An Analysis of Inter-Population Divergence in Visual Display Behavior of the Green Anole Lizard (*Anolis carolinensis*)

Natasha Bloch* & Duncan J. Irschick†

* Department of Biological Science, Universidad de los Andes, Bogota, Colombia
† Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA, USA

Correspondence

Duncan J. Irschick, Department of Ecology and
Evolutionary Biology, 310 Dinwiddie Hall,
Tulane University, New Orleans, LA 70118,
USA. E-mail: irschick@tulane.edu

Abstract

Variation in habitat structure can profoundly affect the evolution of visual displays in animals. We compared the field display behavior of two populations of the green anole lizard (*Anolis carolinensis*) in Southern Louisiana. These two populations occupy habitats varying markedly in structure (clumped vs. continuous), ecological setting (urban vs. natural) and the degree of male competition and predation. We filmed 56 large adult male lizards during the active spring reproductive period and detected substantial divergence in display behavior between populations. We found that (1) relative dewlap areas did not differ significantly between populations, (2) Tulane anoles spent about twice as much time displaying compared with Good Hope field anoles, although the average display duration did not differ significantly between populations, and (3) the two populations differed significantly in the relative frequency of display types: lizards from the Tulane population used a higher proportion of A and B display types, whereas Good Hope Field anoles used C displays more often. Finally, we detected differences in other aspects of display behavior (use of display modifiers, volley length distributions). We suggest that these display differences may result from differences in green anole male density (three times higher at Tulane), combined with habitat differences (clumped vs. continuous).

Introduction

Variation in habitat use among animal populations can profoundly influence how sexual selection operates on social behavior, mating systems and therefore, visual signals (see Arnold 1983; Anderson 1994; Wade 1995; Butler et al. 2000; Baird & Sloan 2003; Baird et al. 2003; Shuster & Wade 2003; Zamudio & Sinervo 2003). Previous syntheses have outlined the complex manner in which factors such as habitat visibility, predation risk, density of conspecifics, food availability or temperature can affect visual displays (Fleishman 1988, 1992; Endler 1992; Ord et al. 2002; Whiting et al. 2003; Zamudio & Sinervo 2003). Habitat visibility (how far can a

visual signal be detected by receivers), may have a strong impact on both the form and intensity of visual signals (Luyten & Liley 1991). Another important factor is whether the available habitat is distributed continuously, or rather arrayed in discrete clumps (Goldberg et al. 2001; Zamudio & Sinervo 2003). Such different habitat arrangements can dramatically influence the distribution of potential mates and resources (Grant 1993; Hews 1993; Baird et al. 1997; Emlen & Oring 1997; Orrell & Jenssen 2003; Zamudio & Sinervo 2003). A third factor is the relative risk of predation (Endler 1983), which can result in a trade-off between displaying to acquire mates and survival (e.g. tungara frogs, Ryan et al. 1982; Ryan 1985).

Comparison of the display behavior among populations of the same species occurring in different habitats, might allow one to examine the effects of the above factors on the evolution of signaling behavior (Foster 1999; Wilczynski & Ryan 1999). Here, we focus on understanding how variation in habitat structure between populations of the green anole lizard (*Anolis carolinensis*) affects the visual displays of adult males. *Anolis carolinensis* is sexually dimorphic (adult males about 1.5 times the body size of adult females), and adult males are highly territorial (Jenssen et al. 2001; Lailvaux et al. 2004). Green anoles have stereotyped headbob display forms: both males and females have a repertoire of displays termed A, B and C patterns that are highly conserved within and among populations (Lovern et al. 1999; Lovern & Jenssen 2001, 2003; Orrell & Jenssen 2003). These displays consist of stereotyped sequences of head bobbing (vertical displacements of the head), which are generally accompanied by extensions of their enlarged throatfans (dewlaps). Green anole displays are used to advertise ownership of territories, attract females (Ruby 1984; Fleishman 1988, 1992; Jenssen et al. 1995; Pough et al. 2001), and probably, as it is the case for other anoline species, to signal to predators (Leal & Rodriguez-Robles 1995, 1997; Leal 1999). Both males and females seem to use all display types across all social contexts, it would therefore be unfounded to assign context-labels to each display type (DeCourcy & Jenssen 1994). Displays can be accompanied by modifiers for increased display visibility at a distance or as indicators of lizard's motivational state. Modifiers may include crest raising, extension of all limbs, sagittal expansion or other body postures, color changes or extra headbobs at the end of the display (Jenssen 1979; Ord et al. 2001). Although previous studies of *Anolis* have focused on inter-population differences in display structure (Jenssen & Gladson 1984; Lovern et al. 1999; Macedonia & Clark 2003), or in dewlap size (Losos & Chu 1998), fewer studies have investigated how variation in habitat use affects display behavior in free-ranging males.

We compared the field display behavior of males between two populations of green anole lizards in southern Louisiana. These sites are close to one another (within 50 km), and consequently are likely to be genetically similar. However, these sites (Good Hope Field and Tulane) differ dramatically in their basic habitat structure (Fig. 1). Previous studies have noted the potential for displays to diverge rapidly among populations (Martins et al. 1998; Foster 1999), suggesting that one might also expect divergence among these green anole populations. We videotaped displays of free-ranging adult males from both populations during the peak of the breeding season (Apr. and May 2004) and observed whether these populations differ in basic aspects of display behavior and/or in the size of their display structure (the dewlap). Finally we estimated male density at both study sites, as density is known to have strong effects on levels of male competition (Stamps 1983; Kwiatkowski & Sullivan 2002), and hence on, the use of visual displays.

Prior studies provide some basis for predictions regarding how visual displays should differ between these two populations. The clumped and simple habitat structure of the Tulane site should induce a higher overall rate of display compared with the more continuous and complex Good Hope Field site. This prediction is based on the assumption that a clumped and simple environment should offer a higher potential for polygyny (see Vehrencamp & Bradbury 1984; McCoy et al. 2003) as well as higher lizard densities. Another reason for this prediction is the substantially lower predation risk in the Tulane population (Irschick et al. 2005), which reduces the cost of normally risky visual displays. Moreover, we expected Tulane and Good Hope Field anoles to use approximately the same proportions of A, B and C displays, following DeCourcy & Jenssen's (1994) recommendation to abandon the function labels on specific display types. Finally, we predicted that anoles should use more display modifiers in the Tulane habitat, in which the potential for male competition is greater (Ord et al. 2001).

Materials and Methods

Field Sites and Videotaping

The Tulane site is a 365-m transect consisting of isolated clumps of simple vegetation separated from one another by 2–10 m (Fig. 1a). Our second site (Good Hope Field) is a 765-m transect that consists of a rarely used dirt road bordered on either side by relatively narrow continuous strips of complex vegetation (about 3–4 m wide between the road and an open water swamp on each side). The vegetation at Good Hope Field is a mixture of dense low-lying shrubs and grass interspersed with larger trees and bushes (Fig. 1b).

We estimated male density at the two habitats from prior work based on mark–recapture studies (D. J. Irschick et al. unpublished data). In both populations, we collected an estimated 75% of all adult
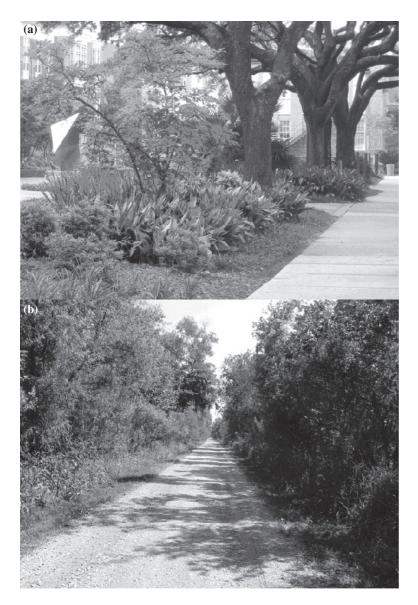
Fig. 1: Images of (a) Tulane University, and (b) Good Hope Field habitat. Note the dramatic difference in the composition of vegetation, and how the vegetation is arranged in discrete clumps at Tulane, but is continuous at Good Hope Field. Photographs by N. Bloch

males (>45 mm SVL) during the non-reproductive seasons of 2002 and 2003/2004 (Good Hope Field, N = 220 and Tulane, N = 56). This 75% estimation was based on repeated sampling until three of every four males captured was marked (D. J. Irschick et al. unpublished data). Subsequently we conducted similar mark–recapture studies in the spring of 2003 and 2004 at Tulane and captured approximately similar numbers of males (spring 2003: N = 86, spring 2004: N = 70), indicating that adult male density does not change dramatically among seasons. To estimate the transect area at Good Hope Field, we measured the widths of the linear habitat strip (distance from road until swamp) at 37 sampling points, every 20 m along the 765-m long transect, alternating left and right sides. We calculated the total two-dimensional area by multiplying the average habitat width on each side [3.45 + 1.09 m (SD)] by the length of the transect (765 m) and summing the areas (total area = 5279 m^2). For the Tulane site, we estimated the width and length of a sample of 10 clumps (average area = 10 m^2) and multiplied the average area by the total number of clumps available (40 clumps, total estimated area = 400 m^2). We then estimated male density for both habitats by dividing the estimated number of males (number of captured males divided by 0.75) (Good Hope Field = 293, Tulane = 75) by the total area accessible to them.

We gathered video focal data for 30 and 26 large free-ranging adult males (>60 mm SVL) from the Tulane Campus and the Good Hope Field,

respectively (total N = 56 males). We videotaped individual males for 5–40 min (average duration: 15 ± 1.32 min SE) until we lost sight of them. We used a Sony mini-DV digital camera with a tripod to film the lizards and maintained a distance of at least 2 m during filming, remaining as still as possible to avoid startling the lizard (following Irschick & Losos 1998). Only one investigator (N.B.) videotaped and analyzed all of the videos of focal males to ensure consistency. We avoided sampling the same area more than once to prevent repeated observations of the same male. The study was conducted from Apr. 1, 2004 to May 20, 2004 when males are actively attempting to acquire and defend territories (Jenssen & Nunez 1998). We only filmed lizards during warm (i.e. shaded ambient temperatures >26°C) and non-rainy weather. A recent study (Lailvaux et al. 2004) showed that green anole males are bimodal, with larger males (>64 mm SVL) exhibiting larger head shapes than smaller males. Therefore, to avoid such confounding effects, we only focused on very large males, although we acknowledge that gathering data on a wide range of male sizes would be informative. To test whether males in the two populations differed in dewlap size, we measured dewlap area on samples (N = 20 per population) of large (>64 mm SVL) adult males. During videotaping we noted if the focal male was displaying to another lizard (male or female) and any signs of aggressiveness, such as crest raising. For each male, we captured digital pictures extending their dewlaps with forceps and then, digitized them using TPSDIG version 1.40 (following VanHooydonck et al. 2005). This method is both accurate and highly repeatable.

Video Analyses

We reviewed the videotapes frame by frame (30 frames per second) to identify specific behaviors. Based on previous descriptions of *A. carolinensis* displays (DeCourcy & Jenssen 1994. Lovern et al. 1999; Jenssen et al. 2000), we quantified different standardized behaviors from each videotape: (1) Headbobs, or vertical head bobbing movements of high amplitude while extending both front limbs; (2) Quick bobs, or shallow simple and double bobs, also called 'shudderbobs' in previous studies (Tinkle 1967; Orrell & Jenssen 2003); (3) The number of times the lizard extended its dewlap. We counted the number of times each of these behaviors was repeated in tandem and the duration of each tandem [by noting the exact moment (minute, second and frame) the first repetition started and the last one

ended]. We also recorded the display type (A, B, or C, or any variant noted) already described by previous studies (Jenssen 1977; DeCourcy & Jenssen 1994). We measured display complexity by recording the following modifiers: quick bobs after the core component of the display (see further description in Jenssen 1979) and 'pushups' which are a full extension of all four limbs during the display. Finally, we recorded if each display was part of a volley or done singly (displays in the same volley had to be <2 s apart, following Orrell & Jenssen 2003).

Data Analysis

We calculated five primary variables for each focal video: (1) percentage of time displaying relative to total observation time; (2) percentage of time exposing the dewlap during displaying; (3) average duration of each display (including headbobs, quick bobs and dewlaping); (4) total headbobs duration; and (5) total quick bobs duration. We used a Principal Components Analysis (PCA) to reduce the dimensionality of these variables and then performed a multivariate ANOVA on these new PCs using population (N = 2) as the sole fixed factor.

To estimate the relative proportions of the A, B and C displays for each study site, we first calculated these proportions for each individual and then evaluated the mean value for each study population. Then, we compared A, B, and C proportions using a chi-square test and used a Kolmogorov–Smirnov test to compare the volley length distributions between populations. We also evaluated the percentage of displays done in volleys and finally calculated the percentage of displays performed with either kind of display modifier and compared them between the populations. A non-parametric Kruskal–Wallis test was used to compare percentages between populations. All data analyses were performed using SYSTAT (version 10, 2000, SPSS Inc., Chicago, IL, USA) and all error bars are standard errors.

Results

Table 1 provides summary statistics for the relevant display variables for the two populations, and Table 2 provides loadings from the PCA. The two study populations did not differ significantly in SVL (F-value = 0.31; p > 0.5), and hence we compared non-size-adjusted values of dewlap area. The average dewlap areas were 2.21 ± 0.10 and 2.29 ± 0.10 cm^2 for the Tulane and Good Hope Field populations, respectively, which did not differ significantly (one-

Table 1: Mean (±1 SE) values for various display variables in the Tulane and Good Hope Field populations

Variable	Tulane	Good Hope Field
% time displaying	9.31 ± 0.84	5.19 ± 0.83
% time exposing dewlap	61.60 ± 2.07	56.34 ± 3.59
Average display duration (s)	4.34 ± 0.18	3.39 ± 0.22
% time headbobs	3.26 ± 0.32	1.91 ± 0.29
% time quickbobs	5.93 ± 0.59	3.09 ± 0.52

Table 2: Loadings from a principal components analysis for various display variables. Substantial loadings are in bold

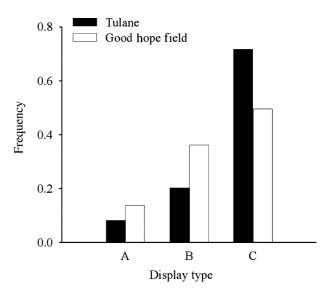| Variables	PC1	PC2
% time displaying	**0.962**	0.247
% time exposing dewlap	0.135	**0.931**
Average display duration (s)	0.272	**0.894**
% time headbobs	**0.967**	0.124
% time quickbobs	**0.941**	0.270
Eigenvalue	2.840	1.815

Fig. 2: Relative frequencies (relative to the total number displays) of A, B and C displays for both the Tulane and Good Hope Field populations. Note the relatively higher proportion of the 'C' display at Tulane, whereas Good Hope Field had higher proportions of 'A' and 'B' displays

way ANOVA, F-value = 0.45; p > 0.5). The estimated green anole male density at Tulane was approximately three times higher than that at Good Hope Field (Tulane: 0.19 males/m², Good Hope Field: 0.06 males/m²). From a total of 577 displays for Tulane and 250 for Good Hope Field, principal component 1 (PC1: 56.8% of variation explained) showed high positive loadings for the percentage of time displaying, percentage of bobbing and percentage of quick bobs. Principal component 2 (PC2: 36.3% of variation explained) had high and positive loadings for the percentage of time dewlaping and the average duration of each display. Therefore, lizards primarily control the length of displays by changing the amount of time they expose their dewlap.

The MANOVA showed that the populations differed significantly only for PC1, indicating a difference in the percentage of time spent displaying (time spent doing headbobs and quickbobs) (Tables 2 and 3). Tulane lizards spent almost twice as much time displaying compared with lizards from Good Hope Field

Table 3: Summary of the analyses of variance (MANOVA) comparing Good Hope Field and Tulane anole populations for the principal components analyses factors

Variable	F-value	df	p-value
PC1	13.49	1.54	0.001
PC2	0.02	1.54	0.890
Wilks' lambda	6.64	2.53	0.003

(Table 1). We obtained ratios for the use of the different display types (A:B:C) of 2:5:18 and 1:3:16 for Tulane and Good Hope Field, which differed significantly (chi-square test, $\chi^2 = 26.46$, df = 2, p < 0.001), Lizards from Good Hope Field used relatively more A and B displays than Tulane lizards (Fig. 2). We also observed an unusual display by four of the 30 Tulane focal males that we term the 'Y' display (following the unusual 'X' display used primarily by green anole juveniles, Lovern & Jenssen 2003). This display appears to be a variation of the usual 'C' display in which the seventh unit is barely noticeable (T. Jenssen, pers. comm.) (see Lovern et al. 1999; Lovern & Jenssen 2003; Orrell & Jenssen 2003, for description of C display).

The average volley lengths were 1.95 ± 0.06 and 2.00 ± 0.12 for Tulane and Good Hope Field, respectively (Fig. 3), with volleys ranging from two to eight displays. The difference in volley length between populations was therefore significant ($D_{max} = 0.17$; df = 9; p < 0.001). By estimating the percentage of displays done in volleys (as opposed to singly) we observed that lizards performed 79.7% and 76.4% of the displays in volleys at Tulane and Good Hope Field, respectively. The Kruskal–Wallis test revealed no significant difference between these percentages (Mann–Whitney U = 257.0; df = 1; p = 0.782). However, when we compared the percentage of displays with modifiers, we detected a
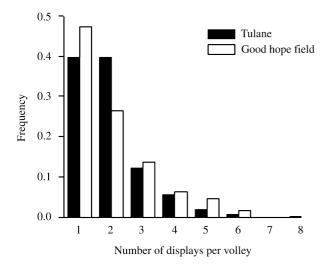
Fig. 3: A frequency histogram of volley length (number of displays per volley) for both the Tulane and Good Hope Field populations. Note that Good Hope Field generally had fewer displays per volley compared with Tulane

significant difference between populations (Mann–Whitney U = 451.5; df = 1; p = 0.001). Tulane males used these display modifiers about 9.0% of the time compared with only 3.2% for Good Hope Field males. Finally, four of the 30 focal males (13%) from Tulane displayed to a female and six (20%) displayed aggressively to another male. At Good Hope Fields these proportions were 4% (1/26) and 8% (2/26), respectively. Although these data generally show a trend toward a greater number of directed displays at Tulane, there was no significant difference in the time each lizard spent displaying to a conspecific between sites (pooling displays toward males and females within each population, Mann–Whitney U = 423.0; df = 1; p = 0.397).

Discussion

Different populations of the same species can diverge in the morphology of the signaling structure and/or their display behavior. In anoles, dewlap size and coloration have been shown to vary greatly among species (Echelle et al. 1971; Losos & Chu 1998) and among populations (Macedonia et al. 2003; Leal & Fleishman 2004). Not infrequently, however, display behavior, as opposed to morphology of the signaling structure, differs among populations of the same species (Macedonia et al. 1994; Macedonia & Stamps 1994; Martins et al. 1998; Downes & Adams 2001 or see Foster 1999 for a review). We detected no significant difference in the relative dewlap areas of

Tulane and Good Hope Field anoles, but documented substantial divergence in several aspects of display behavior, most notably the percentage of time spent displaying (verifying prediction 1).

The amount of time spent displaying is often viewed as an indicator of males' investment toward territorial defense (DeCourcy & Jenssen 1994; Jenssen et al. 1995). Previous research shows that highly polygynous anoles, such as trunk-ground and trunk-crown anoles (see Butler et al. 2000 or Losos 1994 for a definition of *Anolis* ecomorphs), display around 5.7 ± 1.2% and 6.0 ± 1.4% of their time respectively, whereas largely non-polygynous species display only about 1% or less (Hicks & Trivers 1983; Irschick & Losos 1996). In the case of Good Hope field anoles, the percentage of time spent displaying (5.19%) is similar to reported values for polygynous anoles. By contrast, the percentage of time Tulane anoles spent displaying (9.31 ± 0.84%) is extremely high, almost double the highest previously reported. We suggest that the greatly increased display rate at Tulane results in part from the much higher male densities (about threefold) combined with a clumped and simple habitat structure, which forces males into closer proximity. Additionally the reduced risk of predation in the urban Tulane environment (Irschick et al. 2005) may allow males to display more frequently (Fleishman 1988, 1992, 2000). Similar differences have been reported by McCoy et al. (2003) between populations of the territorial *Crotaphytus* lizards living in habitats that differ in structure. The higher percentage of displays directed toward other males at Tulane (20%) compared with Good Hope Field (8%) is consistent with these higher densities (although the proportion of displays directed toward conspecifics did not differ significantly between populations). Larger samples are needed to provide more information on the social context of displays in the two populations.

The *A. carolinensis* display repertoire is highly conserved across widely divergent populations, such as North America and Hawaii (Lovern et al. 1999). We found that green anoles from both Louisiana populations also used the previously described A, B and C display types. As previously demonstrated by Jenssen et al. (2000) and Orrell & Jenssen (2003) males used predominantly C displays. Nevertheless, Good Hope Field anoles used proportionally fewer A and B displays, and more C displays, compared with Tulane anoles, which refuted our second prediction. Orrell & Jenssen (2003) showed that males tended to use more C displays when signaling toward individuals at a distance,

but increase the proportion of A and B displays during encounters at a shorter distance. This latter finding might explain why Tulane anoles use higher proportion of A and B displays, given their clumped population distribution and high densities.

Additionally we found that four of 30 males videotaped at Tulane performed an undescribed variant of the C display (T. Jenssen pers. obs.) that we did not observe at Good Hope Field. The reason we have not seen this display in the past could be that most studies of the green anole display repertoire were primarily conducted under standardized laboratory settings. Further comparative field studies are needed to determine whether the durations of the other display 'units' in this unique display are homologous with the normal version of the 'C' display, and more generally, to ascertain its function.

We found that Good Hope Field anoles used display modifiers only 3% of the time, which is substantially lower than 9% observed for Tulane anoles, verifying our third prediction. Previous authors have suggested that some modifiers could be used to enhance the visibility of the display (Jenssen 1977, 1979; Jenssen et al. 2000), whereas others could be indicators of motivational state during agonistic encounters (Martins 1993; Martins et al. 1998; Ord et al. 2001). Tulane population's high density, and thus intense intrasexual competition, lends support to the latter hypothesis. Finally, during male–male signaling, volley length tends to decrease as the distance between the signaling males decreases (DeCourcy & Jenssen 1994; Orrell & Jenssen 2003). This latter finding is consistent with the fact that Tulane anoles tended to perform shorter volleys more often than do those at Good Hope Field.

In conclusion, we found that our study populations show substantial divergence in their rate and use of headbob displays. However, our findings do not rule out the possibility that such inter-population differences are genetically based, as opposed to being plastic. Reciprocal transplant and/or common garden experiments would be useful for distinguishing environmental vs. genetic causes for divergence in display behavior. We argue that differences in both male density and habitat structure between Tulane and Good Hope Field may be a driving force behind the behavioral differences we document, but as with any two-population comparison (Garland & Adolph 1994), one must be cautious. Further studies that extend our approach to a broader range of habitat types would be useful for understanding the effects of habitats on display behavior.

Acknowledgements

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