

Form Emergence and Fixation of Head Bobbing Displays in the Green Anole Lizard (*Anolis carolinensis*): A Reptilian Model of Signal Ontogeny

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Signal ontogeny was examined in green anoles (*Anolis carolinensis*). From 1,246 head bob displays given by 114 juveniles, it was found that juveniles possessed all 3 display types (A, B, and C) described for adults and that C displays were present at hatching, but A and B displays appeared to emerge gradually from a common precursor. Durations of the head bobs and pauses that make up juvenile displays tended to be more variable (i.e., less stereotyped) than those of adult displays. However, within the juvenile class, sex, age (or size), social context, and rearing environment (field or lab) had no effect on display structure or stereotypy. Thus, in contrast to typical signal ontogeny in songbirds and mammals, components of the green anole signal repertoire are expressed from early development. Similar to signal ontogeny in altricial species, maturation is nevertheless important for the complete and stereotyped expression of the adult signal repertoire.

The ontogeny of communication signal structure and use has received uneven attention across taxa, with comparatively few studies existing outside of the avian and mammalian literature (Groothuis, 1993a, 1993b, 1994). This disparity is partly because the social signals of some taxa (e.g., anurans; Kiestler, 1977; Ryan, 1985; orthopterans; Moore, Reagan, & Haynes, 1995) are not expressed until adulthood and exhibit no apparent period of development. In contrast, studies on birds and mammals have revealed that development of their social signals is typically gradual. As examples, songbirds go through an extended signal development period as juveniles, which includes stages for acquisition, storage, and practice of species-typical song patterns (reviewed in Catchpole & Slater, 1995). Juvenile mammals may begin expressing behaviors like the aggressive and sexual signals of adults in the context of play, during which time the behaviors are comparatively variable and do not carry the functional consequences that they will in adulthood (reviewed in Fagen, 1981; Thompson, 1998; Walters, 1987).

Studies conducted within the contexts of avian and mammalian life histories have suggested the importance of an altricial juvenile stage coupled with an environment that allows for extended contact between parents and offspring, among siblings, or among social groups, in the development of aggressive and sexual signals. From such studies, recurring factors salient to signal development

have emerged: maturation, opportunities for imitation and practice, previous social experience, and motivation (e.g., Burghardt, 1977b; Groothuis, 1994; King, Freeberg, & West, 1996; Liu & Kroodsma, 1999; Mateo & Holmes, 1997; Nordby, Campbell, Burt, & Beecher, 2000; Ramakrishnan & Coss, 2000). It does not necessarily follow that an avian- or mammalian-grade social organization is prerequisite for signals to be shaped by environmental inputs, however (Burghardt, 1988; Groothuis, 1993a, 1993b, 1994). Given the few studies on the ontogeny of aggressive and sexual signals outside avian and mammalian taxa, the extent to which the factors listed above are generally important to signal development remains unresolved (Groothuis, 1993a, 1994).

Reptiles are a relevant taxonomic group for the study of generalized developmental processes in signal ontogeny for several reasons. First, reptiles represent the ancestral lineage that gave rise to birds and mammals. Second, reptilian communication systems involve diverse modalities (e.g., visual, chemical, and vocal sensory systems) related to social organization and species differences in ecology and life-history traits (e.g., Baird, Fox, & McCoy, 1997; Burghardt, 1977a, 1978, 1988; LeMaster, Moore, & Mason, 2001; Steele & Cooper, 1997; Tang, Zhuang, & Wang, 2001). Third, some reptiles, in particular lizards, are known to signal as juveniles (e.g., Burghardt, Greene, & Rand, 1977; Greenberg & Hake, 1990; Phillips, Alberts, & Pratt, 1993; Roggenbuck & Jenssen, 1986; Stamps, 1978), thus affording the opportunity to study signal ontogeny in the absence of environmental features commonly associated with altricial species (e.g., parental care or extensive sibling interactions).

We used the green anole lizard to document when adult-typical displays appear in ontogeny, when they become stereotyped (form emergence and form fixation, respectively; Groothuis, 1993b), and whether environment affects the trajectory of display structure development. In anoles, there is no parental care and no social aggregation of hatchlings, which emerge from eggs immediately and are individually responsible for their own survival (Lovern, 2000; Stamps, 1978). Furthermore, the displays of adult green anole lizards have been thoroughly described (DeCourcy & Jens-

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sen, 1994; Jenssen, Orrell, & Lovern, 2000; Lovern, Jenssen, Orrell, & Tuchak, 1999). Adult males and females share a repertoire of three distinct display patterns labeled *A*, *B*, and *C*, which they use to communicate across a variety of functional contexts (e.g., aggressive and sexual interactions). These displays consist of highly stereotyped cadences of vertical head bobbing movements, and each display type may be accompanied by modifiers such as dewlap (throat fan) extension and/or other morphological traits or body postures designed to enhance display visibility (Jenssen, 1977). Adult temporal display structure is markedly stable, varying neither by sex nor by the social context in which displays are given (DeCourcy & Jenssen, 1994; Jenssen et al., 2000; Lovern et al., 1999). Display use can vary tremendously, however. Display rates; proportions of *As*, *Bs*, and *Cs* used; and the expression of modifiers may vary considerably between the sexes and in different social contexts (DeCourcy & Jenssen, 1994; Jenssen et al., 2000). Finally, although juvenile males and females are known to give head bobbing displays (Lovern, 2000), the form of these displays has not been studied.

Our specific objectives were (a) to document the temporal cadence of juvenile green anole lizards' head bobbing displays; (b) to determine the effects of sex, age (or size), social context, and rearing environment (field or laboratory) on when displays arise and when they become stereotyped; and (c) to compare juvenile display structure with that of adults. These data were used to examine the possible roles of maturation, imitation, practice, and social interaction in the emergence and fixation of adult-typical displays. If maturation (defined here broadly as an age- or size-related effect) plays a role in display development, then several ontogenetic patterns are possible. For example, the three display patterns could emerge at different ontogenetic stages, or intraindividual display stereotypy could increase through ontogeny, approaching that of adults, as juveniles become more capable of consistent repetition of a motor pattern (perhaps through underlying neuromuscular development). Such effects should relate to age or size, regardless of sex, social context, or rearing environment, if causally related to maturation. If imitation of other displaying lizards is important to display ontogeny, then lizards reared socially should converge faster on common display cadences than lizards with less opportunities for social interaction. Such an effect should be manifested in higher interindividual stereotypy in social groups than in isolated lizards. If practice, or repetition, is an important input, then lizards with the opportunity for more social interaction (e.g., those from the field or reared socially in the laboratory) should have higher intraindividual display stereotypy than lizards reared alone, because juveniles do not give displays when no other lizards are present (Lovern & Jenssen, 2001) and hence would not have the opportunity to practice. Finally, if specific features of social interaction per se (e.g., sex of interactants) affect display development, then display structure could differ depending on the social context in which displays are given.

Method

Subjects

A total of 114 juvenile green anole lizards (*Anolis carolinensis*; 65 males and 49 females; < 44 mm snout-vent length [SVL]) was used to document display ontogeny. Displays were videotaped from 9 males and 8 females

observed at our field site in Augusta, Georgia, as part of a study on juvenile social behavior (Lovern, 2000). Displays were also videotaped from 32 males and 19 females reared from hatching in the laboratory and observed in behavior trials at several ontogenetic stages, as described below. Finally, displays were videotaped from 24 males and 22 females collected at our field site and brought to the laboratory for behavior trials, as part of a study on the effects of sex, body size, and context on social behavior (Lovern & Jenssen, 2001). We analyzed a total of 1,246 displays (displays per juvenile, $M = 10.9$, $SE = \pm 0.5$). In addition, 304 displays from 30 adults (8 males and 22 females; > 50 mm SVL) were reanalyzed from Jenssen et al. (2000) for comparison to the juvenile displays in the present study.

Procedure

Displays were collected from juveniles in the field by videotaping them under free-ranging conditions (Lovern, 2000). Each juvenile was videotaped for 30–60 min with a Quasar VM547 video camera. To minimize observer effects, we videotaped from a distance of at least 3 m and did not handle lizards prior to observation. Following observations, lizards were captured and sex was determined by postanal scale size (males have two enlarged postanal scales); they were measured to the nearest millimeter SVL, paintmarked for individual identification, and released.

To rear juveniles, we collected eggs from 16 adult females captured at our field site that were housed in groups of 4 in the laboratory. Eggs were incubated in a 1:1 (mass) vermiculite:water mixture in cups that were covered with plastic wrap and a rubber band and kept between 24 and 30°C on a diel cycle. Hatching success was 89%. Upon hatching, lizards were sexed, measured to the nearest millimeter SVL, and toe clipped for permanent identification. We randomly assigned hatchlings to be reared in isolation or in groups. Those reared in isolation were housed in cages measuring 120 cm × 60 cm × 60 cm and divided into fourths with opaque partitions. Those reared in groups were placed in groups of 4 into cages of the same dimensions but without the partitions. The isolate condition did not exclusively test the effect of social isolation, as physical isolation could conceivably affect display structure as well. However, because social interaction of any kind in juveniles is infrequent even in the field (Lovern, 2000), these laboratory housing conditions did not appear to be excessively atypical. We exposed the lizards to a 14:10-hr light–dark cycle using four 40-W full-spectrum bulbs (Durotest Vita-Lite Plus, Philadelphia, PA) placed on the top of each cage. Temperature ranged 27–34°C during the day and dropped to 23°C at night. These conditions approximated what would have been experienced in the field. Cages were furnished with a peat moss substrate, wooden dowels for perching, and artificial vegetation for ground cover. Each day, we sprayed cages with water for drinking and we fed lizards with vitamin-dusted crickets, mealworms, flour beetle larva, or waxworm larva.

Laboratory-reared juveniles were videotaped at known ages to collect displays during specific ontogenetic stages. At age classes of 0–5, 12–16, 28–32, and 85–95 days, 4 lizards at a time were moved to an observation cage divided into four compartments identical to housing cages. Each juvenile was separated by an opaque, removable partition. After 16–24 hr to allow lizards to become familiar with the new cage, pairs of juveniles from within the same housing condition (isolate or group) but unfamiliar to each other were videotaped in 30-min interactions by removing the partition. We videotaped all interactions from a blind using a Panasonic AG 460 video camera fitted with a video telephoto converter (2.0× magnification). The following day, this procedure was repeated with different pairs of lizards. Each lizard was videotaped twice within each age class, once in a consensual trial (male–male or female–female) and once in a heterosexual trial (male–female). For each group of 4 lizards moved to the observation cage, trial order (consensual or heterosexual) was determined by a coin toss. After interactions, lizards were returned to their housing cages.

A subset of juveniles in this study was collected from our field site and housed singly in the laboratory (Lovern & Jenssen, 2001). We videotaped

displays from these juveniles within 14 days of capture, using the protocol described above. To increase the likelihood of generating displays from each lizard in the pair, we minimized asymmetry in their competitive abilities by size matching them to within 2 mm SVL (e.g., Tokarz, 1995).

Of the total of 1,246 displays recorded, 552 displays from 49 males and 39 females ($M = 6.3, SD = \pm 0.7$) were suitable for temporal structure analysis (i.e., full displays recorded on videotape, displaying lizard unobstructed by the habitat and at appropriate angle to camera). These displays were analyzed by reviewing the videotapes frame by frame (30 frames/s) with a Panasonic AG 1950 VCR. We used the display action pattern (DAP) graph method (e.g., Carpenter & Grubitz, 1961; Jenssen et al., 2000) to identify and categorize displays. This technique plots vertical amplitude of lizard head position and dewlap extension (y-axis) over elapsed time (x-axis) for each display. Displays were divided into naturally occurring units consisting of head bobs and interbob pauses. The duration of the units defined the cadence of the display, and displays of a common cadence were categorized as being of the same type (Jenssen, 1977, 1978). For each display, we recorded display type, sex, and size of the displaying lizard (also age when known); the social context in which it was given (consensual, heterosexual, or unknown); and rearing environment of the displaying lizard: (a) field hatched and observed; (b) lab hatched, reared in isolation, and lab observed; (c) lab hatched, reared in a group, and lab observed; or (d) field hatched and lab observed. We also recorded the total number of head bobs in each display, whether dewlap extension occurred, and unit and total display durations to the nearest 0.033 s (the resolution of the VCR). This technique of display analysis is reliable. Our repeatability of display-type classification was 100% (based on a randomly chosen 20-display subsample), and out of 12 displays DAP graphed by each of us, 96% (92 out of 96) of the units were judged to be of identical durations, and the remaining 4% (4 out of 96) were within one frame (0.033 s). Following identification of display types on the basis of DAP graphs, we recorded the same information as above with the exception of unit and total display durations for the 694 displays not suitable for DAP-graph analysis.

Statistical Analyses

We used a nearest neighbor discriminant analysis (e.g., Hair, Anderson, & Tatham, 1987) to statistically assess our categorization of display types. This multivariate technique assigns a discriminant score to each display (based on the sequence of head bob and pause durations recorded for the display) and then uses the score to assign it to the category (i.e., display type) to which it most likely belongs, thus allowing for a comparison between visual and statistical classifications. Once display types were visually identified and statistically confirmed, subsequent comparisons were performed within displays of the same type among homologous units. We calculated unit duration, total display duration, and number of head bobs per display using intrasubject means to eliminate a sample bias due to different numbers of displays from different lizards. To test for differences among groups, we used analyses of variance (ANOVAs; repeated measures or general linear model [GLM], as appropriate) when the data met the assumptions of normality (tested with Kolmogorov–Smirnov one-sample tests) and homogeneity of variance (tested with Levene’s tests; Glass & Hopkins, 1996). We used nonparametric Kruskal–Wallis tests when either assumption was not satisfied following log transformation of the data. We also calculated the coefficient of variation (CV) for display unit durations for each lizard separately (intraindividual; yielding a CV for each display unit for each lizard that gave more than one display of the same type) and for groups of lizards (interindividual; yielding a single CV for each display unit of each display type), as measures of individual and group display stereotypy, respectively (Barlow, 1977). Comparatively large CVs indicate units with comparatively low stereotypy. All tests were two-tailed with an overall alpha of .05. To protect against Type I errors from multiple statistical tests, we used sequential Bonferroni adjustments (Rice, 1989) to determine whether *p* values from tests on unit durations within a display type indicated significant differences at the displaywide level.

Results

Display Description

The 1,246 displays in our data set were assigned to four categories following visual inspection. Three of these categories constituted display types previously identified for adult green anole lizards (DeCourcy & Jenssen, 1994; Jenssen et al., 2000; Lovern et al., 1999). Therefore, we followed the established convention of labeling these three display types as *A*, *B*, and *C*. These display types are shown in Figure 1a. Table 1 shows the sample sizes of

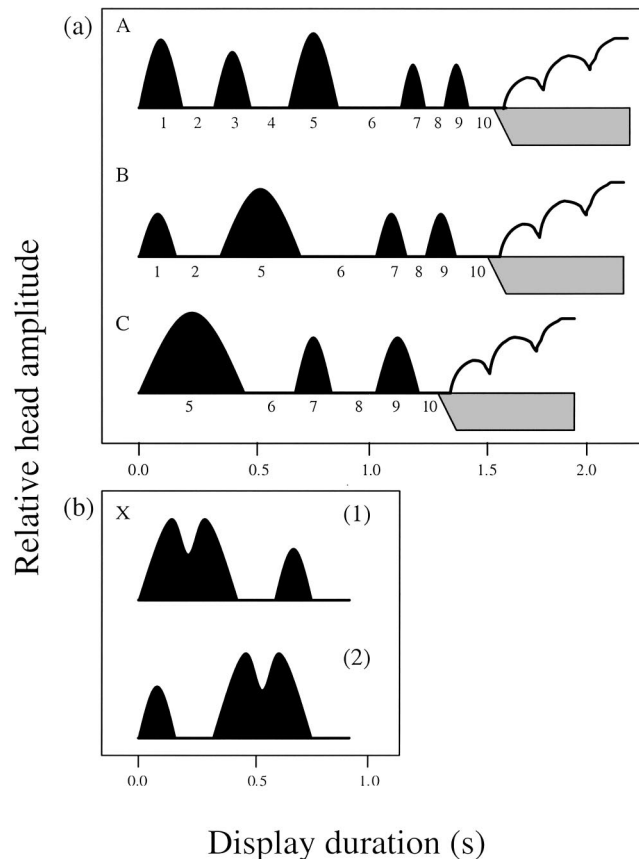


Figure 1. Generalized display action pattern (DAP) graphs for head bobbing display types *A*, *B*, and *C* (a) and the two variants of *X* displays (b) observed in young juvenile male and female green anole lizards. Relative head amplitude is plotted above the *x*-axis over elapsed time. DAP graphs are drawn to approximate the mean head bob and pause durations of 79 Type *A*, 50 Type *B*, 393 Type *C*, and 30 Type *X* displays videotaped from 88 individuals and analyzed at 0.033-s intervals. For Display Types *A*, *B*, and *C*, the core display (i.e., the portion of the display that was always present in every single rendition of that type) is shown in solid black, and terminal, variably produced head bobs are shown by a black line. Numbers correspond to display head bob and pause units, following DeCourcy and Jenssen (1994). Dewlap extension is plotted below the *x*-axis in gray and may be present or absent for each display type. *X* displays were rare, variable in cadence and duration, and therefore lacked the stereotypy found in the *A*, *B*, and *C* display types. As a result, *X* displays were not considered to be stereotyped display types, and only the introductory head bobs, which all *X* displays possessed in one or the other variant, are shown.

Table 1
Sample Sizes of Displaying Lizards (and Head Bobbing Displays) Used to Analyze Juvenile Temporal Display Structure and Stereotypy

Rearing environment and sex	<i>n</i>	Display pattern			
		A	B	C	X
Field					
Males	9	1 (2)	0 (0)	7 (29)	1 (3)
Females	6	0 (0)	1 (1)	5 (27)	0 (0)
Lab reared					
Males	16	7 (14)	2 (2)	16 (150)	6 (14)
Females	13	5 (20)	3 (16)	12 (81)	2 (6)
Field captured					
Males	24	9 (30)	8 (22)	20 (49)	1 (4)
Females	20	6 (13)	4 (9)	17 (57)	2 (3)

juvenile males and females in each recording condition that gave DAP-graphed displays as well as the sample sizes of displays given. Overall, we DAP graphed 79 Type A, 50 Type B, and 393 Type C displays. We observed that both males and females were capable of displaying on the day they hatched. Furthermore, each display type could be given with or without dewlap extension, by both males and females, as reported for adults (DeCourcy & Jenssen, 1994; Jenssen et al., 2000). Because Type C displays were the shortest, with only six units in the core display type (see Figure 1a), we used the first six units of each display type in a nearest neighbor discriminant analysis (which yields a conservative analysis of discrimination, because the bias for comparing display-type categories of different lengths is removed) to confirm our visual classifications of DAP-graphed displays. There was agreement on 492 of 522 (94%) displays (95%, 98%, and 94% for Types A, B, and C, respectively). Thus, even when removing the most obvious difference among display types (i.e., the duration and amplitude of the introductory head bobs; see Figure 1a), three distinct categories clearly remained.

In addition to the three display types shared by juvenile and adult green anole lizards, juveniles exhibited a fourth category of head bobs that we labeled X displays. These displays did not have a discrete cadence of their own (i.e., were not a uniquely distinct display type) but rather exhibited considerable structural overlap with the cadences of the A, B, and C display types. The X displays were the rarest in occurrence, accounting for only 48 (4%) of the 1,246 displays observed, of which 30 were DAP graphed (see Table 1). Individuals from both the field and the laboratory gave X displays, all of which shared the trait that either the first or the second head bob within the display contained a brief dip in head amplitude, as depicted in Figure 1b. The unusual head dip was suggestive of a pause that was in the incipient stage of being added to or removed from a display cadence. The head bob with the dip was always higher in amplitude and longer in duration than any other head bobs within the same display. The remaining two head bobs that always occurred in X displays were intermediate in duration to the final two head bobs in Display Types A and B. Not surprisingly, therefore, nearest neighbor discriminant analysis showed low agreement with our classification of Type X displays, agreeing with only 4 of 30 displays (13%).

Display Emergence

The emergence of the A, B, C, and X displays occurred asynchronously during ontogeny. Figure 2 shows the relative percentages of A, B, C, and X displays given by the 114 juveniles in this study, by size class. The Type C display was most common in every size class, beginning at 90% of the displays for the smallest lizards (Class 1) and steadily decreasing to 72% of the displays for the largest (Class 5). This decrease in the relative frequency of the Type C display corresponded with increasing use of Display Types A and B, which collectively accounted for 1% of displays in Size Class 1 but 27% of displays in Size Class 5. X displays were more common than Display Types A and B in Size Classes 1 and 2 (9% and 10%, respectively), but they declined in relative frequency in Size Classes 3–5 (3%, 1%, and 1%, respectively) as Display Types A and B were increasing in relative frequency. When considering only the laboratory-reared lizards, for which ages were known, the relative frequencies of X displays by age class mirrored the pattern described for size class. X displays were most common in individuals less than 14 days old (13% of displays), after which they continued to drop in frequency at 15–30 days old (9%) and at more than 30 days old (3%).

Display Fixation

Because Display Types A and B were infrequently performed by juveniles, we pooled across size classes and recording conditions to achieve an adequate sample size for statistical analysis. For size class, individuals were scored as 1 (≤ 30 mm SVL) or 2 (> 30 mm SVL). For recording condition, individuals were scored as 1 (field hatched) or 2 (laboratory hatched). No individual performed A or B displays at more than one age or in more than one social context, so each observation used in the analyses was independent. We found no significant sex, size, context, or rearing environment effects on any of the 10 unit durations for the A displays or on any of the eight unit durations for the B displays, nor were total display duration and total number of head bobs per display affected (GLMs, $ps > .05$). Intraindividual display unit stereotypy did not

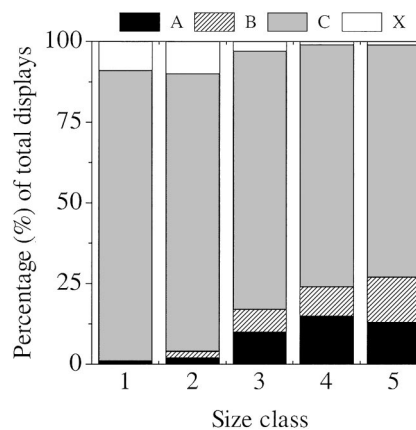


Figure 2. Relative percentages of A, B, C, and X head bobbing displays from 1,246 displays performed by 114 juvenile green anole lizards. Size classes are (1) less than 26 mm snout-vent length (SVL), (2) 26–30 mm SVL, (3) 31–35 mm SVL, (4) 36–40 mm SVL, and (5) greater than 40 mm SVL.

differ among groups for A and B displays (GLMs, $ps > .05$). Similarly, interindividual stereotypy did not differ, as there were no tendencies for display unit CVs grouped by sex, size, context, or rearing environment to be consistently high or low from one group to another.

Type C displays were much more numerous than A or B displays in our data set, and we were therefore able to examine potential effects on their structure and stereotypy in more detail. Like results from the A and B displays, however, we found no significant effects due to sex or rearing environment on any of the six individual unit durations, overall display duration, or total number of head bobs per display (GLMs, $ps > .05$). Interindividual stereotypy showed no consistent effects due to sex or rearing environment. Similarly, intraindividual stereotypy did not differ by sex for any unit of the Type C display (GLMs, $ps > .05$), although it did differ by rearing environment for Unit 6, $F(3, 60) = 7.75, p < .01$. For Unit 6, the CV for individuals reared in the laboratory in groups (43.5%) was significantly higher than the CVs for individuals recorded in the field (20.0%), reared in the laboratory in isolation (27.9%), and captured in the field and recorded in the laboratory (19.6%). Because many ($n = 17$) lizards displayed in consensual and heterosexual contexts or at a minimum of three ages ($n = 10$), we examined potential differences in the C displays due to social context or age by repeated measures ANOVAs. We used individuals as the random effect and context or age as the fixed effect. Age for each individual was scored as 1 (≤ 7 days), 2 (8–30 days) or 3 (> 30 days). For the juveniles represented in the data set only once, a GLM was used to test for context and size effects. Size was scored for each individual as 1 (≤ 25 mm), 2 (26–30 mm), 3 (31–35 mm) or 4 (36–43 mm). Regardless of the type of analysis, however, neither context nor age or size had an effect on unit duration, total display duration, number of head bobs, or intra- or interindividual stereotypy ($ps > .05$).

Comparison of Juvenile and Adult Display Structure

Table 2 compares mean unit and total display durations for Display Types A, B, and C between juveniles and adults. Because juveniles and adults did not show homogeneity of variance for many of the unit durations (9 of the total of 24 display units exhibited heteroscedasticity; Levene’s tests, $p < .05$), comparisons were made using Kruskal–Wallis tests. Unlike comparisons among juveniles, durations for 3 out of 10 units from the Type A display, 3 out of 8 units from the Type B display, and 5 out of 6 units from the Type C display were significantly different between juveniles and adults. Total display duration significantly differed between juveniles and adults for Display Types A and B. When examining the direction of difference, 9 of 12 head bobs were shorter and 11 of 12 pauses were longer for juveniles than for adults (see Table 2). The direction of difference is suggestive of a nonrandom deviation for head bobs, $\chi^2(1, n = 12) = 3.0, p = .08$, and fully supports it for pauses, $\chi^2(1, n = 12) = 8.3, p < .01$.

Interindividual stereotypy, as a measure of group stereotypy, did not consistently differ between juvenile and adult displays. Thus, the range of variation in display unit durations found among juveniles was not consistently greater or less than that found among adults. However, intraindividual stereotypy differed dra-

Table 2
Overall Means, Standard Errors, and Results from Kruskal–Wallis Tests for Differences Between Juvenile and Adult Display Types and Unit Durations

Unit	Juvenile		Adult		H(1)	p
	M (s)	SE	M (s)	SE		
Type A (juveniles, $n = 28$; adults, $n = 14$)						
1	0.176	0.005	0.202	0.008	8.53	< .01*
2	0.117	0.007	0.073	0.008	12.04	< .01*
3	0.148	0.006	0.143	0.003	0.10	.97
4	0.162	0.009	0.134	0.007	5.14	.02
5	0.216	0.012	0.176	0.009	5.05	.03
6	0.307	0.015	0.325	0.019	0.43	.51
7	0.129	0.003	0.139	0.008	0.54	.46
8	0.096	0.006	0.052	0.005	22.64	< .01*
9	0.139	0.005	0.143	0.005	0.56	.45
10	0.169	0.008	0.130	0.013	5.86	.02
1–10	1.660	0.030	1.520	0.024	8.08	< .01*
Type B (juveniles, $n = 18$; adults, $n = 12$)						
1	0.156	0.007	0.182	0.006	7.29	< .01*
2	0.181	0.012	0.108	0.006	16.27	< .01*
5	0.356	0.019	0.370	0.013	0.24	.63
6	0.310	0.020	0.220	0.017	8.85	< .01*
7	0.152	0.004	0.157	0.007	0.84	.36
8	0.075	0.007	0.051	0.007	4.49	.03
9	0.166	0.009	0.162	0.005	0.08	.78
10	0.238	0.013	0.214	0.014	1.62	.20
1–10	1.640	0.041	1.460	0.022	9.43	< .01*
Type C (juveniles, $n = 77$; adults, $n = 24$)						
5	0.456	0.007	0.511	0.009	15.22	< .01*
6	0.211	0.009	0.175	0.014	4.19	.04
7	0.151	0.003	0.182	0.006	14.55	< .01*
8	0.191	0.004	0.130	0.005	39.32	< .01*
9	0.189	0.004	0.213	0.006	9.31	< .01*
10	0.174	0.004	0.139	0.008	11.74	< .01*
5–10	1.370	0.017	1.350	0.019	0.79	.37

Note. Sample sizes shown are numbers of lizards giving each display type. Means of intrasubject means were used to eliminate sample biases resulting from different numbers of displays from individual lizards. Adult data are from Jenssen et al. (2000). All p values marked with an asterisk indicate a significant effect following sequential Bonferroni adjustments.

matically between juveniles and adults. Table 3 compares intraindividual CVs for individual unit and total display durations of A, B, and C displays. The CVs for 7 out of 10 Type A units, 2 out of 8 Type B units, and 1 out of 6 Type C units were significantly different between juveniles and adults. The CVs for total display duration were also significantly different between juveniles and adults for Display Types A and B. In every case in which CVs were significantly different, they were higher for juveniles than for adults, indicating less intraindividual stereotypy for juveniles. Furthermore, for 21 out of the total 24 head bob and pause units of the three display types and for all three total display durations, the CVs were larger for juveniles than for adults, which is much more frequently than would be expected by chance, $\chi^2(1, n = 27) = 16.3, p < .01$.

Table 3
Comparisons of Juvenile and Adult Intraindividual Coefficients of Variation (CVs) for Display Units of Display Types and Results of Kruskal–Wallis Tests

Unit	Intraindividual CV (%)		<i>H</i> (1)	<i>p</i>
	Juveniles	Adults		
Type A (juveniles, <i>n</i> = 21; adults, <i>n</i> = 9)				
1	20.0	6.1	7.95	< .01*
2	33.9	15.1	4.73	.03
3	22.6	8.4	7.82	< .01*
4	33.1	6.1	9.90	< .01*
5	35.0	9.5	7.91	< .01*
6	30.2	3.3	12.13	< .01*
7	13.8	12.1	0.02	.88
8	41.6	27.7	0.86	.35
9	22.5	12.1	6.50	< .01*
10	34.1	7.4	7.80	< .01*
1–10	11.0	1.3	7.03	< .01*
Type B (juveniles, <i>n</i> = 11; adults, <i>n</i> = 10)				
1	15.1	12.8	1.44	.23
2	23.9	14.1	1.28	.26
5	18.8	5.5	9.17	< .01*
6	20.0	9.2	6.26	.01
7	14.6	10.0	0.32	.57
8	49.3	64.5	0.18	.67
9	19.3	19.9	0.03	.86
10	21.8	8.1	10.53	< .01*
1–10	8.0	2.1	7.38	< .01*
Type C (juveniles, <i>n</i> = 58; adults, <i>n</i> = 21)				
5	14.9	10.0	0.04	.85
6	42.6	29.4	0.47	.50
7	23.9	14.6	1.73	.19
8	26.6	22.9	0.93	.33
9	24.1	28.0	0.43	.51
10	36.9	22.5	7.31	< .01*
5–10	13.0	9.8	0.01	.92

Note. Sample sizes shown are numbers of lizards used in the analysis. Adult data are from Janssen et al. (2000). All *p* values marked with an asterisk indicate a significant effect following sequential Bonferroni adjustments.

Discussion

Display Ontogeny and Social Environment

We found no evidence that imitation, practice, or social interaction had any effects on the development of the temporal structure of displays in green anole lizards. The emergence and fixation of displays followed a common trajectory for juveniles, regardless of their sex, rearing environment, or the social contexts in which displays were given. Display unit durations showed no significant tendencies toward longer or shorter durations, and intra- and interindividual display stereotypy were not affected by the sex of the lizard, its rearing environment, or the social context in which displays were given. If imitation or practice were important to display development, inter- or intraindividual stereotypy, respectively, should have been higher in lizards housed socially in the laboratory or observed in the field under natural conditions (be-

cause of the opportunity to imitate or practice displays) than in lizards housed in isolation in the laboratory (that would have neither seen nor given any displays while isolated). If experience from social interactions shaped display structure, then displays recorded from different social contexts should have differed in structure or stereotypy.

Display Ontogeny and Maturation

Age- or size-related factors (i.e., maturation) appear to be important in the development of the display repertoire for green anole lizards. We found that the A, B, and C display types emerged asynchronously during development and did not depend on sex or rearing environment. Juveniles gave C displays throughout ontogeny, beginning as early as the day of hatching, whereas A and B displays gradually emerged during later ontogeny. In contrast, X displays appeared at low frequency in early development and became almost nonexistent in later development. This pattern of display emergence suggests that the X display is an undifferentiated A/B precursor, as proposed in Figure 3. Specifically, Variant 1 of the X display (see Figure 1b) suggests an A display in the process of forming, once the incipient pause is added to split the first head bob into two head bobs. Variant 2 suggests a B display once the waning pause is fully removed from the second head bob.

An examination of individual display behavior supports the idea that the A and B display types emerge from X displays during development. No lizard that gave an X display also gave a Type A or B display during the same observation period, although nearly all of them (85%) gave Type C displays. Furthermore, 9 of 13 laboratory-reared lizards gave X displays early in ontogeny but were later observed to give Types A or B without X. Three of the 4 remaining lizards continued to give X displays for the duration of the study, and one was observed to give several Type B displays but subsequently gave some additional X displays. Similarly,

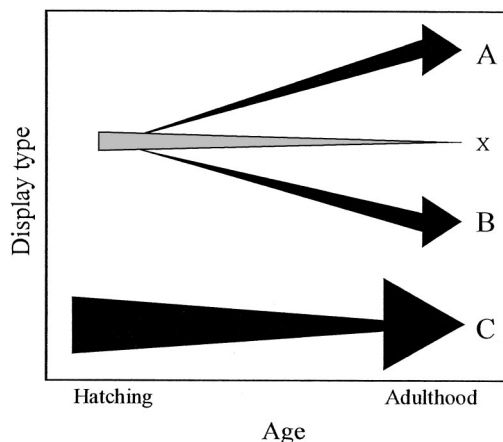


Figure 3. Schematic of the emergence of head bobbing displays seen during ontogeny in juvenile male and female green anole lizards. Stereotyped display types are represented by black arrows (A, B, and C); the hypothesized, developmental precursor to the A and B display types (X) is represented by a gray arrow. Arrowhead size approximates the proportion of use of each display type in adulthood. Increases or decreases in arrow line thickness indicate increases or decreases, respectively, in the proportion of displays of each type observed throughout ontogeny.

Roggenbuck and Jenssen (1986) found an undifferentiated display pattern in the very early ontogeny of the fence lizard, and they reported that this pattern resulted from an incomplete separation of introductory head bobs of the species-typical adult patterns. However, the undifferentiated display pattern observed in fence lizards disappeared within a week of hatching, whereas the X displays that we observed for green anole lizards remained relatively common for at least a month after hatching and persisted in a few individuals over the entire study.

Juveniles, like adults, show no sex differences in display structure. However, comparisons between juveniles and adults reveal that the juvenile display cadences require maturation during ontogeny. Although juvenile display stereotypy did not change with age or size over the course of our study, almost half of the units for Display Types A, B, and C had significantly different mean durations for juveniles and adults, and adults showed higher intra-individual stereotypy for nearly every head bob and pause unit of each display type. Furthermore, when considering unit differences between juveniles and adults, juveniles tended to have shorter head bobs and longer pauses. Thus, the fine temporal structures of the green anole lizard's display types change during the transition from juvenile to adult, with an emphasis on decreasing head bob separation.

Our results demonstrate that maturation in a broad sense affects display structure. However, to say a trait requires maturation does not yield much insight into mechanism, as many potentially inter-related processes could be involved (e.g., Burghardt, 1977b; Groothuis, 1994). It is unclear whether the phenomenon we have termed *maturation* is primarily due to neuromuscular constraints to the performance of displays in ontogeny or perhaps due to underlying physiological or social changes as juveniles grow that adjust the thresholds of producing particular displays (i.e., motivation). That is, are X displays and low stereotypy relative to that of adults the result of a still developing neuromuscular system that coordinates display output or of a juvenile environment that does not require a complete and stereotyped display repertoire? The idea that the X display is an A/B precursor suggests that neuromuscular maturation is more explanatory than motivation. However, Groothuis and Meeuwissen (1992) found that exogenous testosterone (T) given to juvenile black-headed gulls could rapidly induce them to perform stereotyped adult display patterns, at an age when they normally would be producing incomplete displays. In several songbird species, exposure to androgens or estrogens at the appropriate stage in ontogeny is critical to both the song learning process and the production of stereotyped song, and experimental manipulation of these steroids can alter the normal temporal scale of song learning, stereotypy, and production (reviewed in Bottjer & Johnson, 1997). These results suggest that motivation, rather than neuromuscular constraint, is the primary determinant of signal structure for these avian species. Similarly, large juvenile male and female green anole lizards (36–42 mm SVL) given T implants exhibited a higher proportion of A and B displays in social interactions than did juveniles given blank implants (Lovern, McNabb, & Jenssen, 2001). Thus, high T exposure can increase A and B display rates at an age when A and B displays are already being exhibited. It would be interesting to see whether T given to very young juveniles produced a similar, rapid increase in A and B display rates (motivation hypothesis), or

whether X displays were still exhibited as a necessary precursor to A and B displays (neuromuscular maturation hypothesis).

Social Organization Display Function and Evolution

The present study reveals that the development of head bobbing display structure in green anole lizards is refractory to environmental inputs, as compared with the development of social signals in many birds and mammals. This difference in signal ontogeny arises not from deficits in the reptilian system but from differences in life history and the consequent requirements for survival that are faced by precocial juveniles but buffered for altricial juveniles (e.g., Burghardt, 1978; Groothuis, 1993a; Stamps, 1978). It is consistent with the social organization of green anole lizards that imitation, practice, and social interaction had no significant effect on display structure.

The green anole lizard is polygynous; females settle in comparatively small territories, and males attempt to establish territories that overlap those of females (Jenssen, Lovern, & Congdon, 2001; Ruby, 1984). Females lay single-egg clutches at weekly intervals over a 4-month breeding season (Andrews, 1985; Ruby, 1984). Within this social system, there is no parental care by either sex, and juvenile anoles are therefore immediately responsible for meeting their survival needs (Lovern, 2000; Stamps, 1978). Unlike some lizards (e.g., iguanas; Burghardt et al., 1977), juvenile anoles do not socially aggregate and must individually locate suitable habitat for foraging, predator avoidance, and shelter (Lovern, 2000; Stamps, 1978). Juveniles therefore require functional signals to mediate their social interactions, which primarily include agonistic interactions over habitat use (Lovern, 2000; Stamps, 1978, 1983), but they are not likely to have many opportunities for learning and modifying these signals by processes such as imitation and practice. Furthermore, although previous social experience can affect subsequent signal use in green anole lizards (Greenberg & Crews, 1990; Yang, Phelps, Crews, & Wilczynski, 2001) and reptiles in general (e.g., Sakata, Gupta, Chuang, & Crews, 2002; Schuett, 1997), it is unlikely to result in modification of signal structure because social encounters are infrequent and brief, and the communication requirements of juvenile males and females do not differ (Lovern, 2000; Lovern & Jenssen, 2001).

The ontogenetic trajectory of the communication signal repertoire in green anole lizards reported here, along with previous research on juvenile and adult display use, yields insight into the meanings of the A, B, and C display types. As mentioned above, adults show no sex differences in display type structure but many differences in display type use. In agonistic encounters, adult males and females predominantly use C displays (DeCourcy & Jenssen, 1994; Jenssen et al., 2000). As such encounters intensify, males increase the relative proportions of A and B displays, but females do not (DeCourcy & Jenssen, 1994; Jenssen et al., 2000). Adult males also display in two contexts in which adult females do not—stationary advertisement and patrol (DeCourcy & Jenssen, 1994; Jenssen et al., 2000; Nunez, Jenssen, & Ersland, 1997). Stationary advertisement displays are given from prominent locations within the territory and are predominantly Type C, whereas displays given by males as they actively patrol their territories are more frequently Types A and B. During courtship, males predominantly use type C displays, but females use A and B displays (Orrell & Jenssen, in press).

Because the A, B, and C display types are used by both males and females, in multiple contexts, specific function-related labels have not been given to the three categories; such function labeling can be problematic (e.g., Tinbergen, 1951), jeopardizing both the objective description of display structure and the accurate interpretation of display meaning (see DeCourcy & Jenssen, 1994; Lovren et al., 1999). Given the breadth of data on display behavior in green anole lizards reviewed above, an overall pattern of display function is becoming apparent. We suggest that the fundamental display is Type C, as it is used across broad contexts—by all ages of lizards—under typically low-intensity or low-arousal conditions. In contrast, A and B displays may have evolved because of selection pressures associated with breeding, as they become more frequently expressed by males in territory defense and by females in courtship, both of which are comparatively high-arousal contexts experienced only by breeding adults. That juveniles overwhelmingly exhibit C displays relative to A and B displays regardless of context (Lovren & Jenssen, 2001; the present study) is consistent with their signaling requirements (see above) and the notion of low-arousal (C) and high-arousal (A and B) displays.

The ontogenetic trajectory of the signaling repertoire in green anole lizards also may be informative from an evolutionary perspective. For example, parallels between ontogeny and phylogeny have been demonstrated for song in a lineage of sparrows (Irwin, 1988) and for displays among closely related gulls (Groothuis, 1989). These studies demonstrate that ontogenetic trajectory can reflect phylogenetic history when trait modifications occur late in development (e.g., Gould, 1977). The green anole lizard has a display type (C) that is present from hatching and two display types (A and B) that emerge later in development. This pattern is consistent with the idea that the A and B display types are late additions to the developmental trajectory of the signal repertoire, perhaps evolutionarily derived from the C display. By our logic presented above (and in Figure 3), the occurrence of X displays is the developmental clue that A and B display types are evolutionary additions. If ontogenetic trajectory reflects phylogenetic history in this case, then one would expect that Display Type C might be more similar, and Display Types A and B less similar, to the display types of closely related species (e.g., the Cuban green anole lizard; Buth, Gorman, & Lieb, 1980). More quantitative studies on the development of display structure among closely related anoles are necessary to evaluate this possibility.

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