Morphological, Behavioral and Electrophoretic Evidence of Hybridization Between the Lizards, *Anolis grahami* and *Anolis lineatopus neckeri*, on Jamaica

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An adult male hybrid resulting from a cross between *Anolis grahami* and *Anolis lineatopus neckeri* was discovered in Mandeville, Jamaica. Twenty-two diagnostic characters which differentiate the parental species were used to confirm and examine the results of hybridization. These included scalation, body proportion, body color, non-display behavior, display behavior and biochemical characters. Though many of the hybrid's features were intermediate to parental characteristics, some strongly reflected the characteristics of just one parent. This was particularly true of the behavior in which the hybrid was quite *grahami*-like. However, when placed in social situations with a male of one or the other parental species, there was none of the agonistic behavior usually associated with male-male intraspecific interactions; the hybrid did not react as if it were a member of either parental species.

Also included are the first descriptions of the signature displays for *A. grahami* and *A. l. neckeri*.

RECENTLY there have been reports of hybridization between various lizard taxa (Gorman, 1969; Gorman and Atkins, 1968; Gorman et al., 1971; Gorman and Yang, 1975; Hall and Selander, 1973; Jackson, 1973). These instances of hybridization occur within contact zones between parapatric populations or where introduction by man has brought two previously separated species together. The present report, however, describes a hybrid produced from parents of two sympatric species. On 8 July 1971, in Mandeville, Jamaica, I collected an adult male whose parents were *Anolis grahami* and *Anolis lineatopus neckeri*. Hybridization between any of the seven anoline species on Jamaica was previously unknown.

Though sympatric, *A. l. neckeri* and *A. grahami* do not necessarily have the same microdistributions; *A. l. neckeri* is shade-loving (Underwood and Williams, 1959) and *A. grahami* frequents sunny, open perches (Schoener and Schoener, 1971). However, the once-extensive deep-forest habitat of *A. l. neckeri* is now fragmented. As a consequence, Mandeville *A. l. neckeri* can be found in such diverse shaded areas as under house foundations, along and in wide porous rock walls and in thick growths of bushes. The disruption of ancestral habitats has markedly increased the area of interface between *neckeri* and *grahami* habitats (Ernest Williams, pers. comm.). It is surprising more instances of hybridization have not been found.

METHODS

Morphological, behavioral and electrophoretic comparisons were used to confirm and in most instances describe the degree of shared characteristics between the hybrid (Harvard University, Museum of Comparative Zoology, specimen MCZ R-129321) and its parental species.

Morphology.—Underwood and Williams (1959) have described the diagnostic morphological characteristics which distinguish *A. grahami* from *A. l. neckeri*. I followed their lead when choosing the scalation, anatomical proportion and body coloration characters used for describing the relationship of the hybrid to its parents. For meristic characters showing some variability in number, counts were made from five adult male specimens of each parental species (all Mandeville-collected); these data are given as mean ± standard error of the mean and range.

The relative dewlap size was determined by selecting motion picture sequences of the three forms in which the dewlap was fully extended, and in which the animals were oriented laterally to the camera in almost identical positions. For each sequence, the projector was shifted to still projection on the frame depicting full dewlap extension and projected onto graph paper where the dewlap area was outlined. To ensure equal orientation and magnification, three points (the snout tip, eye and ear opening) of an image had to coincide with those same land-

marks of the previously projected animal. The dewlap area was determined for each form with the largest dewlap set at 100% and the other two dewlap sizes expressed as proportions of the largest.

Behavior.—The display behavior of the three forms was quantitatively analyzed. Both parental species have multiple-display repertoires; for the purpose of this report, however, only the most often performed display type in each species' repertoire is described. This display type is functionally analogous to the "signature" display type (Jenssen, 1977). Using displays filmed in field and enclosure, the *A. grahami* signature display analysis was made from 84 displays performed by eight males. The *A. l. neckeri* signature display was analyzed from 93 displays given by four males. All subjects were from Mandeville. The hybrid was collected before its displays were recorded in the field. In the enclosure it did not display readily. Only seven complete displays of good quality have been analyzed.

All behavior sequences were filmed with a Nizo S80 Super 8 camera set at an 18 frames/s filming speed. Captured lizards were placed in a 1.3 m (L) × 0.5 m (W) × 1.0 m (H) enclosure fitted with simulated habitat for observation and filming. Because all three of the forms were wary and *A. l. neckeri* extremely shy, a blind was used in conjunction with the enclosure. Analysis of the resulting films was accomplished frame-by-frame with a Kodak Ektagraphic MFS-8 projector using a technique described in detail by Jenssen and Hover (1976).

Each form's signature display was divided into artificial units. Unit divisions were based on easily detectable features of the display. The duration of each unit was statistically described (mean, standard error of the mean and 95% confidence limits of the mean) to reflect relative degree of stereotypy. Absolute amplitude of display head bobs was not measured; however, the relative relationship of amplitude between the various head bobs within a display is reflected in the summary graphs.

Proteins.—Electrophoretic analysis of the hybrid was done by Preston Webster using techniques described by Webster and Burns (1973).

Results and Discussion

Twenty-two characters were examined on the three forms; of these, the hybrid showed a closer relationship to *A. grahami* for 15 characters and a closer relationship to *A. l. neckeri* for seven characters.

Morphology.—The hybrid reflected affinities for each of its parental species in half of the 10 scalation characters (Table 1). Regarding anatomical proportions, *A. grahami* has wider phalanges with fewer lamellae and a smaller dewlap than *A. l. neckeri.* The hybrid resembled *A. l. neckeri* by having long phalanges in relationship to lamellae width, but also reflected *A. grahami* digits by having numerous lamellae (Table 1, Fig. 1). The hybrid had an intermediate sized dewlap, but was closer to the *grahami*-sized dewlap than to the *neckeri*-sized dewlap. Setting *A. l. neckeri* dewlap area at 100%, *A. grahami* dewlap is approximately 48% and the hybrid dewlap 68% of the *A. l. neckeri* dewlap area (Fig. 2).

Body coloration and pattern is quite different between the parental species. Of the six most prominent differences, the hybrid possessed the *A. grahami* condition for five of the features (Table 1). Unlike *A. l. neckeri,* male *A. grahami* can markedly change their body color. It varies from a darkened state during which males are a deep chocolate brown to a colorful stage at which time they have a magenta tail, yellow sides, and an aqua neck and head. When *A. grahami* and the hybrid were in the darkened state, hourglass-shaped markings were evident along the dorsal midline of the trunk (Table 1). *A. l. neckeri* lacks this pattern.

Non-display behavior.—Behaviorally, the hybrid was similar to *A. grahami* (Table 1). *Anolis grahami* has a repertoire of vocalizations which it emits during social contexts and when handled (Milton, 1974). In contrast, *A. l. neckeri* does not produce sounds other than hisses. The hybrid was found to squeak similarly to *A. grahami* when handled upon capture.

When initially captured, the two parental species have characteristic, but markedly different escape behavior. *Anolis grahami* shows no special defensive postures; interspersed with a quiescent attitude are unpredictable and brief episodes of vigorous struggling accompanied by squeaking sounds. *Anolis l. neckeri,* on the other hand, assumes a head up, dewlap out and mouth open posture when held. Though both species will attempt to bite if the opportunity arises, *A. l. neckeri* does not exhibit the vigorous thrashing nor does it vocalize except to hiss. The hybrid possessed the *A. grahami* escape behavior and vocalizing ability.

TABLE 1. COMPARISONS BETWEEN TWO PARENTAL SPECIES, *Anolis grahami* AND *Anolis lineatopus neckeri*, AND A HYBRID FOR SCALE, ANATOMICAL PROPORTION, BODY COLORATION AND BEHAVIOR CHARACTERISTICS.

Diagnostic Character	*A. grahami*	Hybrid	*A. l. neckeri*
supraorbital semicircle scales	prominence terminates just anterior to the orbits	as in *grahami*	prominence continues almost to nares
anterior subocular scale separated from canthral ridge by:	1 scale 0–1 (0.8 ± 0.2)	1 scale	2 scales 2–3 (2.2 ± 0.2)
interparietal scale separated from supraorbital semicircles by:	4 scales 3–4 (3.8 ± 0.2)	4 scales	6 scales 5–6 (5.4 ± 0.4)
size of interparietal scale in comparison with supraorbital disc	equal in size	approximately ½ as large	approximately ½ as large
description of superciliary scales	granular, only anterior scales just posterior to canthral scales elongate	imbricating, elongate; posterior scales smaller than in *neckeri*; but larger than in *grahami*	all scales markedly elongate and imbricating
number of loreal scale rows	5 rows 5–6 (5.2 ± 0.2)	6 rows	6 rows 6 (6 ± 0.0)
number of subdigital toe scales and lamellae along length of 2nd & 3rd phalanges of 3rd toe on right forelimb	22 scales 21–25 (22.4 ± 0.7)	22 scales	17 scales 17–19 (17.4 ± 0.4)
description of scales of anterior margin of dewlap	slightly swollen, imbricate and *smooth*	slightly swollen, imbricate, *mostly smooth*, and a *few weakly keeled*	swollen, imbricate and *keeled*
description of dorsal and lateral scales of the trunk	swollen, granular, and *without keels*	scales small, slightly swollen and keeled	moderately swollen, small, and *keeled*
description of belly scales	imbricate, broad, *smooth*, and larger than scales on dorsum and sides	imbricate, broad, *distinctly keeled*, and larger than scales on dorsum and sides	imbricate, broad, *distinctly keeled*, and larger than scales on dorsum and sides
ratio of length of 2nd & 3rd phalanges of 3rd toe on right forelimb divided by widest subdigital lamellae on 3rd toe	2.5–2.7 (2.6 ± 0.03)	4.0	4.1–5.1 (4.5 ± 0.18)

TABLE 1. (*Continued*)

Diagnostic Character	*A. grahami*	Hybrid	*A. l. neckeri*
relative area of smaller dewlaps compared with largest dewlap	48%	68%	100%
dewlap color	orange with narrow border of yellow	as *grahami*	very pale yellow with a varying sized patch of faint orange
patch of orange coloration under chin	absent	absent	present
finely patterned spots on dorsum of head and neck	present	present	absent
dark brown hourglass-shaped marking along dorsal midline of trunk	present, evident in darkened coloration state	as *grahami*	absent
magenta coloration on base of tail	present, vivid	present, moderate	absent
greenish line over shoulder and along flank	absent	present	present
ability to vocalize	yes	yes	no
description of characteristic behavior upon initial capture	does not mouth gape or extend dewlap, intermittently thrashes vigorously from side to side, and squeaks	as *grahami*	gapes mouth widely with dewlap usually extended, remains passive except for occasional directed effort to bite collector
habitat type most frequented	open to semi-open habitat; appears to have a relatively high preferred body temperature	found living in same microhabitat with *grahami*—in a direct sun-exposed area	never in direct sunlight except when ambient temperature is cool; shows a strong association with shady microhabitats
descripition of signature display	a series of five "plateaued" bobs separated by short waiting periods; cadence is very stereotyped	as *grahami*, but cadence shows more variability	a series of three continuous "sine wave" bobs; cadence is very stereotyped

The two parental species are separated in Mandeville by distinctly different climatic niches. *Anolis grahami* is found in hot, open to semi-open microhabitats, while *A. l. neckeri* is restricted to heavy shade and seems to prefer cooler temperatures. On the morning when I collected the hybrid, I was filming a male *A. grahami* displaying as he made his territorial "rounds." He was on a small water tower which had no surrounding shade. At places on the

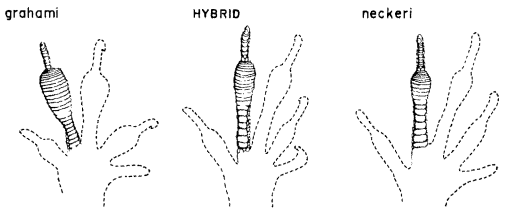

Fig. 1. Subdigital lamellae of the fourth digit on the right forefoot of *Anolis grahami*, the hybrid and *A. lineatopus neckeri*.

water tower the substrate was so hot that when the *A. grahami* stopped to display he curled his toes up off the substrate and moved on as he was finishing the display. It was on the top of this water tower that I first noticed the hybrid. On the basis of this observation, the hybrid did not share the *A. l. neckeri* avoidance of bright, hot habitats.

The conditions under which I first noted the hybrid are noteworthy. The male *A. grahami* which I was filming on the water tower began to move slowly and deliberately, postured and pulsed his dewlap. This indicated another conspecific male had been seen. I then saw the intruder about a meter away from the territorial owner on an upper crossbrace of the tower. The animals dewlapped at each other, but besides several signature displays, the males never progressed into more agonistic display types. In addition, the *A. grahami* male's initial approach did not lead to a close distance "face-off." The hybrid neither approached nor showed marked retreat. This being extremely atypical territorial behavior between conspecific males, I collected the hybrid and only then discovered its mixed origins. Though the *A. grahami* showed initial signs of reacting to the hybrid as a conspecific male, his agonistic behavior waned upon closer approach.

Some social interactions were staged in an attempt to determine if the hybrid would defend a territory against members of its parental species. Would the hybrid consider itself an *A. grahami*, *A. l. neckeri*, both, or neither? After the hybrid had been placed in a 1.3 m (L) × 0.5 m (W) × 0.7 m (H) enclosure for a day, singly introduced male *A. grahami* and *A. l. neckeri* were placed in the enclosure at different times over a two week period. At no time was there extensive agonistic behavior which marks intraspecific male encounters. The hybrid was a large animal (65 mm S-V length, 6.25 g body wt.), and the introduced males were of about the same size. The only interactions evoked

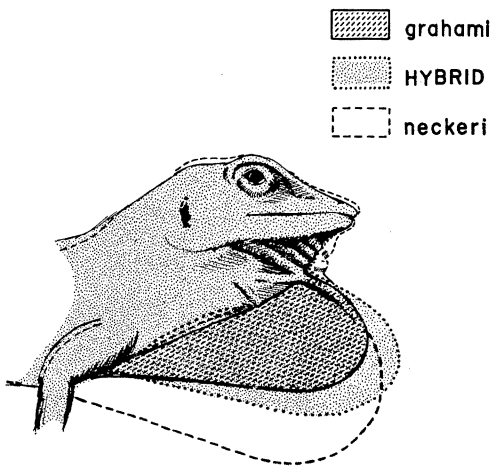

Fig. 2. Overlay of the heads with extended dewlaps of *Anolis grahami*, the hybrid and *A. lineatopus neckeri*.

were those seen during interspecific encounters; the strongest agonistic behavior observed was lateral presentation, slight side flattening and dewlap pulsing. The hybrid did not react as if it recognized males of either parental species as a conspecific.

Display behavior.—The Mandeville *A. grahami* signature display is a series of five "plateaued" head bobs with waiting periods separating the bobs (Fig. 3). The duration of each of the display's nine units was very consistent as evi-

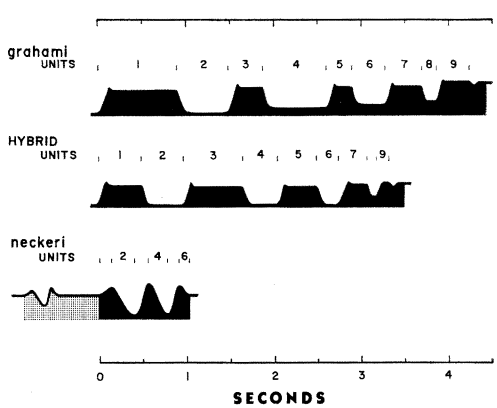

Fig. 3. Display-action-pattern graphs of which the upper edge of the blackened areas represents head amplitude through time. Unit durations are mean values taken from 84 *A. grahami*, 7 hybrid and 93 *A. l. neckeri* signature displays. The stippled area represents a different type of head bob pattern sometimes associated with *A. l. neckeri* signature display.

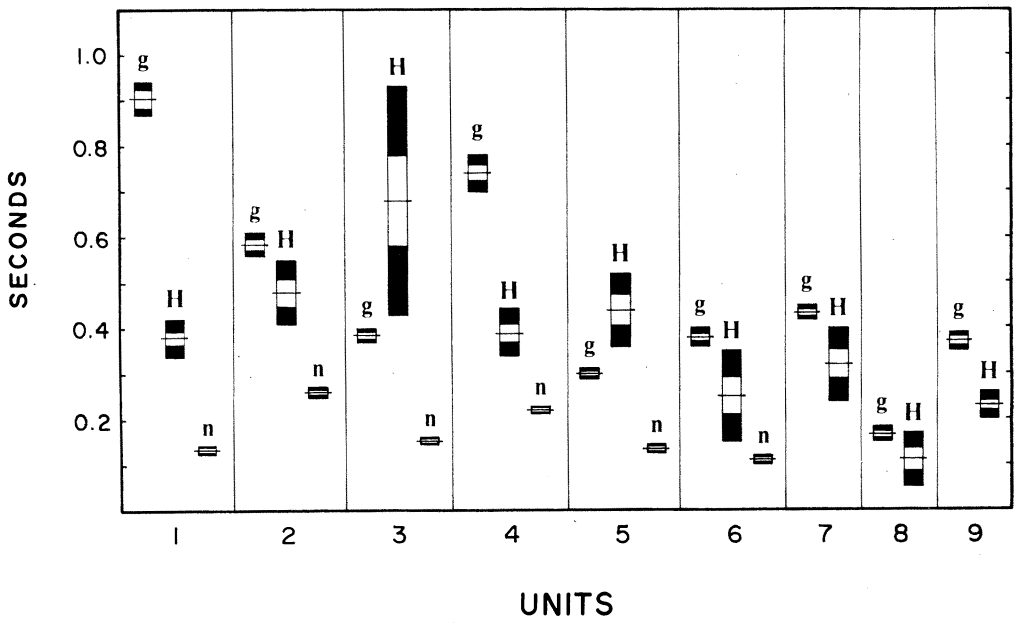

Fig. 4. Descriptive statistics of unit means for 84 *A. grahami* (g), 7 hybrid (H) and 93 *A. l. neckeri* (n) signature displays. Horizontal lines give the unit means, ends of white bars give the standard error of the mean and ends of black bars give 95% confidence limits of the means.

denced by the units' narrow confidence limits for the means (Fig. 4). Amplitude, however, was quite variable. Head bobbing could be very subtle, with the head elevated solely by the neck muscles. The vertical movements of the head could be exaggerated by amplitude components produced by the forelimbs, or even at times involving four-legged push-ups. The durations of the units, however, were not altered regardless of the means by which a lizard effects his signature display pattern.

Fifty-two (62%) of the signature displays were followed by dewlap extension. The number of dewlap pulses varied from a single extension and retraction to a series of five pulses; a single dewlap pulse following the head bobs was most common (40% of displays with pulses) and a five pulse series the least common (5% of displays with pulses). Duration of dewlap pulses was extremely variable; however, the last pulse of a series was of longer duration than the preceeding ones. If dewlapping followed the head bobbing pattern, initiation of dewlap appearance was stereotyped, averaging 0.38 ± 0.05 sec after the ninth unit; the actual dewlapping sequence, however, showed no consistency.

The *A. l. neckeri* signature display does not incorporate the use of the dewlap; dewlapping may infrequently follow the head bob sequence, but its temporal relationship to the signature display is in no way stereotyped. Qualitatively, the head bob pattern is quite different from that of *A. grahami*. Where *A. grahami* has box-like bobs with waiting periods between bobs, *A. l. neckeri* head bobs are like a sine wave with no intervening pauses (Fig. 3).

As was true of *A. grahami* displays, the three-bob signature display pattern of *A. l. neckeri* was very stereotyped; this is reflected by narrow confidence limits of the unit means (Fig. 4). The particular narrowness of the confidence limits for this species' display units, however, is accentuated by the small values of the unit durations. Actually, the coefficients of variability for mean unit durations of both parental species were of a similar magnitude, generally ranging between 14 and 24%.

The *A. l. neckeri* signature display frequently was performed in pairs. About a third of the displays were repeated after an interdisplay pause of 0.32 ± 0.02 sec (range 0.28 – 0.44 sec). When the displays were given in pairs, the second display was shorter in duration than the first (Wilcoxon matched-pairs signed-ranks test, $P = 0.0003$); they averaged 1.08 ± 0.03 and 0.93 ± 0.03 sec, respectively.

The three-bob signature display was often accompanied by fast, double bobs of low am-

plitude (Fig. 3). Observed casually, this kind of bob pattern very much resembled courtship bobs seen in other iguanid species. However, no females were present in the enclosure or in close proximity in the field when the filmed behavior was performed. These rapid head bobs usually appeared before the signature display, but they could also follow the signature display.

To study the relationship between the rapid head bobs and the signature display, 36 filmed signature display sequences were analyzed which recorded the lizard relocating itself before stopping to display. All antecedent behavior to the signature display was thus recorded. Half of these displays were not preceded by the rapid double head bobs, 22% were preceded by the one double bob pattern, 17% were preceded by two double bob patterns and 11% were preceded by three quick successions of the double bob pattern. The social significance of this rapid head bob pattern was not determined.

The hybrid signature display pattern did not show any compromise between the parental signature displays (Fig. 3). This is in contrast to Gorman's (1969) observation that the display of an *Anolis aeneus* × *Anolis trinitatis* hybrid was intermediate to its parental species' displays. The *A. grahami* × *A. l. neckeri* hybrid's head bob characteristics definitely resembled those of *A. grahami*. Comparisons of the hybrid's unit durations with those of the *grahami* display, however, were significantly different ($P < 0.05$) for all but one of the units (Fig. 4). The mean duration of the hybrid's total display (3.28 sec) was also considerably different from that of the *A. grahami* signature display (4.66 sec). The wide confidence limits for the hybrid's mean unit durations show a weaker degree of stereotypy than is characteristic of displays by lizards of the parental species. This is reflected in the large coefficients of variability values for some of the hybrid's unit durations; they ranged from 13–60%.

Proteins.—Preston Webster's tragic death in the fall of 1975 cut short the contributions of a generous and competent person. Webster was conducting an extensive electrophoretic analysis of the Jamaican anoles when he died. However, he had analyzed the hybrid specimen and representative samples of Jamaican *Anolis* to confirm the hybrid's parental species. The following is quoted from a letter to me from Preston Webster. "Of the *grahami-neckeri* hybrid: The chromosomes suggest a hybrid origin by their diversity in morphology, and there is considerable non-disjunction in meiosis. Electrophoretically the animal is indisputably a *grahami-neckeri* hybrid."

Acknowledgments

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Under other circumstances, Preston Webster would have been a collaborator on this paper. The absence of his work here affirms our loss.

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