric procedures (Siegel and Castellan, 1988) were used to test for trends and sample differences of continuous and ordinal data without requiring Gaussian distribution of the data. When performing an analysis of variance within a multivariate model or between two samples, we used Kruskal-Wallis or Wilcoxon rank sums procedures. The α -level ($P < 0.05$) was applied to two-tailed tests for nonspecific null hypotheses and to one-tailed tests when applied to a priori hypotheses with predicted directionality. In cases of multiple testing, we used a modified Bonferroni procedure (Hommel, 1988) to adjust P -values to minimize

making a type I error (i.e., rejecting the null hypothesis when it is true). Statistical procedures were computed using SAS version 8.2 (SAS, Cary, North Carolina).

RESULTS

Display Types Used and their Proportions

Hypothesis 1 (only one display type for nondirected displaying) was unsupported because all males in both events and across both seasons used A, B, and C display types (Fig. 2). In addition, males used A and B displays differentially between the monitor and travel events. The ratio of C:A + B displays was approximately 4:1 during monitor, but shifted to 1:1 during travel—a four-fold increase of A

and B displays; the same event-contingent ratios were consistent across seasons (Fig. 2).

Hypothesis 2 (Type C display best suited for long-distance detection) was supported by frequency data. Type C displays accounted for most of the displays in both seasons (breeding, 62% of 1794 displays; postbreeding, 64% of 514 displays). Of note, the C display was most heavily used during monitoring (breeding, 79% of 566 displays; postbreeding, 84% of 184 displays), the event when the longest broadcast distances might be expected. Statically, all observed percentages for the C display deviated significantly from an expected 33% of a sample ($\chi^2 \geq 418$, $P < 0.0001$, $n = 184$ -1794).

Display Numbers, Rates, and Temporal Spacing

Hypothesis 3 (i.e., greater nondirected signaling from monitoring sites than when traveling) was largely unsupported. The total number and rates of nondirected displays were lowest during monitoring, a trend consistent across seasons (Fig. 2). Using the means from individual males, comparisons of display rates between events by season were all significant (Wilcoxon sign-rank tests: breeding/monitor vs. travel, $Z = -3.034$, $P = 0.002$, $n = 18$; postbreeding/monitor vs. travel, $Z = 2.452$, $P = 0.014$, $n = 18$).

In partial support of Hypothesis 3, volley lengths were longer when males monitored during both the breeding and postbreeding seasons (3.3 ± 0.10 and 3.1 ± 0.14 displays/volley, respectively) and were longer than when they travelled (2.5 ± 0.04 and 2.5 ± 0.08 displays/volley, respectively); these event differences were significant for both seasons (breeding: Wilcoxon sign-rank test, $Z = 10.971$, $P < 0.0001$; postbreeding: Wilcoxon sign-rank test, $Z = 8.400$, $P < 0.0001$).

In contrast, the number of volleys (but not their lengths) and single displays was highest when males traveled. For monitoring, the average of male ratios for volleys:single displays was 1.7:1 (totals: 172 volleys:104 single displays) and 3.6:1 (totals: 62 volleys:17 single displays) for breeding and postbreeding, respectively. For travel, the average of male ratios for volleys:single displays was 0.5:1 (totals: 378 volleys:773 single displays) and

0.5:1 (totals: 99 volleys:203 single displays) for breeding and postbreeding, respectively. Pooling across seasons, the average ratio of volleys:single displays reflected a four-fold shift between events, from approximately 2:1 during monitoring to 1:2 during travel (totals: 234/121 and 477/976, respectively).

Shudderbob Modifier

Hypothesis 4 (i.e., no modifiers should accompany nondirected signaling) was not supported. The “shudderbob” display modifier—a series of rapid, shallow, double head nods (Fig. 1B)—was appended to 39% of the 2308 displays (breeding, 41% of 1794 displays; postbreeding, 31% of 514 displays). When seasons were combined, more displays during travel had shudderbobs (41% of 1558) than during monitoring (34% of 750 displays). Across events and seasons, shudderbobs were more frequently appended to A and B displays (45% of 879 displays) than to C displays (35% of 1429 displays).

Dual Function Evaluation

Hypothesis 5 (i.e., a dual function for nondirected signaling) is evaluated by inference, rather than direct empirical testing. The evaluation is made below (see Discussion, Functional Inferences).

DISCUSSION

Points of Emphasis

Three nondirected display types, not one.—*Anolis carolinensis* males used three stereotyped head-bob patterns (A, B, and C display types) for nondirected displaying during monitor and travel events. Display usage distinctly shifted between the two events in rates of displaying, ratios of the three display types performed, proportions of volleys to single display performances, and numbers of displays per volley; these shifts were consistent among males and across seasons (Fig. 2). The complex usage of multiple display types accentuates an important conceptual issue—a long-observed problem with labeling a signal by a function (Tinbergen, 1972: 30). Obviously, *A. carolinensis* has no “assertion display,” but rather, three display types abstractly labeled A, B, and C. Furthermore, these same three display types appear in aggressive and

sexual contexts (Table 1). Therefore, using functional names (e.g., “challenge display,” “threat display,” “courtship display,” “submissive nod”) in these contexts can seriously obfuscate the communication system, and lead to misinformed experimental protocols (see Introduction, single display assumption).

Multiple advertisement contexts.—Shifts in display usage between the monitor and travel events were a curious observation. Conventional constructs for advertisement signaling (e.g., Bradbury and Vehrencamp, 1998) predict the monitoring sites as the focus for high-duty cycles (i.e., long-distance signaling at high repetition rates). To some extent this seemed the case for *A. carolinensis* males. When monitoring, males performed display volleys of greater length than when traveling (Table 2) and favored the C display pattern (best fit for broadcast attributes; see Fleishman, 1992; Leal and Fleishman, 2004; Fleishman and Pallus, 2010) over the A and B displays (Fig. 2).

For remaining variables, however, the travel event overshadowed monitoring for prolific nondirected signaling. Males performed twice the number of volleys when traveling than when at monitoring sites (Table 2) and at four times the display rate (Fig. 2). Even more provocative, the combined frequencies of A and B displays types shifted from less than 20% of displays during monitor to almost 50% during travel (Fig. 2).

Even though the event-specific signaling profiles were consistent across males and seasons of our study, there remains a question of consistency between populations. Bloch and Irschick (2006) made a careful study of display type usage by two *A. carolinensis* populations, one in a clumped habitat and the other in continuous habitat. They found interpopulation differences in the A, B, and C display profiles, but made no correlations to concomitant activities. Our findings suggest that the habitat differences of the Bloch and Irschick study may reflect a population difference in time spent monitoring (emphasizing C displays) vs. traveling (emphasizing A and B displays), rather than a possible intrinsic difference in the populations' communication systems. That Bloch and Irschick (2006) found more C displays and fewer A and

TABLE 2.—Volleys proportioned by length (display number per volley) performed during the nondirected events of monitoring and travel by 10 free-ranging males of *Anolis carolinensis* during the breeding and postbreeding seasons (n = sample size of volleys).

Displays per volley	Breeding season		Post-breeding season	
	% Monitor ($n = 172$)	% Travel ($n = 378$)	% Monitor ($n = 62$)	% Travel ($n = 99$)
2	31	60	34	64
3	33	30	35	28
4	20	8	22	4
5	11	1	5	2
6	3	<1	2	2
7	1	<1	2	—
9	1	—	—	—
Total	100%	100%	100%	100%

B displays by males in the clumped habitat than in continuous habitat might be explained by our data. Logically, if clumped habitat produces territories with long monitoring distances and discrete boundaries, then males could spend less time patrolling and more time monitoring (increase in C displays by our findings). In contrast, if continuous habitat produced contiguous and overlapping territories with short monitoring distances and indiscrete boundaries, then males would need to spend more time patrolling (four-fold increase in A and B displays by our findings). Thus, interpopulation differences in habitat structure and lizard demography should shift the proportion of time males and females spend in various activities (i.e., events). In turn, those time shifts will affect the event-dependent display features of an *A. carolinensis* population (see Table 1).

“Shudderbob” modifier.—Because modifiers are generally observed during directed social exchanges (see Introduction), it was unexpected to find the shudderbob modifier (Fig. 1B) appended to more than 30% of *A. carolinensis* nondirected displays (all display types and both events and seasons, Table 1). This modifier has been widely observed in the displays of many lizard species (e.g., “courtship nodding” [Carpenter, 1967]; “shudderbobbing” [Cooper, 1977]; “jiggling” [Evans, 1938]; “rapid nodding” [Greenberg, 1977]; “shuddering” [Tinkle, 1967]), and it has been reported across all social milieu (e.g., Ruby, 1977).

To suggest a message for shudderbobbing by inference from a correlated activity has proven elusive. For example, this approach has posited that the shudderbob indicates male courtship intent, male pacification of female, female submissiveness, and high arousal and tendency to attack (e.g., Greenberg and Noble, 1944; Ferguson, 1977; Greenberg, 1977; Ruby, 1977; Greenberg and Crews, 1983). Our data conclusively reject a specific social message (e.g., courtship intent) because the modifier appeared with nondirected displays in both the breeding and postbreeding seasons (Table 1). Therefore, in the absence of a recipient, perhaps the modifier reflects the displayer's internal state (e.g., heightened alertness). Our data even open the discussion to an old idea (Noble and Bradley, 1933)—that simple head nods are a means for better depth perception (i.e., parallax displacement; see *Chamaelinorops barbouri*; Jenssen and Feely, 1991).

Functional Inferences

We use six lines of inference to examine Hypothesis 5, that nondirected displaying has the dual functions of attracting mates (intersexual selection) and repelling rival males (intrasexual selection). All six suggest that nondirected displays of male *A. carolinensis* have been selected primarily to address intermale competition.

Experimental evidence.—Direct experimental evidence for female-choice (intersexual selection) of *Anolis* male signalers and their attributes has been equivocal, including no support that females are attracted by the dewlap of the male Green Anole (e.g., Tokarz, 1995, 2002; Lailvaux and Irschick, 2006; Steller and White, 2010).

Mating system.—The breeding territories of male *A. carolinensis* are not preestablished for the purpose of attracting females (i.e., not resource-defense polygyny), but rather are established around existing female home ranges (i.e., female-defense polygyny; Jenssen et al., 2001). Large male body size correlates positively with winning intermale contests (e.g., Lailvaux et al., 2004; Jenssen et al., 2005) and controlling territories with the most resident females (Ruby, 1984; Jenssen et al., 1995; Jenssen and Nunez, 1998). Thus, males

gain fitness through intrasexual selection, not necessarily by attracting distant females. In this perspective, nondirected displaying is a warning to potential male intruders, not as an allurement to females.

Daily activity.—If male nondirected signaling was selected for mate attraction, then males should optimally choose a few high-visibility perch sites from which to broadcast for long durations and at a high rate. The opposite seems true. Jenssen et al. (1995) reported a frenetic pattern of patrol by free-range male *A. carolinensis*. Average bouts of monitoring were brief (3.3 min/bout, 2.5 displays/bout), interspersed with short, frequent bouts of travel (1.9 min/bout, 6.5 displays/bout, 2.3 m moved/bout).

Signal number.—If nondirected signaling was selected primarily for mate attraction, then a single complex display is predicted (e.g., Bradbury and Vehrencamp, 1998: 577–586). Johnstone (1996) modeled the conditions under which single vs. multiple advertisement signals might be selected as an indication of signaler quality. Under low signal costs, increased investment in one signal occurs at the expense of others, particularly when reinforced by strong preferences in receivers (i.e., sensory driven selection by females; reviewed by Endler and Basolo, 1998). This leads to one highly exaggerated display at model equilibrium.

In contrast to a female-choice prediction, intermale aggression would likely generate multiple threat displays. Andersson (1980) contended that when contestants experience intense conflict and engage in tactics of bluff and assessment (i.e., manipulation and mind-reading; Krebs and Dawkins, 1984), the effectiveness of a signal to predict an attack becomes eroded. Then frequency-dependent selection should shift to a more reliable indicator by building on aspects of the original signal to produce a new aggressive signal, while retaining the original signal in the display repertoire. In the context of an arms race (i.e., manipulators selected for effective signals and assessors selected for accurate signal evaluation), the number of signals is expected to successively evolve (Maynard Smith and Harper, 2003). The nondirected signaling with multiple display types by *A.*

carolinensis males seems a better fit for the intrasexually selected model than that of the intersexually selected model.

Comparison of nondirected signal use with other contexts.—Examining the use of signals by social context provides a valid indicator of signaler intent. Therefore, if nondirected signaling has been selected primarily through female choice, then one would expect similar signals and a common pattern of use with those of female-directed signaling. Conversely, if nondirected displaying is selected primarily through intermale threats, then one would expect nondirected signaling to use the same displays and in a similar manner as those of male-directed signaling.

Heterosexual signaling by *A. carolinensis* males does not resemble nondirected signaling. Courting males almost exclusively use C displays (Orrell and Jenssen, 2003; Table 1), whereas nondirected displays by males use a large proportion of A and B displays (Fig. 2). In contrast to female-directed displays, the signaling by contesting males closely parallels that of nondirected signaling (Table 1). As contesting males approach from long separation distances to close proximity—and as advertising males shift from monitor to travel—the same trends occur: (1) the proportion of A and B displays increase, (2) display rate increases, (3) proportion of single displays increases, and (4) volley length decreases (Table 1).

Comparison of signal use across seasons.—Effects of sexual selection should markedly decrease as males shift from the breeding to postbreeding period. With the shift in season, display function (or functions) could change along with signal attributes and pattern of use. If nondirected signals contain intersexual selected elements for attracting mates or maintaining resident female mating interest, then these elements should drop out in the postbreeding period. Conversely, if nondirected signals contain intrasexual selected elements for repelling male competitors, then these elements should continue in the postbreeding season as warnings to conspecifics, regardless of sex, to maintain individual distance on a foraging home range.

We did not find any signal or signal component during the breeding season to be

missing in the nondirected signaling of postbreeding males, nor was there any difference in the pattern of signal use. Not even the proportion of C displays (a likely female attractant) decreased. Only display rate declined (Fig. 2; Tables 1 and 2).

Future Research

The contrast between the two event-specific signaling profiles suggests that two different fitness-related contingencies exist for monitoring vs. traveling. As indicated in Table 1, nondirected signaling strongly mimics contest signaling. This suggests that nondirected signaling may be risk-modulated as is true for long-range (low-risk) vs. short-range (high-risk) contest signaling (DeCoursey and Jenssen, 1994; Jenssen et al., 2005). The monitor/travel-dependent signaling may indicate that males are cognizant (*sensu* Shuttleworth, 1998) of greater risk during travel. Are traveling males registering an awareness of likely encounters with conspecifics by signaling in an aggressive manner? If cognition is involved, then by definition, learning is too. A number of studies have shown that fish and lizards can be quickly conditioned to cues that predict impending events (e.g., Rothblum et al., 1979; Hollis, 1990; Marcellini and Jenssen, 1991; Hollis, 1999; Hollis et al., 2004). Through associative learning, individuals may likely use conditioned stimuli to anticipate and prepare for the contingencies of an encounter with prey, predator, competitor, or mate, thereby gaining increased performance efficiency. With evidence of spatial cognition in anoles (Jenssen, 2002), patrolling males traveling between monitoring sites may have the ability to associate particular spatial positions within their territories with past social encounters (e.g., competitors or receptive resident females). This is an area of field investigation where baseline signaling or site-specific signaling might be induced to change after an introduced threat or released female along a male's patrol route.

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LITERATURE CITED

- Andersson, M. 1980. Why are there so many threat displays? *Journal of Theoretical Biology* 86:773–781.
- Andrews, R.M. 1985. Oviposition frequency of *Anolis carolinensis*. *Copeia* 1985:259–262.
- Bloch, N., and D.J. Irschick. 2006. An analysis of inter-population divergence in visual display behavior of the Green Anole lizard (*Anolis carolinensis*). *Ethology* 112:370–378.
- Bradbury, J.W., and S.L. Vehrencamp. 1998. *Animal Communication*. Sinauer Associates, Inc. Publishers, USA.
- Carpenter, C.C. 1962a. Patterns of behavior in two Oklahoma lizards. *American Midland Naturalist* 67:32–151.
- Carpenter, C.C. 1962b. A comparison of the patterns of display of *Urosaurus*, *Uta*, and *Streptosaurus*. *Herpetologica* 18:145–152.
- Carpenter, C.C. 1963. Patterns of behavior in three forms of the Fringe-toed Lizards (*Uma*-Iguanidae). *Copeia* 1963:406–412.
- Carpenter, C.C. 1967. Aggression and social structure in iguanid lizards. Pp. 87–105 in W.W. Milstead (Ed.), *Lizard Ecology: A Symposium*. University of Missouri Press, USA.
- Cooper, W.E. 1977. Information analysis of agonistic behavioral sequences in male iguanid lizards, *Anolis carolinensis*. *Copeia* 1977:721–735.
- Davies, N.B. 1991. Mating systems. Pp. 263–294 in J.R. Krebs and N.B. Davies (Eds.), *Behavioral Ecology: An Evolutionary Approach* (3rd Ed). Blackwell Scientific Publishers, UK.
- DeCourcy, K.R., and T.A. Jenssen. 1994. Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. *Animal Behaviour* 47:251–262.
- Emlen, S., and L. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:214–223.
- Endler, J.A., and A.L. Basolo. 1998. Sensory ecology, receiver biases and sexual selection. *Trends in Ecology and Evolution* 13:415–420.
- Evans, L.T. 1938. Courtship and sexual selection of *Anolis*. *Journal of Comparative Psychology* 26:475–492.
- Ferguson, G.W. 1977. Variation and evolution of stereotyped behavior in reptiles. Pp. 405–554 in C. Gans and D.W. Tinkle (Eds.), *Biology of the Reptilia, Ecology, and Behaviour* A. Academic Press, New York, USA.
- 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.
- Fleishman, L.J. 2000. Signal function, signal efficiency and the evolution of anoline lizard dewlap color. Pp. 209–236 in Y. Espmark, T. Amundsen, and G. Rosenqvist (Eds.), *Animal Signals: Signalling and Signal Design in Animal Communication*. Tapir Academic Press, Norway.
- Fleishman, L.J., and A.C. Pallus. 2010. Motion perception and visual signal design in *Anolis* lizards. *Proceedings of the Royal Society B, Biological Sciences* 277:3547–3554.
- Fleishman, L.J., M. Leal, and M.H. Persons. 2009. Habitat light and dewlap color diversity in four species of Puerto Rican anoline lizards. *Journal of Comparative Physiology A* 195:1043–1060.
- Font, E., and L. Rome. 1990. Functional morphology of dewlap extension in the lizard *Anolis equestris* (Iguanidae). *Journal of Morphology* 206:245–258.
- Greenberg, B., and G.K. Noble. 1944. Social behavior of the American chameleon (*Anolis carolinensis* Voigt). *Physiological Zoology* 17:392–439.
- Greenberg, N. 1977. A neuroethological study of display behavior in the lizard *Anolis carolinensis* (Reptilia, Lacertilia, Iguanidae). *American Zoologist* 17:191–201.
- Greenberg, N., and D. Crews. 1983. Physiological ethology of aggression in amphibians and reptiles. Pp. 469–506 in B.B. Svare (Ed.), *Hormones and Aggression*. Plenum Press, USA.
- Greenfield, M.D. 1997. Sexual selection and the evolution of advertisement signals. Pp. 145–177 in D.H. Owings, M.D. Beecher, and N.S. Thompson (Eds.), *Perspective in Ethology*, Vol. 12, Communication. Plenum Press, USA.
- Hebets, E.A., and D.R. Papaj. 2004. Complex signal function: Developing a framework of testable hypotheses. *Behavioral and Ecological Sociobiology* 57:197–214.
- Hollis, K.L. 1990. The role of Pavlovian conditioning in territorial aggression and reproduction. Pp. 197–219 in D.A. Dewsbury (Ed.), *Contemporary Issues in Comparative Psychology*. Sinauer Press, USA.
- Hollis, K.L. 1999. The role of learning in the aggressive and reproductive behavior of Blue Gouramis, *Trichogaster trichopterus*. *Environmental Biology of Fishes* 54:355–369.
- Hollis, K.L., L.A. Blouin, M.C. Romano, K.S. Langworthy-Lam, and J. Siegenthaler. 2004. Maintaining a competitive edge: dominance hierarchies, food competition and strategies to secure food in green anoles (*Anolis carolinensis*) and firemouth cichlids (*Thorichthys meeki*). *International Journal of Comparative Psychology* 17:222–240.
- Hommel, G. 1988. A stagewise rejective multiple test procedure based on a modified Bonferroni test. *Biometrika* 75:383–386.
- Husak, J.F., D.J. Irschick, J.J. Meyers, S.P. Lailvaux, and I.T. Moore. 2007. Hormones, sexual signals, and performance of the Green Anole lizard (*Anolis carolinensis*). *Hormones and Behavior* 52:360–367.
- Jenssen, T.A. 1977a. Evolution of anoline lizard display behavior. *American Zoologist* 17:203–215.
- Jenssen, T.A. 1977b. Display diversity in anoline lizards and problems of interpretation. Pp. 269–285 in N. Greenberg and P.D. MacLean (Eds.), *Behavior and Neurology of Lizards: An Interdisciplinary Colloquium*. National Institute of Mental Health, USA.
- Jenssen, T.A. 1979. Display modifiers of *Anolis opalinus* (Lacertilia: Iguanidae). *Herpetologica* 35:21–30.
- Jenssen, T.A. 2002. Spatial awareness by the lizard *Anolis cristatellus*: Why should a non-ranging species demonstrate homing behavior? *Herpetologica* 58:364–371.

- Jenssen, T.A., and P.C. Feely. 1991. Social behavior of the male anoline lizard *Chamaelinorops barbouri*, with a comparison to *Anolis*. *Journal of Herpetology* 25:454–462.
- Jenssen, T.A., and N. Gladson. 1984. A comparative display analysis of the *Anolis brevirostris* complex in Haiti. *Journal of Herpetology* 18:338–341.
- Jenssen, T.A., and E.L. Hover. 1976. Display analysis of the signature display of *Anolis limifrons* (Sauria: Iguanidae). *Behaviour* 57:227–240.
- Jenssen, T.A., and S.C. Nunez. 1998. Spatial and breeding relationships of the lizard, *Anolis carolinensis*: Evidence of intrasexual selection. *Behaviour* 135:981–1003.
- Jenssen, T.A., N. Greenberg, and K.A. Hovde. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding season. *Herpetological Monographs* 9:41–62.
- Jenssen, T.A., K.S. Orrell, and M.B. Lovern. 2000. Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis*. *Copeia* 2000:140–149.
- Jenssen, T.A., M.B. Lovern, and J.D. Congdon. 2001. Field-testing the protandry-based mating system for the lizard, *Anolis carolinensis*: Does the model organism have the right model? *Behavioral Ecology and Sociobiology* 50:162–172.
- Jenssen, T.A., K.R. DeCourcy, and J.D. Congdon. 2005. Assessment in contests of male lizards (*Anolis carolinensis*): How should smaller males respond when size matters? *Animal Behaviour* 69:1325–1336.
- Johnstone, R.A. 1996. Multiple displays in animal communication: 'Backup signals' and 'multiple messages.' *Philosophical Transactions of the Royal Society of London B* 351:329–338.
- Krebs, J.R., and R. Dawkins. 1984. Animal signals: Mind-reading and manipulation. Pp. 380–402 in J.R. Krebs, and R. Dawkins (Eds.), *Behavioural Ecology: An Evolutionary Approach* (2nd Ed). Blackwell Scientific Publications, UK.
- Kroodsma, D.E., and B.E. Byers. 1991. The function(s) of bird song. *American Zoologist* 31:318–328.
- Lailvaux, S.P., and D.J. Irschick. 2006. No evidence for female association with high-performance males in the Green Anole lizard, *Anolis carolinensis*. *Ethology* 112:707–715.
- Lailvaux, S.P., A. Herrel, B. Vanhooydonck, J.J. Meyers, and D.J. Irschick. 2004. Performance capacity, fighting tactics, and the evolution of life-stage male morphs in the Green Anole lizard (*Anolis carolinensis*). *Proceedings of the Royal Society of London, B* 271:2501–2508.
- Leal, M., and L.J. Fleishman. 2004. Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. *American Naturalist* 163:26–39.
- Licht, P. 1973. Influence of temperature and photoperiod on the ovarian cycle in the lizard *Anolis carolinensis*. *Copeia* 1973:465–472.
- Losos, J.B. 2009. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press, USA.
- Lovern, M.B. 2000. Behavioral ontogeny in free-ranging juvenile male and female Green Anoles, *Anolis carolinensis*, in relation to sexual selection. *Journal of Herpetology* 34:274–281.
- Lovern, M.B., and T.A. Jenssen. 2001. The effects of context, sex, and body size on staged social interactions in juvenile male and female Green Anoles (*Anolis carolinensis*). *Behaviour* 138:1117–1135.
- Lovern, M.B., and T.A. Jenssen. 2003. Form emergence and headbobbing displays in the lizard, *Anolis carolinensis*: a reptilian model of signal ontogeny. *Journal of Comparative Psychology* 17:133–141.
- Lovern, M.B., T.A. Jenssen, K.S. Orrell, and T. Tuchak. 1999. Comparisons of temporal display structure across contexts and populations in male *Anolis carolinensis*: Signal stability or lability? *Herpetologica* 55:222–234.
- Marcellini, D.L., and T.A. Jenssen. 1991. Avoidance learning by the curly-tailed lizard, *Leiocephalus schreibersi*: Implications for anti-predator behavior. *Journal of Herpetology* 25:238–241.
- Maynard Smith, J., and D. Harper. 2003. *Animal Signals*. Oxford University Press, UK.
- McFarland, D. (Ed.). 2006. *Oxford Companion to Animal Behaviour*. Oxford University Press, USA.
- Noble, G.K., and T.H. Bradley. 1933. The mating behavior of lizards: Its bearing on the theory of sexual selection. *Annals of the New York Academy of Science* 35:25–100.
- Nunez, S.C., T.A. Jenssen, and K. Ersland. 1997. Female activity profile of a polygynous lizard (*Anolis carolinensis*): evidence of intersexual asymmetry. *Behaviour* 134:205–223.
- Ord, T.J., and J.A. Stamps. 2008. Alert signals enhance animal communication in "noisy" environments. *Proceedings of the National Academy of Science* 105:18830–18835.
- Orrell, K.A., and T.A. Jenssen. 2002. Male mate choice by the lizard, *Anolis carolinensis*: A preference for novel females. *Animal Behaviour* 63:1091–1102.
- Orrell, K.A., and T.A. Jenssen. 2003. Heterosexual signaling by the lizard *Anolis carolinensis*, with intersexual comparisons across contexts. *Behaviour* 140:603–634.
- Partan, S.R., P. Otovic, V.L. Price, and S.E. Scott. 2011. Assessing display variability in wild Brown Anoles *Anolis sagrei* using a mechanical lizard model. *Current Zoology* 57:140–152.
- Rothblum, L.M., J.W. Watkins, and T.A. Jenssen. 1979. A learning paradigm and the behavioral demonstration of audition for the lizard *Anolis grahami*. *Copeia* 1979:490–494.
- Ruby, D.E. 1977. The function of shudder displays in the lizard *Sceloporus jarrovi*. *Copeia* 1977:110–114.
- Ruby, D.E. 1984. Male breeding success and differential access to females in *Anolis carolinensis*. *Herpetologica* 40:272–280.
- Searcy, W.A., and S. Nowicki. 2000. Male-male competition and female choice in the evolution of vocal signaling. Pp. 301–315 in Y. Espmark, T. Amundsen, and G. Rosenqvist (Eds.), *Animal Signals: Signaling and Signal Design in Animal Communication*. Tapir Academic Press, Norway.
- Shuttleworth, S.J. 1998. *Cognition, Evolution, and Behavior*. Oxford University Press, USA.
- Shuster, S.M., and M.J. Wade. 2003. *Mating Systems and Strategies*. Princeton University Press, USA.

- Siegel, S., and N.J. Castellan, Jr. 1988. Non-parametric Statistics for the Behavioral Sciences (2nd Ed.). McGraw-Hill Book Company, USA.
- Smith, J.M., G. Sinelink, J.D. Fawcett, and R.E. Jones. 1973. A survey of the chronology of ovulation in anoline lizard genera. Transactions of the Kansas Academy of Science 75:107–120.
- Stamps, J.A. 1977. Social behavior and spacing patterns in lizards. Pp. 265–334 in C. Gans and D.W. Tinkle (Eds.), Biology of the Reptilia, Ecology, and Behaviour A. Academic Press, USA.
- Stamps, J.A., and G.W. Barlow. 1973. Variation and stereotypy in the displays of *Anolis aeneus* (Sauria: Iguanidae). Behaviour 47:67–94.
- Steller, J.E., and D.J. White. 2010. Social influences on female choice in Green Anole lizards (*Anolis carolinensis*). Behavioural Processes 83:282–286.
- Tinbergen, N. 1972. The Animal in its World, Vol 1: Field Studies. Harvard University Press, USA.
- Tinkle, D.W. 1967. The life and demography of the Side-blotched Lizard, *Uta stansburiana*. Miscellaneous Publications of the Museum of Zoology, University of Michigan 132:1–82.
- Tokarz, R.R. 1995. Mate choice in lizards: A review. Herpetological Monographs 9:17–40.
- Tokarz, R.R. 2002. An experimental test of the importance of the dewlap in male mating success in the lizard *Anolis sagrei*. Herpetologica 58:87–94.
- Vanhooydonck, B., A. Herrel, R. Van Damme, and D.J. Irschick. 2005a. Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? Functional Ecology 19:38–42.
- Vanhooydonck, B., A. Herrel, R. Van Damme, J.J. Meyers, and D.J. Irschick. 2005b. The relationship between dewlap size and performance changes with age and sex in a Green Anole (*Anolis carolinensis*) lizard population. Behavioral Ecology and Sociobiology 59:157–165.
- Workman, S.W., and K.W. McLeod. 1990. Vegetation of the Savannah River Site: Major community types. Savannah River Site Natural Environmental Research Park Program, Department of Energy Publication, SRO-NERP-19:1–137.

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