



---

Unusual Display Behavior by *Anolis grahami* from Western Jamaica

Author(s): Thomas A. Jensen

Reviewed work(s):

Source: *Copeia*, Vol. 1981, No. 3 (Aug. 26, 1981), pp. 728-733

Published by: [American Society of Ichthyologists and Herpetologists](#)

Stable URL: <http://www.jstor.org/stable/1444588>

Accessed: 21/12/2011 11:05

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



*American Society of Ichthyologists and Herpetologists* is collaborating with JSTOR to digitize, preserve and extend access to *Copeia*.

<http://www.jstor.org>

their opponents with their back legs. During breaks in the fighting, the frogs invariably exchanged rapid click notes, but they seldom gave peeps during encounters. Sometimes a male would give clicks while clasping his opponent, but much of the wrestling was done in silence.

Aggressive defense of territories is common in anurans (Wells, 1977), but has been reported for the genus *Eleutherodactylus* only in a few Puerto Rican species, especially *E. coqui* (Drewry, 1970, 1974; Reyes Campos, 1971). However, such behavior probably is relatively common in the genus, at least in high density populations, and it has been inferred from spacing patterns of males in several species (Drewry, 1970; Lemon, 1971). In *E. urichi*, males apparently defend only their calling sites, a type of territoriality common in other families (Wells, 1977). Eggs probably are laid in leaf litter on the ground (Kenny, 1969), and it seems unlikely that oviposition sites are in short supply.

*Acknowledgments.*—Financial support was provided by the University of Connecticut Research Foundation. I thank Jack Price for his hospitality at Simla, and W. R. Heyer and the Smithsonian Institution for use of equipment to analyze vocalizations.

#### LITERATURE CITED

- CLARK, P. J., AND F. C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445-453.
- DREWRY, G. E. 1970. The role of amphibians in the ecology of Puerto Rican rain forest. Puerto Rico Nuclear Center Annual Report 1970:16-85.
- . 1974. Ecology of *Eleutherodactylus coqui* Thomas in montane rain forest of eastern Puerto Rico (abstract). 54th Annual Meeting, Amer. Soc. Ichthyol. Herp., Ottawa.
- KENNY, J. S. 1969. The Amphibia of Trinidad. *Stud. Fauna Curacao and Other Caribbean Is.* 108:1-78.
- LEMON, R. E. 1971. Vocal communication by the frog *Eleutherodactylus martinicensis*. *Canad. J. Zool.* 49:211-217.
- NARINS, P. M., AND R. R. CAPRANICA. 1976. Sexual differences in the auditory system of the tree frog *Eleutherodactylus coqui*. *Science* 192:378-380.
- , AND ———. 1978. Communicative significance of the two-note call of the treefrog *Eleutherodactylus coqui*. *J. Comp. Physiol.* 127A:1-9.
- REYES CAMPOS, N. B. 1971. Observaciones sobre la conducta del coqui, *Eleutherodactylus coqui*. *Carib. J. Sci.* 11:209-210.
- WELLS, K. D. 1977. The social behaviour of anuran amphibians. *Anim. Behav.* 25:666-693.

———. 1981. Parental behavior of male and female frogs. In: *Natural Selection and Social Behavior: Recent Research and New Theory*. R. D. Alexander and D. W. Tinkle (eds.) Chiron Press, Newton, N.Y., in press.

KENTWOOD D. WELLS, *Biological Sciences Group, University of Connecticut, Storrs, Connecticut 06268*. Accepted 30 June 1980.

*Copeia*, 1981(3), pp. 728-733  
© 1981 by the American Society of  
Ichthyologists and Herpetologists

UNUSUAL DISPLAY BEHAVIOR BY *ANOLIS GRAHAMI* FROM WESTERN JAMAICA.—Observations have been accumulating which indicate that the taxonomy of Jamaican *Anolis* lizards is far from settled. Schwartz and Thomas (1975) have expressed a need for closer scrutiny of the seven species last reviewed by Underwood and Williams (1959). Preliminary evidence by George Gorman and William Hall (Hall, 1974) and by Ernest Williams (1977) and his current students corroborate the opinion of Schwartz and Thomas: for instance, polymorphism in the karyotypes of some Jamaican *Anolis* is now known. In particular, *Anolis g. grahmi* show extraordinary chromosomal complexity, with diploid numbers ranging 30-36. My report provides new behavioral data on two closely related Jamaican species, and gives further indication that the taxonomic status of *A. grahmi* remains an open question.

*Materials and methods.*—The display patterns of *A. grahmi* from western Jamaica (Negril, Westmoreland Parish) were compared with those of *A. grahmi* from central (Mandeville, Manchester Parish) and southeastern Jamaica (Kingston, St. Andrew Parish), and with its near relative, *A. garmani*. Displays of all species were filmed in the field under natural conditions and in large enclosures [1.3 (L) × 0.7 (H) × 0.4 (W)-m]. This analysis used 136 displays by 16 male *A. grahmi* from Mandeville and Kingston, 38 displays by five male *A. grahmi* from Negril, and 22 displays by three male *A. garmani* from Mandeville.

Displays filmed in the field were recorded under two contexts. The first involved undisturbed males giving non-directed displays as they changed perch sites while patrolling their territories. The head bob display appearing in

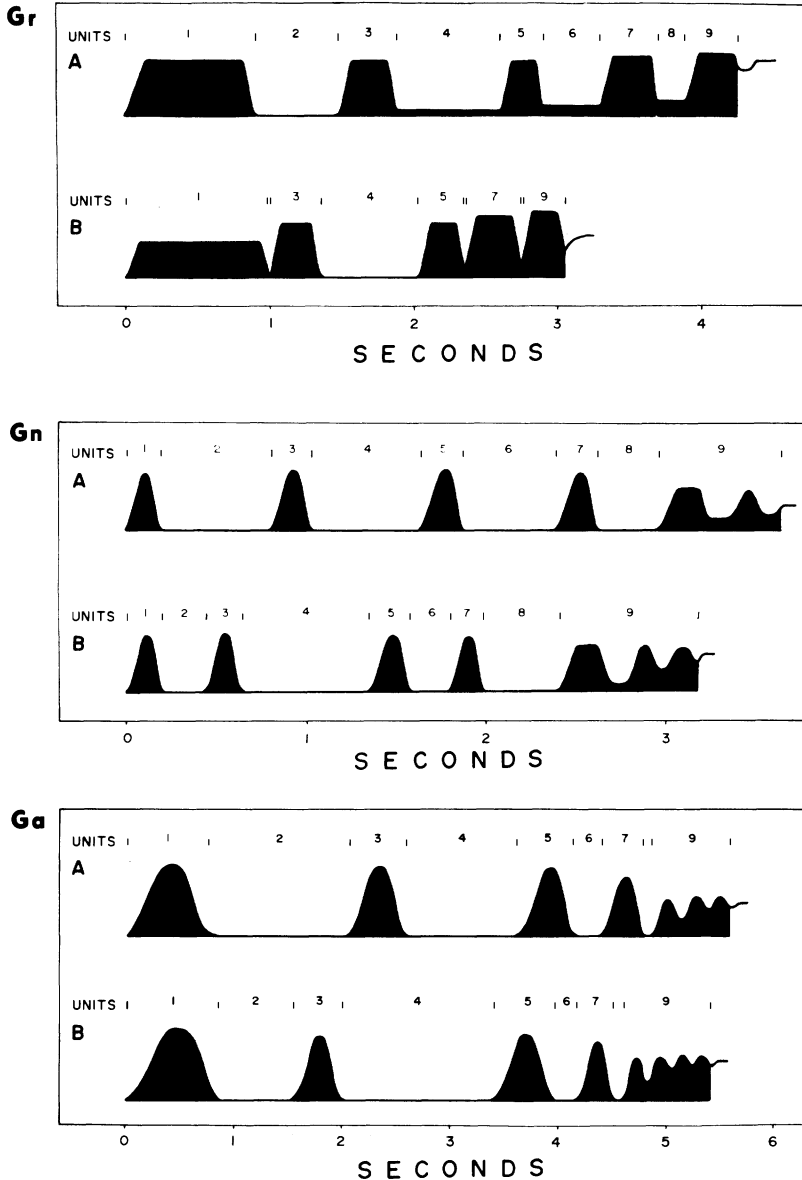


Fig. 1. Display-Action-Patterns of the Type A and B head bob displays for male *Anolis grahami* from Mandeville and Kingston (Gr) and from Negril (Gn), and from *Anolis garmani* from Mandeville (Ga). The relative head amplitude (y-axis) is plotted through time (x-axis).

this "assertion" context is the species-typical "signature" display (Jenssen, 1978), and is designated in this paper as the Type A pattern. The second context was created by releasing an unrestrained conspecific male into a resident's territory. This elicited a second head bob pattern in all observed territorial males, designated the Type B pattern. Both Type A and B display

patterns were performed by the subjects in the male-male or "challenge" context (Jenssen, 1977a, provided an evolutionary interpretation of multiple bob pattern repertoires).

Lab-filmed displays were elicited within an enclosure in a manner similar to those recorded in the field. From a blind, spontaneous displays by solitary males were first filmed; these were

TABLE 1. DESCRIPTIVE STATISTICS AND PERCENT DURATION (% DUR.) FOR EACH UNIT OF THE TYPE A AND B DISPLAYS BY *Anolis grahami* FROM MANDEVILLE AND KINGSTON (GR) AND NEGRIL (GN) AND BY *Anolis garmani* (GA) FROM MANDEVILLE. Sample sizes are given in parentheses with the Display Type; and  $\bar{x}$  durations are in seconds.

Taxa	Display Type	Statistic	Unit 1	Unit 2	Unit 3	Unit 4	Unit 5	Unit 6	Unit 7	Unit 8	Unit 9
Gr	A (84)	$\bar{x}$	0.905	0.585	0.384	0.738	0.298	0.381	0.433	0.166	0.369
		SD	0.716	0.108	0.076	0.178	0.049	0.080	0.080	0.071	0.088
		CV	19%	19%	20%	24%	16%	21%	18%	44%	24%
		% Dur.	21%	14%	9%	17%	7%	9%	10%	4%	9%
	B (52)	$\bar{x}$	1.000	0.000	0.342	0.683	0.316	0.000	0.415	0.000	0.295
		SD	0.170	—	0.103	0.174	0.050	—	0.067	—	0.074
		CV	17%	—	30%	26%	16%	—	16%	—	25%
		% Dur.	33%	—	11%	22%	10%	—	14%	—	10%
Gn	A (27)	$\bar{x}$	0.182	0.620	0.210	0.614	0.228	0.525	0.225	0.340	0.657
		SD	0.026	0.088	0.024	0.094	0.018	0.079	0.013	0.078	0.121
		CV	14%	14%	11%	15%	8%	15%	6%	23%	18%
		% Dur.	5%	17%	6%	17%	6%	15%	6%	10%	18%
	B (11)	$\bar{x}$	0.183	0.254	0.183	0.722	0.222	0.222	0.167	0.437	0.778
		SD	0.027	0.030	0.042	0.101	0.032	0.056	0.032	0.093	0.101
		CV	15%	12%	23%	14%	14%	25%	19%	21%	13%
		% Dur.	6%	8%	6%	23%	7%	7%	5%	14%	24%
Ga	A (14)	$\bar{x}$	0.758	1.345	0.523	1.059	0.516	0.306	0.397	0.059	0.722
		SD	0.091	0.146	0.047	0.122	0.046	0.075	0.037	0.041	0.119
		CV	12%	11%	9%	11%	9%	25%	9%	68%	17%
		% Dur.	13%	24%	9%	19%	9%	5%	7%	1%	13%
	B (8)	$\bar{x}$	0.827	0.716	0.424	1.424	0.549	0.194	0.327	0.077	0.854
		SD	0.117	0.069	0.051	0.148	0.036	0.066	0.036	0.078	0.183
		CV	14%	10%	12%	10%	7%	34%	11%	102%	9%
		% Dur.	15%	13%	8%	26%	10%	4%	6%	2%	16%

all Type A displays. Then a male intruder was introduced into the enclosure and the ensuing agonistic behavior was filmed; the resulting displays were a mixture of Type A and B patterns.

All filmed display sequences were taken with a Nizo S 80 super 8 camera at 18 frame/s and analyzed frame-by-frame with a Kodak MSF-8 projector. The A and B display patterns for each of my four groups of lizards (Negril, Mandeville, and Kingston *A. grahami* and *A. garmani*) were broken down into nine units; each unit measured the duration of a head bob or an inter-bob pause (Fig. 1). Further details of the techniques used appear in Jenssen (1979) and Jenssen and Hover (1976).

The mean ( $\bar{x}$ ) and standard deviation of the mean (SD) were calculated for each unit of a species' display pattern (Table 1). The coefficient of variation (CV = SD  $\times$  100/ $\bar{x}$ ) of each unit was also computed to indicate relative temporal stereotypy (Barlow, 1977). In addition,

the total display duration for each display was expressed as 100% and each unit as a percentage of that whole. This makes every display pattern have an identical duration (Fig. 2). One can then compare display patterns directly, without having to compensate for fast and slow performances of different display types within and between species.

Body markings and coloration appearing in Table 2 were taken from males displaying their most vivid coloration. The description of markings and coloration were determined subjectively from territorial males and recorded in my field notes. These were supplemented with notes taken on the coloration of subjects interacting during male-male encounters in enclosures.

*Results and discussion.*—The display behavior (Fig. 1, Table 1) and body color (Table 2) of *A. grahami* from Negril are strikingly different

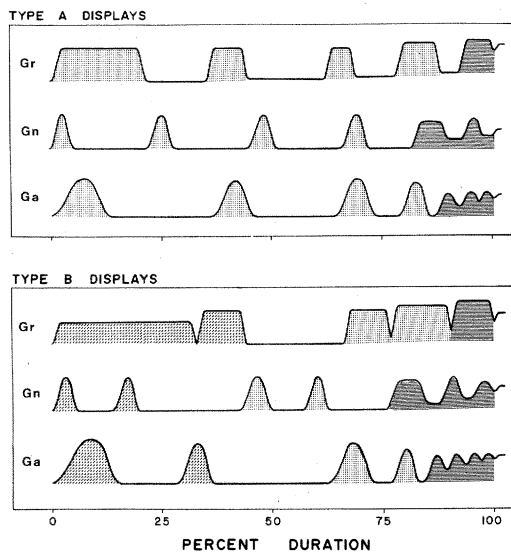


Fig. 2. The Type A and B Display-Action-Patterns (DAP) are compared between three forms: *Anolis grahami* from Mandeville and Kingston (Gr) and from Negril (Gn), and *Anolis garmani* from Mandeville (Ga). The relative head amplitude (y-axis) is plotted through time (x-axis), where duration of each DAP is expressed as 100%. Shaded areas of similar design facilitate inter-DAP comparisons of analogous parts of the display patterns.

from the species in Mandeville and Kingston. Display data from Mandeville and Kingston *A. grahami* were pooled as there were no statistically significant differences between them.

The Negril *A. grahami* have two stereotyped display patterns (Types A and B) in their repertoires as do the *A. grahami* from Mandeville and Kingston. However, the Negril population has a distinctly different bob form in both A and B display types as compared with the Mandeville and Kingston populations. All bobs in the Negril displays are relatively quick up and down movements with no pause at the top of the bob amplitude. The bobs of the Mandeville and Kingston displays, however, are definitely "plateaued" (Fig. 1). Furthermore, the cadence of the two Negril display patterns is uniquely different from the other *A. grahami* populations, especially for the Type B pattern (Fig. 1; Table 1).

Species members from a particular population performed their display patterns with marked consistency. Within a given display pattern, there were no variations in bob form and no disruptions to the temporal relationship of

the bobs and inter-bob pauses (i.e., bob cadence). The expected temporal variation in unit durations of a given pattern were small; almost all unit CV values were well below the 35% level which Barlow (1977) suggests as an upper limit for ritualized behavior. Therefore, the magnitude of differences when comparing the Type A and B patterns of Negril *A. grahami* with the corresponding display patterns of Mandeville-Kingston *A. grahami* is significant. No such divergence in bob form and bob cadence has been previously described for iguanid lizards thought to be of the same taxon. It is noteworthy that a case of hybridization between *A. grahami* and *A. lineatopus neckeri* in Mandeville produced a hybrid whose signature display (Type A pattern) was much more similar to its parental *A. grahami* pattern (Jenssen, 1977b) than the resemblance of Negril *A. grahami* Type A pattern to the Mandeville-Kingston *A. grahami* Type A pattern.

In addition to the display features, the general appearance of Negril *A. grahami* is quite different from *A. grahami* in central and south-eastern Jamaica. The bodies of the Negril lizards have an obvious greenish cast in contrast to the aquamarine, tan and magenta colors seen in Mandeville and Kingston *A. grahami* (Table 2). Furthermore, at another locality in the west (Anchovy, just south of Montego Bay, St. James Parish), I have found the *A. grahami* to be unequivocally green over the entire body. Only the lighter colored "worm marks" on the head and nuchal region gave an immediate clue to the lizards' identification. From the display data and the more subjective evidence of markings and coloration, it is very likely the western populations of *A. grahami* may be a separate subspecies from those of Mandeville and Kingston.

As an aside, it was found that the form of the Negril *A. grahami* head bobs (rounded up and down movements) are much more similar to those of its closest relatives, *A. opalinus* (Jenssen, 1979: Fig. 1) and *A. garmani* (Figs. 1, 2), than the "plateaued" bobs of the Mandeville and Kingston *A. grahami*. Even more curious is the close resemblance of the Negril *A. grahami* Type A and B display patterns to the Type A and B patterns of the *A. garmani* displays (Figs. 1, 2); it is also of interest that *A. garmani*, as a species, is the only bright green lizard on Jamaica.

The data presented here encourage a systematic investigation of the *A. grahami* series species, and raise some possible questions as to whether or not western *A. grahami*: 1) represent a case

TABLE 2. COMPARISONS OF BODY COLORATION AND MARKINGS OF MORE THAN 50 MALE *Anolis grahami* OBSERVED IN OR COLLECTED FROM NEGRIL, MANDEVILLE AND KINGSTON, JAMAICA.

Body parts	Negril <i>A. grahami</i>	Mandeville and Kingston <i>A. grahami</i>
Head		
Color	Grey-brown snout, grading posteriorly to a grey-green	Deep blue snout, grading posteriorly to an aquamarine
Markings	Pronounced light colored worm marks	Light colored dots half the size of those on the Negril specimens
Trunk		
Color	Green	Aquamarine; slight yellowish tan appearance to sides of abdomen in Mandeville males
Markings	Light colored worm markings anteriorly, progressing to dots posteriorly; no hourglass markings	No dots beyond the neck region; faint darker transverse hourglass markings on dorsum
Hind limbs		
Color	Grey-brown	Deep blue
Markings	—	—
Tail		
Color	Grey-brown	Deep blue with a tint of magenta at the base, grading to a brownish tan
Markings	—	—
Dewlap		
Color	As in the Mandeville and Kingston populations	Orange, with a narrow border of yellow
Markings	—	—

of character convergence with sympatric *A. garmani*, 2) reflect a past instance of introgressive hybridization with *A. garmani* or 3) represent a more ancestral form of *A. grahami* than those populations in central and southeastern Jamaica. There is definitely a need for comparative morphological, karyotypic, and electrophoretic study of these anoline species, including especially their western populations.

*Acknowledgments.*—I wish to thank David West, Ernest Williams and Risa Jenssen for their comments on this manuscript and Pam Hollands-worth for typing it. Parts of this study were supported by NIMH (postdoctoral fellowship 6F02M4 33435-01A1 to T. A. Jenssen) and NSF (grants DEB 74-20143 to T. A. Jenssen and B 019801X to E. E. Williams).

#### LITERATURE CITED

- BARLOW, G. W. 1977. Modal action patterns, p. 98–134. *In*: How animals communicate. T. A. Sebeok (ed.). Indiana Univ. Press, Bloomington.
- HALL, W. 1974. Research report, p. 12–13. *In*: The second *Anolis* newsletter. E. E. Williams (ed.). Mus. Comp. Zool., Harvard Univ., Cambridge, MA.
- JENSSEN, T. A. 1977a. Evolution of anoline lizard display behavior. *Amer. Zool.* 17:203–215.
- . 1977b. Morphological, behavioral, and electrophoretic evidence of hybridization between the lizards, *Anolis grahami* and *Anolis lineatopus neckeri*, on Jamaica. *Copeia* 1977:270–276.
- . 1978. Display diversity of anoline lizards and problems of interpretation, p. 269–285. *In*: Behavior and neurology of lizards: An interdisciplinary conference. N. Greenberg and P. MacLean (eds.). NIMH, Rockville, MD.
- . 1979. Display behaviour of male *Anolis opalinus* (Sauria, Iguanidae): A case of weak display stereotypy. *Anim. Behav.* 27:173–184.
- , AND E. L. HOVER. 1976. Display analysis of the signature display of *Anolis limifrons* (Sauria: Iguanidae). *Behaviour* 57:227–240.
- SCHWARTZ, A., AND R. THOMAS. 1975. A checklist of West Indian amphibians and reptiles. *Carnegie Mus. Nat. Hist., Special Publ.* 1.
- UNDERWOOD, G., AND E. E. WILLIAMS. 1959. The

anoline lizards of Jamaica. Bull. Inst. Jamaica Sci. Series 9:5-48.

WILLIAMS, E. E. 1977. Species problems, p. 132-151. In: The third *Anolis* newsletter. E. E. Williams (ed.). Mus. Comp. Zool., Harvard Univ., Cambridge, MA.

THOMAS A. JENSSEN, *Biology Department, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061*. Accepted 17 June 1980.

*Copeia*, 1981(3), pp. 733-734  
© 1981 by the American Society of  
Ichthyologists and Herpetologists

**SUTURE ZONE DYNAMICS: TEXAS POPULATIONS OF *RANA BERLANDIERI* AND *R. BLAIRI*.**—Recent investigations (Brown, 1973; Pace, 1974) involving analysis of mating calls, morphological assessment, laboratory crosses and electrophoretic surveys of protein differences demonstrated that the North American component of the *Rana pipiens* complex consists of several species. Although largely allopatric, sympatry among species pairs with contiguous ranges is well documented. Several papers (Littlejohn and Oldham, 1968; Mecham, 1968; Platz, 1972, 1976; Platz and Platz, 1973; Salthe, 1969; Gillis, 1975; Axtell, 1976; Dunlap and Kruse, 1976; Lynch, 1978; Sage and Selander, 1980) contain reports of naturally occurring hybrids. Hybridization levels are generally less than 10% (but see Gillis, 1975; Lynch, 1978; Sage and Selander, 1980). Among reports, the distinction between F<sub>1</sub> and backcross individuals was usually lacking; most also fail to differentiate between juvenile vs. adult categories as well. To date no study has provided such information for any contact zone for two periods of time separated by several breeding seasons. The present study was designed to provide such comparative analysis of the contact zone between *R. berlandieri* and *R. blairi* in Texas.

The first report (Platz, 1972) based on data gathered in 1969 indicated that *R. berlandieri* and *R. blairi* were sympatric in Coke and Mitchell counties. Morphological comparisons of allopatric populations indicated differences in lip stripe, condition of vestigial oviducts in males and head shape. Both species were monomorphic for different alleles at the albumen locus which was subsequently employed as an aid in estimating levels of hybridization. Eight of 138 individuals (5.8%) from the contact zone were identified as F<sub>1</sub> hybrids (Table 1). Limited introgression (2.9% backcrosses) was inferred on the basis of four individuals homozygous for one albumen or the other, but judged otherwise to be hybrids on the basis of intermediate morphology.

In 1975 I returned to the contact zone to reexamine it as part of a broader study involving interactions of *R. blairi* in several sympatric situations with three members of the *R. pipiens* complex. During this second analysis, individuals from allopatric and sympatric populations were screened electrophoretically for 16 loci. Because the 1969 allopatric populations of *R. blairi* no longer exist (locale 1 no longer has water; locale 2 is now an active oil field) a sample (n = 37) was obtained from Hwy. 60, 3.2 km E. Panhandle, Carson County, Texas. Locale 5, San Angelo, Tom Green County, Texas, in 1969 yielded only *R. berlandieri*, but the 1975 sample included seven juvenile *R. blairi*. Consequently, allopatric *R. berlandieri* (n = 27) were obtained from 4.5 km NW of Uvalde, Uvalde County, Texas. Electrophoretic results from allopatric populations provided four marker loci (sod<sub>1</sub>, mdh<sub>2</sub>, ldh<sub>1</sub> and albumen) with which to evaluate 94 individuals from the contact zone (Table 1). Among these were five adult and one juvenile backcross individuals confirming my 1972 conclusion.

A number of points of general interest are apparent when comparisons between the two sets of data are made. First, a significant change

TABLE 1. HYBRID CENSUS DATA. Expected values appearing in the 1975 census were derived by using the percentage figures from the appropriate columns of 1969 data.

	1969 - N = 138 (58 adult; 80 juvenile)						1975 - N = 94 (63 adult; 31 juvenile)					
	Juvenile		Adults		Totals		Juvenile		Adults		Totals	
	No.	(%)	No.	(%)	No.	(%)	No.	(%)	No.	(%)	No.	(%)
F <sub>1</sub>	7	(8.7)	1	(1.7)	8	(5.8)	0	(2.7)	0	(1.1)	0	(5.9)
Backcrosses	2	(2.5)	2	(3.4)	4	(2.9)	1	(0.8)	5	(2.2)	6	(2.9)