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## Display Repertoire Analysis of *Anolis townsendi* (Sauria: Iguanidae) from Cocos Island

THOMAS A. JENSSEN AND LINDA M. ROTHBLUM

Male *Anolis townsendi* have a large agonistic social display repertoire of 4 display types (displays A-D). The type A display appeared analogous in function to the signature display of other anoles. All 4 display patterns were performed during male-male territorial encounters, with types C and D being rarely observed. The 2 most commonly performed display types (A and B displays) were quantitatively analyzed. Both display patterns had a unique feature of being composed of a series of 4 complex motor patterns (acts) which appeared in a fixed sequence. Though these acts were relatively stereotyped, the number of acts performed during a display was variable. One way analysis of variance components indicated that 97% of the variability of display duration for both A and B displays was attributed to intraindividual variation and only 3% of the temporal variability was ascribed to interindividual variation; this shows that all sampled lizards could vary the durations of their displays to a similar extent. The way in which display types B-D diverged from the basic signature display (A display) was strikingly similar to the situation found in *Anolis limifrons*, a species which also has a large display repertoire.

**A**N impressive number of studies have been conducted on iguanid lizard display behavior during the past 15 years. For the most part these investigations have characterized lizards as

having limited repertoires of stereotyped displays. The usual described repertoire is composed of 2 display types: 1) a sequence of rapid low amplitude head bobs which is associated with

courtship and is interspecifically similar in form, and 2) an "assertion-challenge" display pattern which is species-typical and can vary, depending upon context, from a low intensity version (assertion) to a more elaborate version (challenge) (Bussjaeger, 1971:34-36; Carpenter, 1967; Jenssen, 1977). Recently, however, studies of *Anolis limifrons* (Hover and Jenssen, 1976), *Phenacosaurus heterodermus* (Jenssen, 1975) and *Anolis aeneus* (Stamps and Barlow, 1973) have described repertoires of more than two display types. *Anolis townsendi* also has a large repertoire; description of its display types adds to the growing realization that the social signals of iguanid lizards may be more extensive and complex than previously believed.

#### METHODS AND MATERIALS

Cocos Island, sole locality of *A. townsendi*, is a small Pacific island (5.6 × 5.4 km) approximately 500 km from Costa Rica. Cocos is characterized by almost continuous precipitation which feeds its many streams, a rugged topography bordered by cliff-edged shoreline, and an extraordinarily luxuriant rain-forest vegetation including continuous stands of tall hardwood trees, groves of tree ferns in the deep ravines, and palms on the higher slopes. *A. townsendi* is the only diurnal lizard on the island (Hertlein, 1963). It is abundant and widely dispersed within the many microhabitats on the island.

From 13 to 15 August 1973, in the vicinity of Chatham Bay, T. A. Jenssen and E. L. Hover made field observations, collections and film records of *A. townsendi*. During the infrequent periods of sunshine, displays from 5 males were filmed in the field using the following methods: 1) the observer moved to within 3 m of an animal and followed its activities with a Nizo S80 super 8 camera; a telephoto lens gave sufficient magnification to allow accurate analysis of the resulting filmed displays; 2) a distant male was captured and released, unrestrained, into the territory of a lizard under observation; and 3) an aquarium containing a few males was placed at the base of a resident male's usual perch which produced a predictable site of encounter and permitted the camera to be set up close to where the displays would be performed.

Captive *A. townsendi* were also observed and filmed at the Smithsonian Tropical Research Institute, Balboa, Canal Zone, during 18-24 August 1973. Using the Nizo S80 camera and Colortran Quartz-King 500 flood lights with heat filters, displays of 2 males were recorded

by placing a subject in a 1.2 m (L) × 0.6 m (W) × 0.9 m (H) photographic chamber. Three different social conditions were provided: several females alone with the subject, several females and a rival male with the subject, and one session when an *Anolis notopholis* of similar size as the subject was present. At no time, including the session with the *A. notopholis*, did captivity have any noticeable effect upon the display characteristics of male *A. townsendi*.

A total of 28 field and 82 laboratory-filmed displays from 7 males were used in this study. A larger sample was planned, but the 50 specimens brought back to our laboratory at Virginia Polytechnic Institute and State University died within 2 weeks. More data are necessary to make a thorough analysis of all display types of *A. townsendi*; however, the consistency of the data collected, the unusually large repertoire of the species, and the species' relative inaccessibility prompt this report.

Films were analyzed frame-by-frame and graphs of head and dewlap movement plotted using a Kodak Ektagraphic MFS-8 projector and a technique already reported elsewhere (Jenssen and Hover, 1976).

Four different display types (A, B, C and D) were recognized during observation periods on Cocos Island and later confirmed from films. However, there were only sufficient numbers of filmed displays for a statistical analysis of the type A and B displays. Display variability was measured within the A and B displays by dividing the 2 stereotyped patterns into their 4 naturally occurring acts (see definition of act by Barlow 1968:219-220) and into 13 units chosen by the investigators. These 13 artificial units were delineated by unequivocal landmarks in the display-action-patterns (DAP).

Descriptive statistics of A and B displays included mean duration, standard error of the mean, and 95% confidence limits of the mean for each of Units 1-7 (encompassed by Acts I-II). For Units 8-13 (encompassed by Acts III-IV), however, just the mean durations and their standard errors were computed because the sample sizes were small for these units. Most A and B displays contained Act II, but few were performed through Acts III-IV. Durations for Units 1-7 were also analyzed for the amount of variance within and among lizard groups via the one-way analysis of variance test.

Each of the first 7 unit durations within an A or B display was also expressed as a percentage of Acts I & II of the display in which it appeared. After arcsine transformations of the

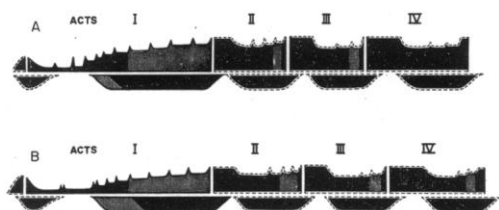


Fig. 1. DAP graphs from mean unit durations showing the *Anolis townsendi* A and B display types resulting from analysis of 68 displays from seven males. Upper block of each figure represents relative intradisplay head amplitude and lower block dewlap extension. Solid black areas are display movements which were always present within an act. Stippled areas denote display movements which were intra- and interindividually variable within an act. Breaks in the DAP graphs show the divisions between the acts. Dashed lines outline those acts and display movements which were optional.

unit percentages to normalize the data, descriptive statistics were computed in the same manner as for unit duration. The unit percentage analysis was conducted to see how much the proportionality of the units varied. For example, displays of a particular type might be performed over a wide range of durations, but each unit within the displays could maintain its percentage value regardless of whether it was in a fast or slow display.

## RESULTS

*Display repertoire.*—*Anolis townsendi* has at least 4 distinct types, designated here as A, B, C and D (Fig. 1, 2). The A display was the most frequently observed display type. From field observations, the type A display is analogous to the signature displays of *Phenacosaurus heterodermus* (Jenssen, 1975), *A. limifrons* (Jenssen and Hover, 1976), and *A. aeneus* (Stamps and Barlow, 1973). Though seen in other contexts, the A display was most predictably performed just after a male reached a new perch site within his territory, even when other conspecifics were not evident (assertion context). This signal seems to function like territorial singing by birds and sign posting by mammals. The other display types of male *A. townsendi* did not appear in this context. Display type A was also seen in agonistic encounters. It was elicited along with B, C and D displays when a second male appeared in or near the first male's territory. Only during intense male-male interactions were C and D displays performed, and these occurred infrequently.

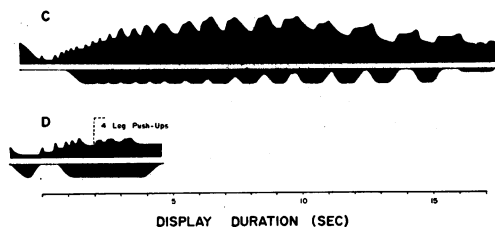


Fig. 2. Specific DAP graphs of the *Anolis townsendi* C and D display types.

*Display types A and B (the acts).*—Display types A and B share a unique feature. The 2 displays are made up of several complex motor patterns which are performed in a fixed order (Fig. 1); however, the entire sequence was not necessarily completed in any one display. The lizards can terminate their A and B displays at any of 4 possible points. This unusual organization of having several naturally occurring subdivisions to the display patterns comes close to the concept of fixed action patterns (FAP) being subdivided by "acts" (Barlow, 1968). Barlow states that if a FAP consists of several components, say W, X, Y and Z, these acts will occur in a predictable sequence. Furthermore, the numbers of the acts can vary which reflect the relative intensity or completeness of the FAP (e.g. low intensity pattern was WX, while high intensity pattern has WXYZ). At no time, however, is the sequencing of the acts disrupted (e.g. never see XW or YX). These criteria which define acts of fixed action patterns also describe the optional, complex motor patterns comprising the *A. townsendi* A and B displays. We will use the term, "act", to distinguish those behaviors appearing between the naturally occurring subdivisions of the displays (Fig. 1), and the "units" (artificial subdivisions) which we imposed upon the display patterns (Fig. 3).

The A and B displays could contain as many as four acts. All displays, of course, contained Act I; however, it was infrequent that a display contained all four acts. For 35 filmed A displays, Acts II, III and IV appear in 94, 66 and 14%, respectively, of the displays. For 33 filmed B displays 79, 27 and 9% of the displays contained Acts II, III and IV, respectively. A displays usually contained more acts than B displays.

*Display types A and B (act I).*—During every A and B display, Act I contained at least 6 head bobs; no Act I had more than 10 bobs (Fig. 1).

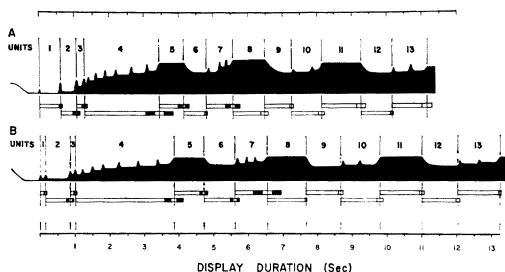


Fig. 3. DAP graphs based on mean unit durations of 35 **A** and 33 **B** display types of *Anolis townsendi* showing unit divisions and unit duration variability. Under the graphs are the descriptive statistics: unit means (vertical lines), standard errors of the means (outer ends of white bars), and 95% confidence limits of the means (outer ends of black bars); 95% C. L. only calculated for Units 1-7.

Those displays which had more numerous head bobs during the first act also tended to have a proportionally longer Act I. When plotting the percent duration of Act I [ $\text{Act I} / (\text{Act I} + \text{II}) \times 100$ ] against the number of head bobs in Act I, correlation coefficients of 0.80 and 0.66 were obtained for the **A** and **B** displays, respectively. Act I had mean durations of  $3.4 \pm \text{SE } 0.1$  s (**A** displays) and  $3.8 \pm \text{SE } 0.1$  s (**B** displays), and an average of  $8.1 \pm \text{SE } 0.5$  (range 6-10) head bobs for **A** displays and  $8.4 \pm \text{SE } 0.3$  (range 6-10) head bobs for **B** displays.

The variance components resulting from one-way analyses of variance run on Act I durations indicate that 97% of the temporal variability was attributed to the within group component (intraindividual variability) and only 3% to the among group component (interindividual variability) for both **A** and **B** displays (Table 1). This means that within the limits of the sample's total temporal variability, each lizard was capable of varying its Act I duration to almost the same extent as any of the other sampled individuals. The amount of intraindividual variability in display duration was more in *A. townsendi* than for *A. limifrons* (64% within group and 36% among group variance, Jenssen and Hover, 1976) and dramatically different from *A. nebulosus* (2% within group and 98% among group variance, Jenssen, 1971).

Of the *A. townsendi* units within Act I, Unit 4 had the greatest percentage of variability for the within group variance component, being 89% (**A** display) and 99% (**B** display). With the exception of very short units (e.g. Unit 1, **B** display; Unit 3, **A** and **B** displays) where shutter speed of the camera introduced a significant

TABLE 1. PROPORTION OF VARIANCE FOUND WITHIN AND AMONG GROUPS RESULTING FROM SINGLE CLASSIFICATION ANALYSES OF VARIANCE APPLIED TO UNIT DURATIONS OF ACT I FROM 68 *Anolis townsendi* DISPLAYS BY SEVEN MALES.

Display Component	Percent Variance Component	
	Within Groups	Among Groups
<b>Display Type A</b>		
Unit 1	73.0%	27.0%
Unit 2	50.4	49.6
Unit 3	35.2	64.8
Unit 4	88.7	11.3
Act I	96.8	3.2
<b>Display Type B</b>		
Unit 1	64.2%	35.8%
Unit 2	20.5	79.5
Unit 3	27.7	72.3
Unit 4	99.3	0.7
Act I	96.9	3.1

source of variation, Unit 4 of Act I **A** and **B** displays also showed the largest coefficients of variation (Table 2). The interindividually variable durations of Unit 4 (Fig. 3) along with the varying number of head bobs performed in Unit 4 (Fig. 1) may serve to signal shifts in motivational intensity of the performer.

Dewlap extension during Act I could be initiated as early as the third head bob in both display types. In the **A** display dewlap extension always began before the sixth bob, but could begin as late as the seventh bob in the **B** display (Fig. 1). No correlation was found between when the dewlap was extended during the first act and the number of head bobs in Act I or the total number of acts performed in the corresponding displays.

The primary diagnostic feature distinguishing **A** from **B** displays is the cadence of the first three bobs (Units 1 and 2) in the two display patterns. There was a statistically significant difference when comparing both duration and percentage values for Units 1 and 2 of **A** displays with the corresponding values from **B** displays. The 95% confidence limits for Units 1 and 2 do not come close to overlapping when comparing corresponding units from the two display types (Fig. 3, 4). Under field conditions this cadence difference was apparent to the human eye. All filmed **B** displays began with a quick double bob (Unit 1/Unit 2 < 1, with resulting mean of  $0.17 \pm \text{SE } 0.01$ , 95% C.L. of 0.05-0.29),

TABLE 2. THE COEFFICIENT OF VARIATION [(STANDARD DEVIATION)/MEAN  $\times$  100] AND THE MAXIMUM UNIT DURATION AND UNIT PERCENTAGE VALUES FOR EACH OF THE FIRST SEVEN UNITS OF 35 A DISPLAYS AND 33 B DISPLAYS FROM SEVEN *Anolis townsendi* MALES.

Unit	Display Type	C.V. (%)	Duration (sec.)	Percentage (%)
1	A	5.6	0.33–0.67	9.3–12.5
	B	25.4	0.11–0.22	1.5– 3.8
2	A	11.4	0.33–0.50	6.5–10.9
	B	8.7	0.61–0.83	9.5–16.1
3	A	22.3	0.17–0.33	2.8– 5.7
	B	20.8	0.11–0.22	1.5– 4.3
4	A	17.5	1.33–2.83	27.2–44.8
	B	18.6	1.61–3.83	31.2–50.7
5	A	10.0	0.61–0.94	10.2–17.0
	B	9.1	0.72–1.11	10.6–16.5
6	A	11.2	0.50–0.89	9.6–14.6
	B	11.2	0.89–1.22	11.4–21.5
7	A	17.1	0.61–1.11	10.1–15.7
	B	36.6	0.33–1.33	5.9–16.2

while all filmed A displays lacked this feature (Unit 1/Unit 2  $>$  1, with resulting mean of  $1.37 \pm$  SE 0.03, 95% C.L. of 1.06–1.67). These 2 cadences showed no tendency to merge as evidenced by non-overlapping ranges of Unit 1 values from A and B displays (Table 2). Delineation of 2 distinct display patterns is justified on the basis of differences in: 1) initial bob cadences, 2) probabilities of including successive acts and 3) social circumstances eliciting the displays.

An infrequent pattern variation of the B display was filmed on 8 occasions (5 males). In these displays the first 2 bobs were apparently fused into a brief plateau having the same duration normally devoted to the quick double bobs. The fused double bobs were the only aspect of the display to deviate from the usual B display pattern.

*Display types A and B (acts II–IV).*—Acts II–IV of both the A and B displays have the same general features. These acts begin with the dewlap retracting and the head being raised and held. Near the termination of this “plateau” period, the dewlap is again stretched. The head is then lowered, 1–3 head bobs performed and the act concludes with the head raised once more and the fan retracted.

Acts II–IV of both A and B displays were

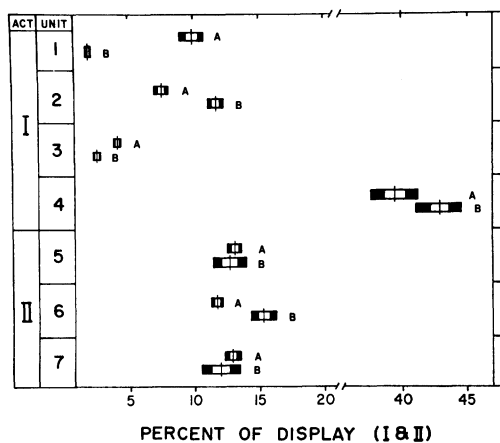


Fig. 4. Unit durations for *Anolis townsendi* display types A and B expressed as a percentage of combined display duration for Acts I and II. Analysis is based on 35 A and 33 B displays. Vertical lines indicate unit means, outer ends of white bars signify the standard errors of the means, outer ends of the black bars denote the 95% confidence limits of the means.

similar in appearance; however, subsequent acts within a display were not identical replications of each other, but varied in their durations. With the exception of Act IV of the B displays, each successive act in the Act II–IV series was found to be significantly longer ( $P < 0.01$ ) in duration than the preceding act using the Student-Newman-Keul (SNK) procedure for measuring differences among means (Sokal and Rohlf 1969:239). For A displays, Acts II, III and IV averaged  $2.16 \pm$  SE 0.03 s,  $2.66 \pm$  SE 0.07 s and  $3.13 \pm$  SE 0.15 s, respectively, while B display Acts II, III and IV had mean durations of  $2.65 \pm$  SE 0.06 s,  $3.12 \pm$  SE 0.11 s and  $3.26 \pm$  SE 0.21 s, respectively.

In summary, the type A and B displays are relatively stereotyped. Variability, however, did occur for a number of measured parameters. For instance, the initial head bob pattern (first 6 bobs) was stereotyped, while the remaining 4 possible bobs of Act I were optional. The number of quick head bobs could also vary between 1–3 within Acts II, III and IV (see stippled areas in Fig. 1 and large C.V. values of Unit 7, Table 1). The performance of Acts II–IV was optional, with few displays having all 4 acts present. The initial extension of the dewlap was not strictly correlated to the appearance of a particular head bob, since it could be extended between the third to seventh head bobs of Act I. Duration of display units and unit percentages showed some variability. For some of the mea-

sured display parameters the variability was subtle (e.g. duration and percentage values for most of the units), while for others it was observable (e.g. number of acts performed, number of bobs in Unit 4, and the presence of modifiers—see below).

*Display type C.*—The **C** display starts out like a type **A** display in the pattern of initial head bobs, but then deviates by following with a long series of head bobs which gradually develop a broadening plateau (Fig. 2). In coordination with the head movements, the dewlap retractions deepen until there is total folding of the dewlap during the head bob plateaus. The number of bobs was variable, ranging from 13 to 24 in the 6 **C** displays analyzed.

*Display type D.*—Although seen several times in the field, display type **D** was only filmed twice, so few generalizations can be made. However, this behavior pattern, like the **C** display, also contained an initial head bob sequence similar to that of the **A** display (Fig. 2). The initial head bobs were followed by a series of 4-legged pushups.

*Display modifiers.*—As other anoles, *A. townsendi* augments its displays with various postures and movements (see discussion of static and dynamic modifiers in Jenssen and Hover, 1976; Jenssen, 1977). These behaviors are not always present with any one particular display type; hence their appearance can be considered as modifying the original display message. The following display modifiers were observed in *A. townsendi*: 1) erection of nuchal crest, 2) lateral compression of body (appeared during agonistic encounters, 3) tongue out (less frequently seen during **A** and **B** than with **C** and **D** displays), 4) lip smacking (mouth opened and closed rapidly, observed after displays performed during aggressive encounters) and 5) introductory head roll (an exaggerated raising and lowering of the head, with or without dewlap extension, added to the front of **A**, **B**, **C** and **D** displays during agonistic interactions).

#### DISCUSSION

This study presents 2 new insights into the behavior of the little-known *A. townsendi*. First, a statistical analysis quantifies the degree of stereotypy in the 2 most frequently observed display patterns (**A** and **B**); each of these patterns is somewhat different from the single display pattern reported for this species by Car-

penter (1965). Second, a large display repertoire is documented for *A. townsendi*.

Male *A. townsendi* have at least 4 distinct display patterns which can be used in aggressive encounters. The *A. townsendi* agonistic repertoire contains a basic "signature" display (**A**), a second type (**B**) which is similar to the **A** display, a third pattern (**C**) which appears to take the first act of the **A** display and add to it a long series of gradually slowing head bobs and coordinated dewlap pulses and a fourth display pattern (**D**) which incorporates a pattern of initial head bobbing similar to the **A** display and follows this with a series of 4-legged pushups. The **A** and **B** displays are performed much more frequently than the **C** and **D** types.

*Anolis limifrons*, a lowland anole of Central America, also has a large display repertoire (Hover and Jenssen, 1976). Even though *A. townsendi* and *A. limifrons* have their own unique signature display, both species have evolved display repertoires having certain features in common. As in *A. townsendi*, the *limifrons* repertoire contains 2 display types of close likeness (one being the signature display) used during initial aggressive contacts between males, a third display type which adds a long series of head bobs to a near version of the beginning of the signature display, and a fourth display having the initial elements of the signature display to which is added 4-legged pushups. *Anolis limifrons* also performs a fifth display type seen only when disputing males are in close proximity (several cm) to each other. It is suspected from the parallels between the other display patterns of the *townsendi-limifrons* repertoires that *A. townsendi* may also have a close-range display type.

Because of the above similarity of repertoire one might hypothesize that there is a close phylogenetic relationship between the two species. Both *A. townsendi* and *A. limifrons* are placed in the Beta Section of *Anolis* and occur in closely related species groups; *A. townsendi* is in the *chrysolepis* Series and *A. limifrons* is in the *fuscoauratus* Series (Etheridge, 1960). Our findings support the speculation of Echelle et al. (1971) that *A. townsendi* originated from ancestral stock of *Anolis cupreus* (also a *chrysolepis* Series anole). The **A** display of *A. townsendi* is remarkably similar to the pattern of *A. cupreus* presented by Echelle et al. (1971). If *A. cupreus* has a large display repertoire like *A. townsendi* and *A. limifrons*, it would be instructive to compare the number of displays and the patterning and function of the displays

from *A. cupreus* with its proposed relative on Cocos Island.

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