

THE EFFECTS OF CONTEXT, SEX, AND BODY SIZE ON STAGED SOCIAL INTERACTIONS IN JUVENILE MALE AND FEMALE GREEN ANOLES (*ANOLIS CAROLINENSIS*)

by

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Summary

We documented the ontogeny of headbobbing display use in green anoles (*Anolis carolinensis*) by determining the effects of social context, sex, and body size on juvenile social interactions. Juveniles only gave displays in social interactions (never while isolated), and activity levels in general were much higher during interactions than during isolation. Neither social context (consexual or heterosexual) nor sex affected the type or quantity of displays and related behaviors (perch shifts, display modifiers, color changes, and approaches or retreats). Interactions always appeared to be aggressive in nature and qualitatively similar to interactions between adult females. Both males and females tended to increase overall activity during interactions with body size, including the use of displays and related behaviors, and large juvenile males performed more headbobbing displays than did large juvenile females. These results suggest that juvenile social interactions are agonistic in nature and that they function to defend both immediate and future resources (prospective resource hypothesis). It is likely that resource protection confers the immediate benefits of suitable habitat for foraging, thermoregulation, and predator avoidance, and it is hypothesized that the primary future benefit is the acquisition of the eventual breeding territory that juveniles will hold as adults.

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Introduction

The structure and use of communication signals have been well documented for many species, but their development has received comparatively less attention (Burghardt, 1977; Groothuis, 1993, 1994). In recent textbooks on animal communication, ontogeny is not covered in one (Bradbury & Vehrencamp, 1998) and, in the other, restricted to discussion of the comparatively well studied examples of song development in birds and alarm calling and social signals in squirrels and primates (Hauser, 1996). However, research thus far suggests that, in contrast to what might be inferred from these textbooks, patterns of signal ontogeny can vary greatly across taxa, depending on life history constraints and social organization.

There are at least three general ontogenetic patterns by which signals arise in their adult form. The 'adult-emergence' pattern occurs when there is no obvious signal development during the juvenile stage. The social signals used by adults are not expressed until adulthood, when they appear as (usually) sex-specific and fully developed signals (*e.g.* orthopterans: Otte, 1977; Moore *et al.*, 1995; fishes: Brown & Colgan, 1985; anurans: Kiester, 1977; Ryan, 1985). Social organization in these species generally gives juveniles little opportunity for acquiring the signals via social processes (*e.g.* parent-offspring or group interactions), and little need for using the adult-typical signals, because interactions among juveniles are infrequent or entirely unlike those of adults.

At the other extreme is the 'juvenile-flexible' pattern of signal ontogeny, characterized by an extended period of signal development. Songbirds acquire song as juveniles during discrete developmental stages for acquisition, storage, and practice, during which time the songs progress from crude to stereotyped species-typical patterns (Catchpole & Slater, 1995). Many mammals begin expressing the signals used in adult social interactions during play in the juvenile stage (Fagen, 1981, 1993; Walters, 1987; Thompson, 1998). Birds and mammals share a comparatively altricial juvenile life stage, thus creating a social environment that allows for reliable interactions between parents and offspring, among siblings, or among extended social groups, in the development of social signals. During ontogeny, the expression of these signals is typically variable or incomplete, and the juvenile signals do not elicit the same social consequences that they will in adulthood (Fagen, 1981; Catchpole & Slater, 1995), although it is possible that they still carry information (Groothuis, 1994).

The third pattern of signal ontogeny, 'juvenile-structured', is one in which social signals appear in juveniles as structurally similar or identical to those of adults (*e.g.* lizards: Cooper, 1971; Stamps, 1978; Roggenbuck & Jenssen, 1986; Greenberg & Hake, 1990; Phillips *et al.*, 1993; Lovern, 2000a). In this pattern, experience appears to play a comparatively minor role; juveniles are capable of giving adult-like displays at hatching, and sex, age, and social context have little effect on display structure (Stamps, 1978; Roggenbuck & Jenssen, 1986; Lovern, 2000a). Because juvenile lizards receive no parental care, and because most do not form aggregations (but see Burghardt *et al.*, 1977; Burghardt & Rand, 1985), juveniles are immediately and individually responsible for their own survival. Functionally, therefore, this life history pattern precludes any substantial opportunity for acquiring displays via social processes, yet it suggests that juveniles need displays to settle conflicts over resources (*e.g.* Phillips *et al.*, 1993; Ruby & Baird, 1993; Stamps, 1994).

We examined the relationship between social organization and the ontogeny of display use in the green anole lizard, *Anolis carolinensis*, a species that bests fits the juvenile-structured pattern of signal ontogeny. Juvenile males and females give headbobbing displays beginning at hatching that are very similar to those of adults (Lovern, 2000a). There are three display types in this common display repertoire (labeled A, B, and C), each of which is distinguishable by its unique temporal pattern of headbobs and inter-bob pauses (DeCourcy & Jenssen, 1994; Jenssen *et al.*, 2000; Lovern, 2000a). Although adult males and females possess common display structures, display use shows dramatic sex differences due to intrasexual selection acting on males and the resulting sex differences in reproductive strategies emerging from a polygynous social organization (Ruby, 1984; Jenssen *et al.*, 1995; Nunez *et al.*, 1997; Jenssen *et al.*, 2000). To achieve high reproductive success, adult males have 8-fold larger territories than do females, and males attempt to exclusively overlap as many breeding females as possible (Jenssen & Nunez, 1998). Consequently, adult males display 8-fold more frequently than adult females overall, 10-fold more frequently during aggressive interactions, and only males display in a territory advertisement (*i.e.* solitary) context (Nunez *et al.*, 1997; Jenssen *et al.*, 2000). Furthermore, male displays are more conspicuous because males can extend dewlaps (red throat fans) with 7-fold greater area than those of females (Jenssen *et al.*, 2000). Interactions between males involve frequent use of the dewlap and display modifiers that can optionally be added to displays to increase apparent body

size (Greenberg, 1977; Jenssen, 1977). Males alter the relative proportion of display types performed with decreasing interaction distance, such that more A and B displays occur at closer distances (DeCourcy & Jenssen, 1994). Male aggressive display behavior is embedded in a ritualized combat scheme (*i.e.* 'fixed-sequence contest'; Bradbury & Vehrencamp, 1998) consisting of approaching, circling, jaw-sparring, and ultimately jaw-locking (Greenberg & Noble, 1944; Jenssen *et al.*, 2000). Male-male interactions can be intense, sometimes lasting over an hour and resulting in injury to one or both participants (Greenberg & Noble, 1944; Jenssen *et al.*, 2000). In contrast, interactions between adult females involve low display rates, comparatively infrequent use of a diminutive dewlap and display modifiers, no shifts in the relative proportions of display types performed with interaction distance, and a lack of the ritualized combat scheme found in males (Nunez *et al.*, 1997; Jenssen *et al.*, 2000). During adult male-female interactions, males also display at high rates with dewlap extension, but without display modifiers and ritualized combat (Greenberg & Noble, 1944; Jenssen & Nunez, 1998). Courted females also give displays that lack modifiers but, unlike males, females do not use dewlaps in courtship interactions (Greenberg & Noble, 1944).

Although dramatic sex differences in signal use by adult *A. carolinensis* have been well-documented, it is unclear how those differences develop. In this study, we examined the influence of social context, sex, and size (age) on the ontogeny of display use by staging social interactions between juveniles of various sex and size classes in different social contexts, and then comparing juvenile signal responses to those previously described for adults (DeCourcy & Jenssen, 1994; Jenssen *et al.*, 2000). In general, we expected that display use would differ between juveniles and adults, based on the assumption that function of, and selection for, juvenile signaling is different than for adults. Display use in adults mainly involves communication in reproductive contexts. In contrast, juveniles do not participate in courtship interactions and their habitat requirements do not include breeding considerations (*e.g.* exclusive overlap of female territories by males, or defended oviposition sites by females). Therefore, juvenile males and females should not differ in their basic needs (*e.g.* Stamps, 1994), and their social interactions should reflect competition over the resources necessary for survival, regardless of the sex of the lizards. Based on these assumptions, we first hypothesized that display behavior would only function in agonistic social

encounters with other lizards, not to advertise territories when individuals were alone. Second, because juvenile requirements do not appear to be sex-specific, we hypothesized that juveniles would not differ in display behavior during interactions, regardless of their sex, body size, or the social context of the interaction (consexual or heterosexual).

Methods

Subjects and housing

In July and August of 1997, we collected 68 juvenile *A. carolinensis* (34 males and 34 females) from a field site near Augusta, Georgia, USA, and brought them back to the laboratory. For each individual, we recorded sex by post-anal scale size (males have two enlarged post-anal scales) and snout-vent length (SVL) to the nearest mm, and we applied a unique dorsal paintmark to each for identification. To ensure that the collected lizards were juveniles in their summer of hatching, we used growth rates for *A. carolinensis* from Michaud (1990) to determine the maximum SVL a lizard in its first summer could attain by any collection date, assuming a field hatch date of 15 May (Gordon, 1956). Lizards were divided into four size classes, all within the juvenile size range: (1) <26 mm SVL; (2) 26-30 mm SVL; (3) 31-35 mm SVL; and (4) 36-42 mm SVL. Based on growth rates (Michaud, 1990), these size classes approximated age classes of <14 d, 14-37 d, 38-61 d, and 62-100 d. Juvenile *A. carolinensis* show no sex differences in SVL or mass at hatching, although males grow faster than females (Gordon, 1956; Michaud, 1990). However, even by 100 d, the magnitude of difference in SVL between males and females is <2 mm, so the size classes we chose contained males and females of the same range of ages.

All lizards were housed singly in cages measuring 30 × 60 × 60 cm. We exposed the lizards to a 14:10 h light:dark cycle using four 40W full-spectrum bulbs (Durotest Vita-Lite Plus) placed on the top of each cage. Temperatures inside each cage were 27-34°C during the day (depending on site within the cage) and 23°C at night. Cages were identically furnished with multiple wooden dowels for perching and numerous pieces of artificial vegetation. We watered and fed lizards daily on vitamin-dusted crickets, mealworms, and flour beetle and waxworm larva.

Experimental design and procedure

We observed 60 lizards (30 males and 30 females) individually and during pairwise interactions with conspecifics and heterospecifics to investigate the potential effects of context and size on behavior (Table 1). After 7-14 d in the laboratory, lizards were moved to observation cages set up identically to housing cages. Prior to the trials, lizards were isolated by opaque, removable partitions. Then, 16-24 h after moving lizards to the observation cages, trials were conducted by videotaping pairs of lizards for 30 min alone (designated as the 'isolation' period) and then 30 min together following the removal of the partition (designated as the 'interaction' period). After the 60 min trial, each lizard was again separated by replacing the partition. The following day this procedure was repeated with different pairings. Thus, each lizard was observed in two trials, but no two lizards interacted with each other more

TABLE 1. *Sample sizes for pairwise trials, by size class (snout-vent length) and social context*

Size class	Lizards		Trial context			Total
	Males	Females	Male-male	Female-female	Male-female	
1 (<26 mm)	6	6	4	4	4	12
2 (26-30 mm)	7	9	5	5	6	16
3 (31-35 mm)	9	7	6	4	6	16
4 (36-42 mm)	8	8	6	5	5	16
Total	30	30	21	18	21	60

than once. All interacting lizards had SVLs within 2 mm of each other. An additional eight lizards (four males and four females; one of each sex from each of the size classes described above) were used once in partition control trials. Housing and trial protocols for these lizards were identical to those described above, except that following partition removal there was no adjacent lizard, which allowed us to determine whether responses by lizards were to each other or simply to partition removal.

Behavioral data were collected by videotaping all trials from a darkened blind using a Panasonic AG 460 video camera fitted with an Aztec video telephoto converter (2.0 \times). To examine overall differences in behavior among trials from different social contexts and size classes, we created a behavior index (BI; Ortiz & Jenssen, 1982; Lovern *et al.*, 2001) that represented behavioral intensity for each lizard during isolation and during interactions. Each behavior listed in the BI was assigned a point value that reflected the position of the behavior in a sequence of increasingly socially-motivated behaviors (Table 2). Behaviors with low point values typically appear early in social interactions, or even when lizards are not interacting, whereas behaviors with high point values appear later in prolonged interactions and rarely or never when lizards are not interacting (Ortiz & Jenssen, 1982). Thus, in addition to headbobbing displays, the BI included behaviors that might arise in the context of display interactions, allowing us to fully assess potential differences in juvenile responses among social contexts and size classes. We calculated BIs by summing the points of the observed behaviors for each lizard individually (individual BIs) and for each pair of interacting lizards (trial BIs).

Data analyses

We used Wilcoxon signed-ranks tests (test statistic = z) to compare paired BIs for individuals when they were alone and when they were in interactions (averaged from the two trials in which each lizard participated) and Mann-Whitney tests (test statistic = U) to compare BIs between control and interaction trials. We used Kruskal-Wallis tests (test statistic = H) to examine sex, context, and body size effects on BIs. Trial BIs were statistically independent from one another because each pair of interacting lizards was unique. When our objective was to examine specific behaviors (*e.g.* to examine sex or body size effects), we averaged individual responses and examined results using Fisher's exact tests (for 2×2 tables with small samples sizes), chi-square tests (test statistic = χ^2), or Kruskal-Wallis tests where appropriate. As a measure of how the interaction BI of one lizard related to the interaction

TABLE 2. *Definitions of behavior and point values used in the behavior index*

Behavior	Definition	Point value
Head-up ¹	Posture reflecting alertness to the environment; >60 s (consecutively) with head raised higher than body	1
Perch shift	Any movement > 1 body length (excluding tail) from one perch site to another; movements > 15 s apart were scored as separate perch shifts	2
Tongue touch ²	Potential chemosensory behavior involving brief touch of the tongue to the substrate	3
Color change ^{1,2}	Change in lizard body color between green, olive, or brown as a potential indicator of social stress or arousal	4
Headbob ³	Series of vertical head movements in species-specific temporal cadences used for communication; noted display type (A, B, C), separation distance between displaying lizards, and whether dewlap extension also occurred	5
Eyespot ^{1,4}	Development of dark skin patch posterior to each eye indicating increased adrenergic activity	6
Engorged throat ^{1,2}	Display modifier in which the ventral throat area remains enlarged	7
Sagittal expansion ^{1,2}	Display modifier in which the lateral view of the lizard becomes enlarged	7
Approach/retreat	A perch shift directly toward or away from another lizard when the separation distance is <30 cm	8
Attack	Lunge toward another lizard, within 10 cm, with actual or attempted physical contact, such as biting	9

¹ These behaviors were scored a maximum of once for each the isolation and interaction portions of trials for each lizard.

² Greenberg, 1977.

³ Following descriptions in DeCourcy & Jenssen, 1994; Lovorn, 2000a.

⁴ Hadley & Goldman, 1969.

BI of the other lizard, we used Spearman rank correlations (test statistic = r). Descriptive statistics are reported as mean \pm SE. We used Minitab (version 10Xtra) for all statistical analyses, and hypothesis tests were two-tailed with an overall $\alpha = 0.05$. In cases where the same statistical comparison was made for multiple groups, sequential Bonferroni adjustments of the p -value were performed to maintain a group-wide $\alpha = 0.05$ (Rice, 1989).

Results

The behavior indices (BIs; see Table 2) from the partition control trials did not differ from the BIs of isolated lizards ($N = 8$, BI = 7.8 ± 2.9 and

$N = 60$, $BI = 12.6 \pm 0.8$, respectively; $U = 2156$; $p = 0.19$). Thus, behaviors elicited during interactions were due to the interaction between lizards rather than to partition removal. Furthermore, individual interaction BIs were unaffected by trial order ($N = 60$, $z = 1003$, $p = 0.52$), indicating that there was no habituation or priming effect on lizard behavior from their first to their second interactions.

Effects of interaction on the BI

BIs of isolated lizards remained relatively consistent, regardless of sex ($H_1 = 1.2$, $p = 0.28$) or size class ($H_3 = 7.1$, $p = 0.07$). However, individual BIs were significantly lower for lizards when they were isolated than they were during interactions (12.6 ± 0.8 and 56.1 ± 5.3 , respectively; $z = 1753$, $p < 0.001$). This difference in behavioral intensity held regardless of the sex or size class of the lizard, or the social context of the interaction (all $p < 0.05$). Of the 10 behaviors in the BI, only the four lowest in intensity (head-up posture, perch shift, tongue touch, color change; Table 2) were ever observed while lizards were alone. Isolated lizards frequently exhibited the head-up posture and perch shifting (53 and 48 out of 60 lizards, respectively), and to a lesser extent exhibited tongue touching and color changing (16 and 13 out of 60 lizards, respectively). In contrast, all 60 and 59 out of 60 lizards showed a head-up posture and perch shifting behavior, respectively, during interactions, and 38 and 47 out of 60 exhibited tongue touching and color changing.

Effects of social context, sex, and body size on the BI

We compared trial BIs among different social contexts. Within size classes, trial BIs from consensual (male-male or female-female) and heterosexual (male-female) contexts did not significantly differ for any of the four comparisons (Kruskal-Wallis tests; all $p > 0.05$). However, in size class 4, trial BIs for male-male interactions were suggestively higher than trial BIs for female-female and male-female interactions ($BI_{\text{male-male}} = 239.2 \pm 35.6$, $BI_{\text{female-female}} = 125.4 \pm 35.2$, $BI_{\text{male-female}} = 117.9 \pm 52.5$; $H_2 = 4.8$, $p = 0.09$). After pooling size classes to increase sample size, trial BIs still did not differ by context ($H_2 = 0.04$, $p = 0.96$). However, the types or frequencies of behaviors that comprised the BI could have differed across contexts. Therefore, we examined trials from each social context to

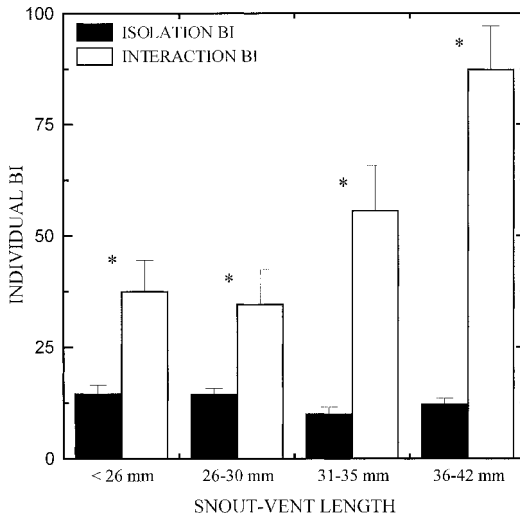


Fig. 1. Mean (+SE) individual isolation and interaction behavior indices (BI) by size class for juvenile male and female *Anolis carolinensis*. See Table 1 for sample sizes, and Table 2 for definitions of the behaviors included in the BI. The BIs from the two trials in which each lizard participated were averaged to create the individual BIs. Overall Wilcoxon signed-ranks test; $N = 60$, $z = 1753$, $p < 0.001$. **Post-hoc* pairwise comparisons indicated significant differences between isolation and interaction BIs within each size class following sequential Bonferroni adjustments.

determine whether the proportion of trials containing any of the behaviors in the BI differed. We found no such effect; whether a particular behavior was observed did not depend on the social context of the trial (Fisher's exact tests; all $p > 0.05$).

Because the social context of a trial did not affect the behavior of individual lizards, we averaged their responses from the two trials in which they participated and focused on potential sex and body size effects on individual BIs and on the particular behaviors that were expressed. Sex did not affect the interaction BI overall ($H_1 = 0.1$, $p = 0.82$) and, within each age class, males and females were equally likely to exhibit each of the behaviors in the BI (Fisher's exact tests; all $p > 0.05$). However, lizard size had a significant effect on interaction BIs ($H_3 = 19.0$, $p < 0.001$). Individuals of different size classes did not differ in their BIs while alone (see above), but their interaction BIs increased, from 37.5 ± 7.0 in size class 1 to 87.3 ± 9.8 in size class 4 (Fig. 1). This was due to a tendency for larger lizards to perform more behaviors in the BI (Table 3). Only attacks

TABLE 3. *Behavior of juvenile Anolis carolinensis of four size classes (snout-vent length) during social interactions*

Behavior	Size class				<i>p</i>
	<26 mm	26-30 mm	31-35 mm	36-42 mm	
Head-up	12/12	16/16	16/16	16/16	1.00
Perch shift	11/12	16/16	16/16	16/16	0.44
Tongue touch	6/12	10/16	10/16	14/16	0.04
Color change	7/12	12/16	13/16	15/16	0.03
Display	6/12	11/16	15/16	14/16	0.04
Eyespot	0/12	0/16	3/16	3/16	0.17
Engorged throat	4/12	6/16	6/16	8/16	0.21
Sagittal expansion	4/12	6/16	6/16	8/16	0.21
Approach/retreat	4/12	6/16	7/16	9/16	0.15
Attack	0/12	0/16	0/16	0/16	1.00

Table entries show number of animals performing the behavior/number tested and *p*-values of Fisher's exact tests comparing the smallest and largest size classes (all non-significant following sequential Bonferroni adjustments). The 'head-up' posture was always observed, 'attack' was never observed, and the remaining eight behaviors all increased in likelihood of expression ($\chi_1^2 = 8.0$, $p = 0.005$).

were never observed, and eight of the remaining nine behaviors increased in probability of expression with increasing size class, which is higher than would be expected by chance ($\chi_1^2 = 8.0$, $p = 0.005$). The head-up posture, the only observed behavior not to increase with size, was exhibited by every lizard in each size class.

Individual display behavior

Juveniles gave 515 type A, B, and C displays during interactions. They also gave an additional 18 displays that were not one of the three species display types, but rather followed the pattern previously labeled as X and inferred to represent a developmental precursor to display types A and B (Lovern, 2000a). These few X displays are not included in the present analyses.

None of the juveniles displayed when alone, although 80% (24 of 30) of the males and 73% (22 of 30) of the females did so during interactions, thus indicating no sex difference in the likelihood of displaying ($\chi_1^2 = 0.38$, $p = 0.54$). Overall, 9% of juvenile displays were type A, 11% were type B, and 80% were type C. There was no sex difference in the relative proportion of display types given ($\chi_2^2 = 4.6$, $p = 0.21$), there was no effect of

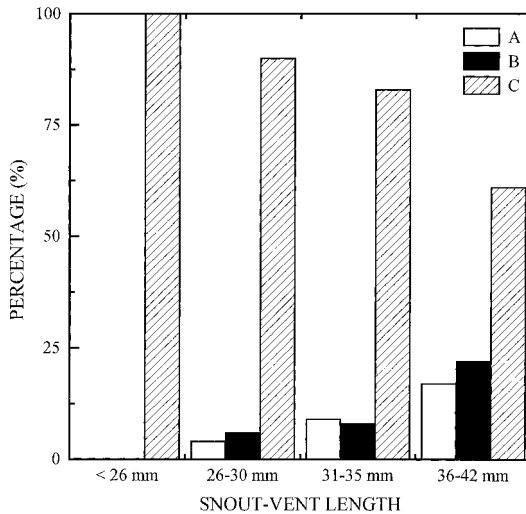


Fig. 2. Relative percentages (%) of 515 headbobbing displays given by 60 juvenile *Anolis carolinensis* during pairwise interactions that were type A, B, and C, by size class.

interaction distance (long, >30 cm; short, <20 cm; $\chi_1^2 = 2.1$, $p = 0.73$), and there was no effect of social context ($\chi_2^2 = 3.8$, $p = 0.28$). Thus, males and females gave the same display types in the same proportions regardless of whether they were in consensual or heterosexual interactions. However, relative display type proportions differed by size class (Fig. 2), with types A and B increasing in frequency with larger size classes. Chi-square tests followed by sequential Bonferroni adjustments indicated that all pairwise comparisons between the relative display type proportions of different size classes were significant (all $p < 0.005$) except for the comparison between size classes 2 and 3 ($\chi_2^2 = 1.9$, $p = 0.39$).

Juvenile males and females also did not differ in the proportion of displays that were accompanied by dewlap extension (59% and 52% of displays for males and females, respectively; $\chi_1^2 = 2.2$, $p = 0.14$). Furthermore, males and females were each equally likely to use their dewlaps in consensual or heterosexual interactions ($\chi_1^2 = 0.1$, $p = 0.76$; $\chi_1^2 = 0.3$, $p = 0.70$; for males and females, respectively). However, size again played a role in the expression of behavior. Displays were accompanied by dewlap extension 77% of the time in size class 1, 60% and 61% of the time in size classes 2 and 3, and 46% of the time in size class 4. This trend of decreasing dewlap use with increasing body size was significant for the comparison between size

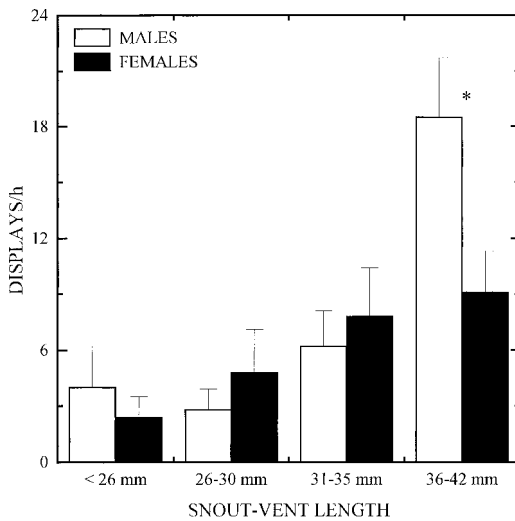


Fig. 3. Mean (+SE) hourly display rate by size class during pairwise interactions for 30 juvenile male and 30 juvenile female *Anolis carolinensis*. Overall Kruskal-Wallis test for size class; $H_3 = 15.7$, $p = 0.001$. *Mann-Whitney test; $N_1 = N_2 = 8$, $U = 89$, $p = 0.03$.

classes 1 and 4 following sequential Bonferroni adjustments ($\chi_1^2 = 18.4$, $p < 0.001$), and appeared at least partly related to the increased use of display types A and B. Only 9% and 5% of A and B displays, respectively, were accompanied by dewlap extension, in contrast to 74% of C displays.

Juvenile males and females were nearly identical in the behaviors expressed during social interactions. However, display rates were sexually dimorphic (Fig. 3). For size class 4, display rates were higher in males than in females ($N = 8$, $18.5 \pm 3.2/\text{h}$ and $N = 8$, $9.1 \pm 2.2/\text{h}$, respectively; $U = 89$, $p = 0.03$). Even with this sex difference in the largest size class, there was an overall significant effect on display rates due to size class ($H_3 = 15.7$; $p = 0.001$). From size class 1 to 4, display rates (displays/h) were $3.0 (\pm 1.3)$, $4.1 (\pm 1.5)$, $6.5 (\pm 3.1)$, and $14.3 (\pm 3.1)$, respectively.

Individual responses to interaction

The behavior expressed by one lizard of an interacting pair could affect the behavior of the other. Furthermore, this relationship could change with social context or size class, if the relative impact of the behaviors differs by whether they are expressed by males or females, or by the age of interacting lizards.

Overall, there was a very strong positive correlation between the BIs of interacting lizards ($r = 0.62$, $p < 0.001$), such that lizards tended to match behavioral intensities during interactions. When examined by social context, male-male ($r = 0.74$, $p = 0.005$), male-female ($r = 0.78$, $p < 0.001$), and female-female ($r = 0.49$, $p = 0.03$) contexts all showed significant positive correlations between the BIs of interacting lizards. However, the degree of correlation between the BIs of interacting lizards increased with size class. The BIs in size class 1 ($r = 0.26$, $p = 0.39$) and size class 2 ($r = 0.51$, $p = 0.07$) were not significantly correlated, but were significantly positively correlated in size class 3 ($r = 0.73$, $p = 0.006$) and size class 4 ($r = 0.67$, $p = 0.009$).

Discussion

Our first hypothesis, that display behavior would only be observed during social interactions, was supported. None of the 60 juveniles displayed while alone, and overall individual behavior levels, as measured by the BI, were comparatively low ($BI = 12.6 \pm 0.8$). In contrast, 77% (46 of 60) of the juveniles displayed during interactions, during which time individual behavior levels were comparatively high ($BI = 56.1 \pm 5.3$).

Our second hypothesis, that juveniles would not differ in display use, regardless of sex, body size, or social context, had mixed support. Social context (consexual or heterosexual interactions) had no effect on juvenile behavior levels or the types and frequencies of behaviors observed. Sex generally had no effect on display behavior, either, with the single exception that juvenile males in the largest size class had display rates that were double those of females. In a separate study using the same testing protocol, Lovern *et al.* (2001) found very similar results; large juvenile males had display rates that were more than double those of large juvenile females (19 vs 8 displays/h). Contrary to our second hypothesis, however, body size had a nearly ubiquitous effect on juvenile display behavior. Larger juveniles had higher behavior levels, involving the expression of more behaviors at greater frequencies. Body size also affected the extent to which interacting lizards matched behavior levels, which were not correlated in size classes 1 and 2 (≤ 30 mm SVL), but were highly positively correlated in size classes 3 and 4 (31-42 mm SVL).

TABLE 4. *Comparison of display behavior by juvenile and adult Anolis carolinensis*

Behavior	Juveniles		Adults	
	Males	Females	Males	Females
A, B, C display types	Yes	Yes	Yes	Yes
Display type proportions				
Shift with context	No	No	Yes	Yes
Shift with distance	No	No	Yes	No
Average displays/h				
Solitary context	0	0	18	0
Interaction	10	9	168	17
Ritualized aggression	No	No	Yes	No
Display modifier use				
Consexual context	Yes	Yes	Yes	Yes
Heterosexual context	Yes	Yes	No ¹	No ¹
Dewlap use				
Consexual context	Yes	Yes	Yes	Yes
Heterosexual context	Yes	Yes	Yes ¹	No ¹

Data on juveniles are from the present study. Data on adults marked 1 are from Greenberg & Noble (1944); all other adult data are from Jenssen *et al.* (2000).

Juvenile interactions, regardless of sex, appeared much more similar to adult female-female agonistic interactions than to either adult male-male agonistic or male-female courtship interactions (Introduction; Table 4). Unlike adult males, juveniles did not display alone in an advertisement context, nor did they show any evidence of a ritualized aggression pattern. Juvenile interactions involved comparatively low display rates, incorporating all three species-specific A, B, and C display types regardless of social context or separation distance between lizards. These interactions produced occasional close (<30 cm) approaches and/or retreats without any ultimate physical contact. Given the similarity between juvenile and adult female-female interactions, it appears that juveniles, like adult females, display in an agonistic context as a means of protecting resources. However, the outcomes of juvenile interactions, like those of adult females, carry comparatively few immediate consequences as the resources important to juveniles (habitat for foraging, thermoregulation, predator avoidance) and to adult females (additionally habitat for oviposition) do not appear to be limiting (Nunez *et al.*, 1997; Jenssen & Nunez, 1998; Lovern, 2000a, b). Field observations suggest that, across all contexts, juvenile display rates are low, averaging

about 3 displays/h for both males and females (Lovern, 2000b). Even in the present study, when interactions were forced, display rates were not much higher, averaging about 10 and 9 displays/h for juvenile males and females, respectively (similar to the 17 displays/h observed in agonistic adult female encounters, but much lower than the 168 displays/h given by adult males in agonistic encounters; Table 4). These laboratory interactions are likely to reflect the most intense encounters in which juveniles participate, as all individuals were size-matched to within 2 mm SVL and therefore potentially competing for the same resources with little asymmetry in resource-holding potential (Bradbury & Vehrencamp, 1998).

We have argued that the outcomes of juvenile interactions carry comparatively few immediate consequences. However, given the clear and consistent effects of body size on behavior that we observed, it is possible that the consequences increase during ontogeny. Ecologically, a shift in resource value could occur if there is not only a present, but also a future, benefit at stake. This possibility has been called the prospective resource hypothesis (Stamps & Tollestrup, 1984), and it appears to explain the positive relationship between body size and interaction intensity that we found in the present study. Stamps & Tollestrup (1984) examined the social interactions of the lizard, *Anolis aeneus*, and found that smaller juveniles defended their territories more aggressively than did larger juveniles. They interpreted this as evidence for prospective resource defense relative to the value of territories to small and large juveniles. In *A. aeneus*, hatchlings migrate to clearings and maintain territories for about a month, after which they return to the shaded forest habitat where they will remain as adults (Stamps, 1983). This habitat shift is due to predation; hatchlings are preyed upon by *Anolis richardi* in the forest, and these predators are absent in the clearings (Stamps, 1983). After about a month of growth, juveniles are too large for *A. richardi* to prey upon them, permitting their return to the forest (Stamps, 1983). Thus, in *A. aeneus*, juvenile territories have more prospective value for small juveniles than for large juveniles, as small juveniles will remain on territories for more days than large juveniles, that are closer to leaving (Stamps & Tollestrup, 1984). In contrast, juvenile *A. carolinensis* do not migrate to habitats separate from where adults are found (although they do tend to be associated with grasses, vines, and ground cover vegetation more often than do adults, which are typically found on larger plants and trees; Jenssen *et al.*, 1998; Minesky, 1999),

perhaps in part due to the fact that juveniles historically have not been under congeneric predation pressure. Therefore, because of limited dispersal by juvenile *A. carolinensis*, we suggest that the prospective value of juvenile territories increases, related to the eventual acquisition of breeding territories in adulthood.

Additional field studies offer support for the prospective resource hypothesis in *A. carolinensis*. In *Anolis limifrons*, juvenile home ranges are typically close to or contained within their eventual home ranges as adults (Andrews & Rand, 1983). Similarly, in a field study with *A. carolinensis*, Lovern (2000b) found that a majority of juveniles (32 out of 37 in the study) could be re-sighted within 2 m from where they were originally observed, up to four weeks after initial sighting (when presumably paintmarks that identified lizards wore off). These observations suggest that juvenile home ranges develop into adult home ranges in at least some anoline species. Furthermore, the prospective resource hypothesis could account for the sex difference in display rate observed in large juveniles. Juvenile males may become more aggressive towards other juveniles because of the comparative importance of holding a large adult territory to reproductive success (Ruby, 1984; Nunez *et al.*, 1997; Jenssen & Nunez, 1998). It is known that plasma testosterone concentrations become higher in juvenile males than in juvenile females during the latter stages of juvenile ontogeny, and this could influence natural aggression levels (Lovern *et al.*, 2001). However, the protocol we used for creating social interactions clearly indicated that juvenile females were equally likely to express the behaviors seen in males, and that all interactions, regardless of context, were aggressive. Because adult male territories are defended only against other males, large juvenile males could have more aggressive consensual than heterosexual interactions. Indeed, we found suggestive evidence for this, as average BIs for male-male interactions in large juveniles (size class 4) were approximately twice those of either female-female or male-female BIs, although high variance and small sample sizes may have precluded these differences from being significant.

In summary, and in accord with the juvenile-structured pattern of signal ontogeny, *A. carolinensis* is equipped from hatching with communication signals like those of adults for resolving conflicts over resources. However, unlike adults who show dramatically sexually dimorphic display behavior, juveniles initially show virtually no sex differences. This is not surprising, since juveniles are not yet reproductive and therefore do not differ in resource

requirements. However, as juveniles develop toward the adult stage, size clearly affects display behavior in both sexes. Interactions are more intense, and activity levels of interacting lizards are more closely correlated, between larger than between smaller juveniles. These results suggest that juvenile display use functions to defend resources for their present as well as future value, thus supporting the prospective resource hypothesis. It is likely that resource protection confers the immediate benefits of suitable habitat for foraging, thermoregulation, and predator avoidance. We suggest that the age-related increases in behavioral intensity present in both sexes, as well as the increased display rates expressed by large juvenile males, are being selected by the future benefit of acquiring a breeding territory in adulthood.

References

- Andrews, R.M. & Rand, A.S. (1983). Limited dispersal of juvenile *Anolis limifrons*. — *Copeia* 1983, p. 429-434.
- Bradbury, J.W. & Vehrencamp, S.L. (1998). Principles of animal communication. — Sinauer Associates, Inc., Sunderland, Massachusetts.
- Brown, J.A. & Colgan, P.W. (1985). The ontogeny of social behaviour in four species of centrarchid fish. — *Behaviour* 92, p. 254-276.
- Burghardt, G.M. (1977). Ontogeny of communication. — In: How animals communicate (T.A. Sebeok, ed.). Indiana University Press, Bloomington, p. 71-97.
- —, Greene, H.W. & Rand, A.S. (1977). Social behavior in hatchling green iguanas: life at a reptile rookery. — *Science* 195, p. 689-691.
- — & Rand, A.S. (1985). Group size and growth rate in hatchling green iguanas (*Iguana iguana*). — *Behav. Ecol. Sociobiol.* 18, p. 101-104.
- Catchpole, C.K. & Slater, P.J.B. (1995). Bird song: biological themes and variations. — Cambridge University Press, Cambridge.
- Cooper, W.E., Jr. (1971). Display behavior of hatchling *Anolis carolinensis*. — *Herpetologica* 27, p. 498-500.
- DeCourcy, K.R. & Jenssen, T.A. (1994). Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. — *Anim. Behav.* 47, p. 251-262.
- Fagen, R. (1981). Animal play behavior. — Oxford University Press, New York.
- — (1993). Primate juveniles and primate play. — In: Juvenile primates (M.E. Pereira & L.A. Fairbanks, eds). Oxford University Press, New York, p. 182-196.
- Gordon, R.E. (1956). The biology and biodemography of *Anolis carolinensis carolinensis* Voigt. — PhD dissertation, Tulane University, New Orleans.
- Greenberg, B. & Noble, G.K. (1944). Social behavior of the American chameleon (*Anolis carolinensis* Voigt). — *Physiol. Zool.* 17, p. 392-439.
- Greenberg, N. (1977). A neuroethological study of display behavior in the lizard *Anolis carolinensis* (Reptilia, Lacertilia, Iguanidae). — *Am. Zool.* 17, p. 191-201.
- — & Hake, L. (1990). Hatching and neonatal behavior of the lizard, *Anolis carolinensis*. — *J. Herpetol.* 24, p. 402-405.

- Groothuis, T.G.G. (1993). A comparison between development of bird song and development of other displays. — *Neth. J. Zool.* 43, p. 172-192.
- — (1994). The ontogeny of social displays: interplay between motor development, development of motivational systems and social experience. — In: *Causal mechanisms of behavioral development* (J.A. Hogan & J.J. Bolhuis, eds). Cambridge University Press, Cambridge, p. 183-211.
- Hadley, M.E. & Goldman, J.M. (1969). Physiological color change in reptiles. — *Am. Zool.* 9, p. 489-504.
- Hauser, M.D. (1996). *The evolution of communication*. — MIT Press, Cambridge, Massachusetts.
- Jenssen, T.A. (1977). Evolution of anoline lizard display behavior. — *Am. Zool.* 17, p. 203-215.
- —, Greenberg, N. & Hovde, K.A. (1995). Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. — *Herpetol. Monogr.* 9, p. 41-62.
- —, Hovde, K.A. & Taney, K.G. (1998). Size-related habitat use by nonbreeding *Anolis carolinensis* lizards. — *Copeia* 1998, p. 774-779.
- — & Nunez, S.C. (1998). Spatial and breeding relationships of the lizard, *Anolis carolinensis*: evidence of intrasexual selection. — *Behaviour* 135, p. 981-1003.
- —, Orrell, K.S. & Lovorn, M.B. (2000). Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis*. — *Copeia* 2000, p. 140-149.
- Kiester, A.R. (1977). Communication in amphibians and reptiles. — In: *How animals communicate* (T.A. Sebeok, ed.). Indiana University Press, Bloomington, p. 519-544.
- Lovorn, M.B. (2000a). Social and hormonal effects on the ontogeny of sex differences in behavior in the lizard, *Anolis carolinensis*. — PhD dissertation, Virginia Tech, Blacksburg.
- — (2000b). Behavioral ontogeny in free-ranging juvenile male and female green anoles, *Anolis carolinensis*, in relation to sexual selection. — *J. Herpetol.* 34, p. 274-281.
- —, McNabb, F.M.A. & Jenssen, T.A. (2001). Developmental effects of testosterone on behavior in male and female green anoles (*Anolis carolinensis*). — *Horm. Behav.* 39, p. 131-143.
- Michaud, E.J., III. (1990). Geographic variation of life history traits in the lizard, *Anolis carolinensis*. — PhD dissertation, University of Tennessee, Knoxville.
- Minesky, J.J. (1999). Development and application of a genetic algorithm-informational modeling approach to exploratory statistical modeling of lizard-habitat relationships. — PhD dissertation, University of Tennessee, Knoxville.
- Moore, A.J., Reagan, N.L. & Haynes, K.F. (1995). Conditional signalling strategies: effects of ontogeny, social experience and social status on the pheromonal signal of male cockroaches. — *Anim. Behav.* 50, p. 191-202.
- Nunez, S.C., Jenssen, T.A. & Ermland, K. (1997). Female activity profile of a polygynous lizard (*Anolis carolinensis*): evidence of intersexual asymmetry. — *Behaviour* 134, p. 205-223.
- Ortiz, P.R. & Jenssen, T.A. (1982). Interspecific aggression between lizard competitors, *Anolis cooki* and *Anolis cristatellus*. — *Z. Tierpsychol.* 60, p. 227-238.
- Otte, D. (1977). Communication in Orthoptera. — In: *How animals communicate* (T.A. Sebeok, ed.). Indiana University Press, Bloomington, p. 334-361.

- Phillips, J.A., Alberts, A.C. & Pratt, N.C. (1993). Differential resource use, growth, and the ontogeny of social relationships in the green iguana. — *Physiol. Behav.* 53, p. 81-88.
- Rice, W.R. (1989). Analyzing tables of statistical tests. — *Evolution* 43, p. 223-225.
- Roggenbuck, M.E. & Jenssen, T.A. (1986). The ontogeny of display behavior in *Sceloporus undulatus* (Sauria: Iguanidae). — *Ethology* 71, p. 153-165.
- Ruby, D.E. (1984). Male breeding success and differential access to females in *Anolis carolinensis*. — *Herpetologica* 40, p. 272-280.
- — & Baird, D.I. (1993). Effects of sex and size on agonistic encounters between juvenile and adult lizards, *Sceloporus jarrovi*. — *J. Herpetol.* 27, p. 100-103.
- Ryan, M.J. (1985). The túngara frog: a study in sexual selection and communication. — University of Chicago Press, Chicago, Illinois.
- Stamps, J.A. (1978). A field study of the ontogeny of social behavior in the lizard *Anolis aeneus*. — *Behaviour* 66, p. 1-31.
- — (1983). The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). — *Behav. Ecol. Sociobiol.* 12, p. 19-33.
- — (1994). Territorial behavior: testing the assumptions. — *Adv. St. Behav.* 23, p. 173-232.
- — & Tollestrup, K. (1984). Prospective resource defense in a territorial species. — *Am. Nat.* 123, p. 99-114.
- Thompson, K.V. (1998). Self assessment in juvenile play. — In: *Animal play: evolutionary, comparative, and ecological perspectives* (M. Bekoff & J.A. Byers, eds). Cambridge University Press, Cambridge, p. 183-204.
- Walters, J.R. (1987). Transition to adulthood. — In: *Primate societies* (B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker, eds). University of Chicago Press, Chicago, Illinois, p. 358-369.
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