BEHAVIORAL COMPARISON OF ANOLINE COMPETITORS:
ANOLIS COOKI AND ANOLIS CRISTATELLUS
(REPTILIA: SAURIA: IGUANIDAE)

By

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"As species of the same genus have usually, though by no
means invariably, some similarity in habits and constitution,
and always in structure, the struggle will generally be more
severe between species of the same genus, when they come
into competition with each other, than between species of
distinct genera." (Darwin, 1859 p. 84).

PERSPECTIVE

Competition is the active demand by two or more individuals of

the same species population (intraspecific competition) or members of

two or more species at the same trophic level (interspecific competition)

for a common resource or requirement that is actually or potentially

limiting (sensu Clements and Shelford, 1939). Some investigators

view competition as the main explanation for such observed phenomena

as the adjustment of the local population density of a species; the

ecological diversity of faunas (Udvardy, 1969); the determination of the

ecological equilibria between species, and adaptive radiation (Schoener,

1977). For an extensive review see Diamond, 1978. Others, however, still

question the reality of competition in natural systems (See review by

Wiens, 1978). The reason for this conflict is that the evidence for

competition has been drawn from simplistic laboratory experiments, the

construction of mathematical models and few data from natural

populations (Miller, 1967). The validity and effects of competition

in natural systems is still based on speculation and indirect evidence.

Two types of competition have been recognized, exploitation and

interference. My study deals with interference competition and follows

the meaning given to it by Miller (1969). Competitive interference is

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considered a strategy in which some form of space is substituted for

a resource and is the proximate object of competition. Interference

thus operates in a spatial context, e.g. territoriality which may

manifest itself as a dispute for posession of a structural resource

such as a nest site or song post (Miller, 1967). Documenting this type

of competition will involve first hand observation of behavior such

as fighting, side stepping or displacement (Schoener, 1977).

My investigation studies the apparent case of interspecific

territoriality between two syntopic Puerto Rican lizards, Anolis cooki

and Anolis cristatellus. These two species have apparently not yet

established a competitive equilibrium (which could result in exclusion

of one species), and so they furnish an excellent opportunity to examine

the importance of competition as a process molding niche dimensions

and geographic distributions.

Anolis cooki and A. cristatellus are medium sized anoles (50 - 70

mm in maximum male snout-vent length) only recently being recognized

as separate species (Gorman, Thomas, and Atkins, 1968). Anolis cooki

is restricted to the xeric lowlands of southwestern Puerto Rico while

A. cristatellus is widely distributed from sea level to mid-elevation

in forest or open habitats (Williams, 1972). They are sympatric in

southwestern P. R. from Cabo Rojo east to the Reserva Forestal de

Guanica and on the islet of Caja de Muertos (Fig. 1).

Recent studies have shown that these two anoles have broadly

overlapping structural habitat (Lister 1976a; P. Ortiz pers. obs.)

and, being physiologically adapted to the desert-like conditions

of their sympatric zone, have similar water loss rates and critical

activity periods (Hillman and Gorman, 1977). Studies of their thermal

biology have found them to be very similar in their relative occur-

rence on perches in full sun (a measure of basking incidence) and in

their mean (MBT) and preferred (PBT) body temperature (Huey and

Webster, 1976).

Based on the above data, A. cooki and A. cristatellus have broadly

overlapping niches and are suspected to be strong competitors for

perch sites. This suspicion has been supported by field observations

of intense congeneric encounters (G. C. Gorman, pers. comm.; P. Ortiz,

pers. obs.). Thus, A. cooki and A. cristatellus appear to be an ideal

species pair with which to investigate the behavioral interactions

which produce interference competition.

In order to study the dynamics of the cooki-cristatellus aggression,

I established five objectives. The first was to make an ethogram for

each species so that I was familiar with their behavioral repertoire;

this was imperative if a quantitative and comparative study was to

be conducted. The second objective was to test the utility of display

behavior for establishing phylogenetic relationships. The third was

to quantify the level of aggressive behavior exhibited during cooki-

cristatellus interactions, and to compare this aggressive intensity with

that measured for conspecific interactions by the two species. The

fourth was to examine whether agonistic interactions were as intense

between similarly appearing species as those interactions between

A. cooki and A. cristatellus. The last objective was to compare the

aggressive intensity of interactions between congeners having broad

resource overlap with those of congeners having little resource overlap.

COMPARATIVE ETHOGRAMS

Introduction

The amount of information accumulated during the last 17 years on
the display behavior of anoline lizards is impressive. Some investigators
have found limited repertoires of stereotyped displays (see Jenssen,
1975; 48 for references), while others have found species with complex
repertoires (Crews, 1975; Hover and Jenssen, 1976; Jenssen, 1977, 1978;
Jenssen and Rothblum, 1977; Stamps and Barlow, 1973). There exist
considerable interspecific differences not only with respect to the size
of the repertoire, but also in the parts of the body used in displays,
the temporal patterning of body movements, and the degree of display
stereotypy (Jenssen, 1978). Such differences are not surprising con-
sidering the enormous ecological and social structure diversity in the
genus.

In most Anolis species the head bobbing patterns appear to be
central to the communication system (Jenssen, 1978). Each species has
one or more sterotyped bob patterns believed to function in species
recognition and mate selection (Jenssen, 1977). Around these stero-
typed behavioral patterns other elements are optionally added which
indicate motivational states. These optional components are not always
associated with a particular display. They seem to physically modify
a display and its information content. For this reason they are referred
to in the literature as modifiers (Jenssen, 1977, 1978; Jenssen and Hover,
1976). Modifiers can be postures (static modifiers) or body movements

(dynamic modifiers). When performed as modifiers to the species head bob display, their progressive addition appears to provide an index to the displayer's relative arousal.

Together, the head bobbing displays and their modifiers make up the majority of signals in a species communication repertoire. It is with these signals that a lizard ritualistically interacts with conspecifics and congeners alike. In order to make a detailed study of interspecific territoriality, one must have an appreciation for the signals with which the combatants effect their ritualized aggression.

There are very few reports of interference in lizards (reviewed by Schoener, 1977). Active interference has been documented most frequently between competing species of lizards (Ferguson, 1971, Jenssen, 1973; Montanucci, 1974; Rand, 1961 and 1967), while one (Talbot, 1979) reported the absence of interference in potentially competing species. None of these studies, however, actually quantified the level of aggression between species. Such a quantification is necessary before the extent of interference can be evaluated.

To my knowledge no other study of anoles has attempted to use display behavior and its modifiers to characterize the level of ag-gression during congeneric encounters. Toward this purpose an etho-gram of the species involved is a prerequisite for the determination of the quality of interspecific competitive interactions.

Previous attempts (Carpenter, 1967, 1978; Clarke, 1965; Echelle, et al., 1971; Ferguson, 1971; Gibbons, 1979; Gorman, 1968; Ruibal, 1967) to use displays as a systematic criterion have met with mixed results.

Those studies which have contributed most to systematic problems have dealt with small numbers of forms, while more encompassing studies have provided few insights. One reason for this is that we still do not know how much weight to give to behavioral data. When species displays are compared against a phylogeny based on traditional morphological characters, as is the usual case, the ethologist permits the morphologically based phylogeny to have sway if major conflicts appear. We have not yet adequately tested lizard behavior criteria against a phylogeny constructed from many types of evidence.

Now there is a good model. Recently, Williams (1972) constructed an evolutionary history of the Anolis radiation in Puerto Rico; it is a synthesis of ecological, electrophoretic, and karyotypic studies. This phylogenetic tree is firmly planted on a diversity of corroborating data. My study begins the data collection of species displays to make the evaluation.

The present study documents the behavioral repertoire of the Puerto Rican cristatellus species group (Williams, 1976), A. monensis, A. cooki, and A. cristatellus. It also describes the display modifiers which appear in conspecific and congeneric interactions of the above species and for two other Puerto Rican anoles, A. evermanni and A. gundlachi. With these ethograms, I have the data base to quantify the intensity of interspecific territoriality and initiate the evaluation of head bob displays as a criterion of phylogenetic relationships.

Materials and Methods

The display behavior analysis involved 56 lab filmed displays by seven male Anolis cooki, 152 displays by five male A. cristatellus (sympatric with A. cooki), 33 displays by two male A. cristatellus (allopatric with A cooki), and five displays of a male A. monensis.

All the A. cooki and five of the A. cristatellus came from the Salt Plant area in Cabo Rojo in Southwestern Puerto Rico where A. cooki and A. cristatellus are sympatric. The allopatric A. cristatellus specimens were collected in Carolina, in northeastern Puerto Rico.

The A. monensis came from the island of Mona located off the western coast of Puerto Rico. It is the only anole on the island.

For the study of the modifiers used by the lizards during agonistic interactions, two other Puerto Rican anoles, were used. The sample consisted of four A. evermanni and four A. gundlachi males. These were collected on the Mt. Britton trail at El Yunque, in Luquillo.

More individuals for all the species were collected, but mortality during the first two weeks in the lab decreased the sample size. The numbers reported for each species were those who survived.

Specimens were collected during January 5-8, of 1978 and 1979. Each individual collected was toe clipped for permanent identification and its snout-vent length and weight recorded.

The lizards were brought to the laboratory at VPI and SU. They were housed in 1.2 m (1) x 0.6 m (w) x 0.7 m (h) glass-fronted plywood enclosures. Each enclosure held one adult male and two to four adult

females. The cages contained stumps, branches, and artificial plants. The lizards were fed small crickets and Tenebrio larvae year round. Water was provided in dishes and by spraying the cages daily. The lab was kept at approximately 24C and the lights set on a 12L-12D cycle.

An enclosure similar to the housing enclosures was prepared for filming. Male displays were filmed under several conditions; (1) with no other animal visible or present in the cage with the resident male, (2) while interacting with females, (3) and while interacting intensively with other males. These conditions provided assertion, courtship, and agonistic contexts, respectively.

The techniques used in the analysis of their social behavior were those established in other display analyses (Jenssen and Hover, 1976; Jenssen and Rothblum, 1977).

All displays were filmed with a Nizo S80 Super 8 camera using Kodachrome II film at 18 frames per second. Lighting was provided by two colortran Quartz King 500 floodlights fitted with heat filters.

Filmed displays were analyzed frame by frame using a Kodak Ektagraphic MSF-8 projector, support box, mirror, clipboard and clip-board guide (Jenssen and Hover, 1976; Fig. 1). Each sequentially viewed frame was projected off the mirror onto the graph paper mounted on the clipboard. Head and dewlap positions were plotted for each frame, and the clipboard was progressively moved along a guide to receive each sequential frame of the movie. The rubber-backed clipboard guide was adjusted before each display so that the

projected head movement would be parallel with the y-axis of the

graph paper. The movable clipboard guide also allowed compensation

during occasional display sequences when the camera moved slightly

or the lizard's perch moved. Characteristic body movements other

than that of the head were noted on each display graphed, along with

other postural features such as erected nuchal crest, extented throat,

orbed eyes, opened mouth, and protruded tongue (Jenssen and Hover,

1976; Jenssen, 1978).

To facilitate the analysis, the displays of all the species were

artificially divided into units which delineated head bobs and inter-

bob pauses. Unit duration was calculated by counting the number of

cinema frames which were needed to record a bob; the number of frames

was then multiplied by 1/18 to convert to seconds. Descriptive

statistics of the unit duration (mean, standard deviation, standard

error, and confidence limits of the mean) were calculated on each of

the units, for every individual's display type.

The coefficient of variation (CV) was calculated for every unit

to give an estimate of relative stereotypy, where stereotypy in-

creases as CV values decrease (Barlow, 1977). One way

analyses of variance (ANOVA) were run for each unit to determine the

intra-individual (within) and inter-individual (among) variance for

each display type. If a unit demonstrated large variance (large CV

values), the variance was partitioned by the ANOVA to see how

the variability was distributed among and within each lizard's display

performances. If the majority of unit variance appears in the within

group, this would indicate that the variability was shared by all

lizards of the sample; one might suspect that this unit duration could covary with the displayer's relative arousal. If the majority of unit variance appears in the among group, this would indicate strong inter-individual differences; one might then suspect that this unit duration could indicate individual recognition within the population.

The modifiers performed by my studied species were filmed from approximately 50 interactions between pairs of conspecific lizards (male-male and male-female). Records of kinds of modifiers and their sequencing also resulted from pilot encounters performed in the lab involving intra- and inter-specific male-male pairings. It became apparent during these observations that the modifiers were being used in a hierarchical fashion, being progressively added to the displays during prolonged encounters where dominance was not rapidly established. A similar conclusion was made from the studies of the display behavior of Anolis limifrons (Jenssen and Hover, 1976; Hover and Jenssen, 1976) and Anolis opalinus (Jenssen, 1979). Those modifiers that appeared at the beginning of an interaction were also the most frequently used, while those that were rare appeared at the end of prolonged encounters.

In addition to the kinds and sequencing of the modifiers, other behaviors not directly associated with the head bobbing displays ("actions") were earmarked as important to the lizards' social interactions. These actions were also recorded and found to have a sequential consistency in prolonged and escalated encounters.

Results - Displays

Anolis cooki

Only a single head bob pattern was observed for A. cooki. The
vertical head movements of the display were produced primarily by
the front legs, although in some cases the alternate extension and
flexion of the four legs (push-ups) were responsible for such head
movement.

The display was used in assertion, courtship, and challenge contexts.
Usually, the display in aggressive interactions was accompanied by
movements of the dewlap and the presence of certain modifiers (sensu
Jenssen, 1977, 1978; Jenssen and Hover, 1976). The dewlap movements,
however, did not show any specific pattern from display to display.
The modifiers that appeared with the display were: rocking intro-
ductory movements, erected crest, extended throat, orbed eyes, opened
mouth and protruded tongue.

The core display (that portion of the display which was always
performed) consisted of 5 head bobs (Fig. 2), although an additional bob
was added at the end by some males. The number of head bobs for all
displays ranged from 5-6 ($\bar{x}$ = 5.4 $\pm$SE 0.06). A characteristic of the
cooki pattern is the high amplitude and long duration of the second and
third bobs, units 3 and 5 respectively. In 83% of all the displays the
third bob was the most dominant (i.e. greatest in amplitude and of
longest duration).

Calculation of coefficients of variance indicated strong stereotypy
for all units (Fig. 9, Table 1), except for those of short duration. For
all these units the confidence limits of the mean were narrow.

The mean total duration for the _cooki_ display was 4.69 ± SE 0.02s, with mean durations for individual lizards ranging from 3.99 - 5.39s.

Anolis _cristatellus_ (sympatric)

Two distinct display types (A and B) were performed by all five male _A_. _cristatellus_. There is little resemblance between the two patterns (Fig. 3 and 4). The type A is quite simple and consists of three equally spaced bobs, and the type B consists of 4 bobs separated in two groups by a conspicuous pause between the second and third bob. Their similarities are as follows: (1) both are highly sterotyped in their temporal sequencing; (2) each pattern consists of a series of "plateaued" bobs; and (3) both displays show little variability in the total number of bobs ($\bar{x}$ = 3.06 ± SE 0.05 for A displays, and $\bar{X}$ = 4.4 ± SE 0.06 for B displays).

The type A appears to be the species' "signature" display (see Jenssen, 1977, 1978 for discussion of term) because it was used for non-directed displaying within the assertion context.

Although the type A display was also seen during male-male encounters, the type B display was only performed in the challenge context and never in the assertion context.

Type A Display. — This three bob display was not performed with dewlap movements (Fig. 3). The bobs within the display progressively decreased in duration while the amplitude remained the same.

The duration of each of the head bobs was highly stereotyped as indicated by the low CV values (Table 3). The total mean duration for these three bobs from all displays was 2.75 ± SE 0.01s., with 95% confidence limits for the mean being 2.73 - 2.77s.

Type B Display. -- The type B core display consists of four bobs, though a fifth bob was occasionally added by all males. These bobs are arranged in a distinct pattern, having the first two bobs as the most dominant in amplitude and duration, with a most conspicuous pause after the second bob. This pause produces a break in the display giving the overall impression of a "two large-one small-one smaller" bob pattern.

Movements of the dewlap also form part of this display. The dewlap appears shortly before the first bob and it is pulsed several times (2-5) during the head bobbing portion of the display. The dewlap movements are not stereotyped, however, producing a different pattern from display to display. One of the many patterns observed is shown in Fig. 5.

The units composing the males' B display, except for the shortest units, showed little temporal variability (Fig. 9, Table 5). Proportionment of the variance for the short units indicated that most of the variability is found within males (Table 6) suggesting that these units might be used to express the relative arousal of the performer.

The total mean duration for the four bobs within the B display was 3.39 ± SE 0.02s, with the 95% confidence limits for the mean being 3.35 - 3.43s; mean durations of the four bobs for individual lizards ranged from 3.16-3.64s.

The appearance of modifiers during this display was common. Considering the agonistic context in which the display is used, the frequency of appearance of these modifiers seem to indicate the increasing arousal of the displaying lizard.

Anolis cristatellus (allopatric)

Two head bob patterns were also found in this sample of cristatellus. The patterns closely resembled those of sympatric A. cristatellus in form, but not in finer details of unit durations. The patterns performed by sympatric and allopatric A. cristatellus are indistinguishable to the human observer, but some unit durations were significantly different.

Type A Display. -- The display showed most of the features discussed for the sympatric cristatellus. It consisted of three bobs interspaced by similar-length pauses and no dewlap pulses were observed during its performance. However, the allopatric cristatellus display lacks the progressive reduction in bob duration that is present in the sympatric cristatellus pattern. This is caused by the slightly longer duration of the third bob when compared to the second (Fig. 5).

The context in which the display appeared is similar to that of sympatric A. cristatellus, assertion and courtship.

All the units composing the A display are strongly stereotyped as was indicated by their low CV values (CV 15%) (Table 7). The total mean duration for the three head bobs was $3.41 \pm$ SE 0.02s, with the 95% confidence limits for the mean being 3.36 - 3.46s. The mean durations of these three bobs for individual lizards ranged from 2.79 - 3.51s.

Type B Display. -- This display showed close similarities to that of sympatric A. cristatellus. These similarities were, as follows: (1) it consisted of four head bobs separated in two groups by the very conspicuous pause after the second bob, (2) non-stereotyped movements

accompanied the display, (3) used in the challenge context, and (4) the first two bobs are also the most dominant in amplitude and duration, but the first one is the more dominant of the two, being this in contrast to the pattern of sympatric A. cristatellus.

Except for units 1, 2 and 7, strong stereotypy was found for most units, as evidenced by the low CV values (Table 9). Proportion-ment of the variability found in the three variable units indicated that for units 1 and 7 most of the variability was explained when comparing between lizards. This indicates intra-individual stereotypy which should promote individual recognition. For unit 2 the variability found was higher within individuals suggesting that the relative arousal of the displayer is being indicated.

Anolis monensis

The data available for A. monensis display behavior are based on five displays by one male and on notes taken during 25 h of close observation. Thus, they are presented only as tentative information.

Only one head bob pattern was found, consisting of five head bobs. The second and third bob are the most dominant in duration giving the impression of a "one small-two big-two small" bob pattern. The average display of this male contained 5.29 ± SE 0.19 head bobs. There is considerable similarity between this male's display pattern and the cooki pattern. The pattern of both species showed a similar decrease in inter-bob pause duration for the first three bobs, followed by an increase in pause duration in the last two. Considering both species appeared to have only one display pattern in their repertoires, the

pattern was used in all three contexts, assertion, courtship and challenge.

Strong stereotypy was suggested by the low CV values for all except units 4 and 6 (Fig. 9, Table 11). The total duration of the five head bobs from all displays was 3.20 $\pm$ SE 0.08s, with the 95% confidence limits for the mean being 2.98 - 3.42s.

Results - Modifiers

Display modifiers are divided into "static" modifiers (i.e. postures and held configurations of certain body parts which alter the appearance of the displays) and "dynamic" modifiers (i.e. moved body parts which do not create the core display, but add to the core display and alter the appearance of the display). Within each division of modifiers, I have ordered the modifiers from those most likely to be present early in a display to those which are the last to be added to a display.

Static Modifiers

Erected crest. -- The erectible crest is a dorsal fold of skin projecting upward from the neck and usually along the length of the body and part of the tail. In some males it is quite impressive (e.g. A. cristatellus, A. cooki, A. monensis, and A. gundlachi), and in others it is miniscule (e.g. A. evermanni). It is raised during social inter-actions with a visible antagonist. In the observed interactions the erected crest was a prolonged response and could be up when the animal was not displaying as well as during display. It was always associated with prolonged male-male interactions, rarely seen in male-female interactions, and never observed without a conspecific present.

Extended throat. -- This modifier is effected when the lizard lowers its hyoid apparatus, giving the throat a swollen appearance. It frequently appeared along with erected crest, both being the first two modifiers to appear. The extended throat was the first to appear in unexpected encounters by two males at close range. If males approached each other from a distance, however, the erected crest preceded extended throat. The extended throat was not necessarily held throughout an encounter. This static modifier was seen in all the species involved in this study.

Orbed (rounded) eyes. -- This modifier consists of pupil dilation and widely opened eyelids. The effect was rounded eyes of larger than normal dimensions. Because it is a graded response, subtle expression of this modifier probably went undetected. It appeared only in agonistic interactions between males. It was also seen in all the species.

Opened mouth. -- The mouth is held partially opened in this modifier. Though the extend was variable, the mouth was never widely gaped. This posture appeared only in male-male interactions. It seems to be an intention behavior to bite, and is used by disputing males when they are at close range. It was observed in all the species.

Lateral compression of body (sides flattened). -- This modifier is almost always associated with a lateral presentation toward the object of display. It was associated with prolonged male-male inter-action and not observed without a conspecific present. It was not seen as frequently as some of the other modifiers. This might be explained by the difficulty to recognize it when subtlely expressed, especially

in stout-bodied lizards such as A. cristatellus and A. evermanni.
In A. monensis, A. cooki and A. gundlachi it was easily observed.

Protruded tongue. -- The tongue was pushed forward between the
lips as a pointed protrusion. Its appearance is associated with male-
male interactions. It was observed in all the species in this study.

Stretch posture. -- This posture consisted of the lengthwise
stretching of the body by the lizard, while its tongue was protruded
and the eyelids partially closed. The stretch posture appeared only
in male-male interactions and was often seen at the moment when a
lizard approached his contender. It was observed in each of the species
involved in this study.

Dynamic Modifiers

Dewlap pulses (dynamic modifiers). -- This was the first modifier
to appear in most male-male interactions. The dewlap was extended as
soon as each lizard spotted its adversary. It was frequently followed
by erected crest and extended throat. It was also seen during courtship.
The pulses usually occurred before or after a display.

Head rolls. -- Infrequently a display was preceded by a moderate
raising and lowering of the head. At times the amplitude of these
movements were exaggerated giving the impression of "bowing". It
appeared during courtship and challenge contexts, but was not seen
without a conspecific present. It was observed in all the species.

Tail movements. -- The tail movements consisted of two types: an
upward arching of the tail with the tip held high, and laterally moved
tail wags. The latter was graded from twitches to full swinging wags.
The lateral tail movements were the most common of the two kinds,

occurred many times independently of the head bob displays, and were performed by all species. The vertical tail movements, however, were closely associated with displays and were performed only by the species representing the _cristatellus_ species series (A. _cristatellus_, A. _cooki_ and A. _monensis_). Tail movements in general appeared during male-male interactions at close range and during courtship.

Rocking introductory movements. -- This modifier consisted of a raised stance on the four legs and back and forth movements of the body caused by the flexion and extension of the front leg. It was performed by a male before initiating a display. Most frequently seen in prolonged interactions between two males, it was observed in all the species, but the conspicuousness of its performance varied from species to species, being most impressive in A. _cooki_.

Actions

Approach. -- This is the reduction of the distance between the two lizards brought about by the movement of one lizard towards the other, or by their mutual movement.

Supplant. -- A lizard moves to the site where another is perched and drives it off, but does not follow the supplanted individual.

Chase. -- This occurs when a lizard consistently keeps on following another lizard throughout the enclosure driving him off every perch he takes.

Attack. -- This occurs when one male approaches the other, getting within striking distance. Biting attempts are usually seen.

Jaw sparring. -- In jaw sparring, two males are faced off head-to-head, with mouths partially opened. One male will initiate the sequence

by swinging his head toward the side of his opponent's head. Contact may or may not be made. The second male immediately responds in a like manner by rapidly pivoting his head laterally toward the first male's head. In instances where no contact is made, there is a series of faints and retreats in which each lizard alternately parries the other's ritualized attempts to bite. If contact does take place between them, it results in a head slap after which the recipient responds by pushing off on the other's head with the same offensive move. Jaw sparring with contact usually culminates in one male loosing his grip on the perch due to a head slap or both males locking jaws.

Jaw locking. -- This usually follows jaw sparring. The two combatants come together with their mouths open, and bite each other's jaw or rostrum. The first to let go is usually the loser and dominance is established at this point. Jaw locking is the climax of prolonged interactions, and the same for all species of the study.

Discussion

In display analysis of A. monensis, A. cooki, and A. cristatellus, revealed stronger affinities between A. monensis and A. cooki than between A. cristatellus and either of the other two species. All three species had displays composed of "plateau-like" bobs and the appearance of non-stereotyped dewlap movements during male-male interactions. However, A. monensis and A. cooki shared a single display type repertoire, a five bob core display, and a similar display pattern. In contrast, A. cristatellus had a two display type repertoire (Types A and B), of which the Type A core display had three bobs and the Type B four bobs. Inspection of the species DAP graphs (Fig. 2-4 and 7) shows

that of the four display patterns, those of A. monensis and A. cooki most closely resemble each other.

Based strictly on display behavior, I would consider A. monensis and A. cooki to be the most closely related of the three species. Interestingly enough, Gorman and Stamm (1975) found the karyotypes of A. monensis and A. cooki to be indistinguishable, both having a diploid number of 29, while A. cristatellus has a karyotype of 27 chromosomes. Gorman and Stamm hypothesized that the monensis-cooki karyotype is primitive and the A. cristatellus karyotype is the more derived.

The modifiers are of limited phylogenetic interest. As has been true in other studies of modifiers (see Jenssen, 1979), most of the described display modifiers are shared broadly among the anoles. This is also true of the species in my study. However, one modifier, vertical tail movements, was not observed in all five species. Tail lifts were performed by the cristatellus series species (A. monensis, A. cooki, A. cristatellus, and A. gundlachi), but not by A. evermanni, a member of the bimaculatus series (Williams, 1976). Moreover, the erectible crest of A. evermanni is quite small, whereas the other four species have pronounced crests which extend beyond the nuchal area, down the length of the body.

AGGRESSIVE INTERACTIONS

Introduction

In complex anoline communities, where sympatric pairs of species are common, interspecific competition seems to be reflected by the divergence of these species in some dimensions of their niches. The major niche dimensions involved in the ecological segregation of sympatric species are: the structural (perch height and diameter: Rand, 1964), the thermal preferenda or climatic component (preferred body temperature: Ruibal, 1961; Rand, 1964; Huey and Webster, 1976), and the food component (distribution of the prey sizes or taxa taken: Schoener, 1975, 1977). Low overlap in at least one or more of these dimensions has been observed. This suggests that by resource partitioning, the lizards reduce interspecific competition. However, conclusions concerning these differences in niche dimensions are not based on actual observations of competition.

Most studies supporting competition have arrived at their conclusions mainly by two approaches. One approach, the manipulative experiment, involves a species being introduced to or removed from a locality occupied by a closely related species. Over the course of time, if changes in the abundance or a shift in the niche characteristics of the species are observed, then the results are attributed to competition (see review by Connell, 1975 and Colwell and Fuentes, 1975). The other approach, the natural experiment, involves the comparison of the niche of a species in an area shared and an area not shared with a related species. Competition theory is invoked if niche characteristics

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of the species differ in areas where the "competitor" is present and where it is absent (see review by Diamond, 1978).

The main concern of the above approaches has been to show that competition is the agent bringing about stable coexistence of related species through niche divergence and resource partitioning. Nevertheless, both have failed to question whether competition first manifested itself as exploitation or as interference. Many studies assumed that it has been through exploitation simply because components of interference have not been observed (Colwell and Fuentes, 1975). Furthermore, few studies have observed actual competitive interactions between species at the moment when their ranges first overlapped. It is then not surprising to find past studies provide little evidence of interference. Therefore, to document interference, first hand observations of behavior such as fighting or displacement are needed (Schoener, 1977).

In reptiles little is known about either the populational or the individual aspects of interference (Schoener, 1977). Information on interspecific interference is scarce and only a few examples can be found in the literature (e.g. Ferguson, 1971; Jenssen, 1973; Rand, 1961, 1967a).

Sympatric A. cooki and A. cristatellus are an excellent pair of species with which to study competitive interference. Because they apparently have yet to come to a competitive equilibrium, they provide an opportunity to examine the role that behavioral interactions play in molding niche dimensions and geographic distributions. Several

observations suggest that their present association represents the initial phase of competitive interference. First, both species are moderately large and similarly sized, conditions Schoener (1975: 244-245) found likely to augment the intensity of competitive interactions. Second, previous studies have shown that their structural habitat niche and climatic niche are very similar. Third, field observations suggest that A. cooki interacts with A. cristatellus as intensely as they do with conspecifics (G. C. Gorman pers. comm.; P. Ortiz pers. obs.).

The object of this study was to evaluate three hypotheses. The first hypothesis: aggressive interactions are more intense between individuals of the same species than between individuals of different species. Recent studies have been able to relate the degree of aggression toward other species to the degree of overlap in diet (Ebersole, 1977; Branch, 1975; Low, 1971; Stimson, 1970, 1973). Considering that overlap in any dimension of the niche is the highest among members of the same species, it is expected that the highest values of aggressive interactions will be between conspecifics.

Applying these criteria to the cooki-cristatellus situation it is predicted that the highest intensity will be found for the conspecific interactions. Lower values are expected for the other interspecific interactions conducted in the study, especially for allopatric pairs of species.

The second hypothesis: interactions between a sympatric pair of species are more intense than between allopatric pairs of species. We might logically expect that the more nearly alike the ecological

requirements of two species are and the greater the amount of intersection in their niches, the more intensely the species will interact (Miller, 1967). Stamps' (1977b) model on the intensity of conspecific aggression may be extrapolated to the intensity of interspecific aggression. She found that the more overlap in certain resources (e.g. food and mates) conspecifics have, the more agonistic behavior is exhibited. This suggests that the congeners will exhibit more interspecific aggression when a greater overlap in shared resources occur. Thus, the intensity of interactions between allopatric species with different ecological requirements should be low. For sympatric species the intensity of interactions should reflect the magnitude of their resource overlap. If their sympatric situation is recent and they have similar requirements, the intensity of their interactions should be high. This may arise because insufficient time has passed for divergence in their ecology to occur (Orians and Willson, 1964). Old sympatric situations should reflect low intensity interactions as we expect divergence to have taken place to reduce competition for limited resources.

The third hypothesis: the intensity of interspecific interactions is not a function of similarity of appearance between the matched pair of species. I tested whether high intensity interspecific interactions are cases of mistaken identity (sensu Murray, 1971). Murray has argued that interspecific territoriality is misdirected intraspecific territoriality. However, others point out that there is strong selective advantage(s) for interspecific territoriality (see Catchpole, 1972; Davies, 1978; Low, 1971; Myrberg, 1972a;

Myrberg and Thresher, 1974; Thresher, 1976).

Pairings of very similar appearing species were made in my study to see whether the level of aggressive interaction was high, thus supporting the "mistaken identity" argument or whether only those pairings between species with wide resource overlap show high aggressive intensity, thus supporting the alternative argument. It was predicted that the cooki-cristatellus pairing would show high intensity values because of their wide resource overlap. Other pairings involving cristatellus or cooki and a similar-appearing species were expected to show low intensity values.

Methods

In order to test the level of aggression in agonistic interactions within and between species, pairings were made between similar sized lizards. Conspecific pairings of A. cooki and A. cristatellus, and congeneric pairings of A. cooki, A. cristatellus, A. evermanni, A. gundlachi, and A. monensis were performed.

The above interactions were staged in the lab in a 0.6 x 1.3 x 2 - m enclosure having a central sliding partition. The enclosure contained simulated habitat arranged in such a way that the observer could always see the lizards as they moved about. A lizard was placed in each end of the enclosure and allowed to adjust to the enclosure for 24 h. Then the partition was removed and the lizards were allowed to interact. This way of introducing the subjects eliminated a "resident-intruder" relationship, since both subjects were residents.

Interaction was limited to a 60 min match. Each match consisted

of a variable number of subject-determined interactions, termed

"rounds", interspersed by periods of non-interaction. The duration of

each round and the frequency of occurrence of the different actions

and modifiers exhibited by each lizard during the round were recorded.

These events were recorded with a stopwatch, timer, and tape recorder

from a blind. The data were tabulated so that for each round of a

match, I knew: (1) the placement of the round within a match (e.g.

round 1, round 2, etc.); (2) the duration of each round within a

match; (3) the opponents, I.D., snout-vent length and body weight;

(4) the species to which each opponent belonged and so characterizing

the match as being conspecific or congeneric; and (5) the different

displays, modifiers, and actions exhibited by each opponent within the

round (Table 13).

Pilot studies of the species' modifiers revealed that they

were used in a hierarchical manner. It became clear, then, that the

progressive addition of the modifiers reflected the increasing arousal

of the displayers as interactions became prolonged. Therefore, the

sequence and frequency of appearance of the modifiers and other

significant actions associated with an encounter were recorded by

giving each modifier, display and action a numerical value with respect

to its initial appearance in the sequence of agonistic behaviors.

In this way the intensity with which any one male reacts to an ag-

gressive encounter could be quantitified (Table 12). Not only would

this method operate in conspecific interactions, but also in inter-

specific interactions due to the apparent universality with which

modifiers seem to be shared in the genus Anolis (Jenssen, 1977).

My "grading scale" was determined from approximately 50 filmed

interactions and recorded encounters between males; these served as

the pilot study for the present experiments. The assignment of values

in the grading scale of aggression intensity was also influenced by

the reports of Jenssen (1978, 1979) and Jenssen and Hover (1976).

The graded scale of values for each behavior in the aggressive

repertoires of the species was used to compute the aggression index

(AI) for each lizard of a match. The AI represents a simple summation

of the values for each behavior that a lizard performed during a match.

The greater the AI, the more a lizard contributed to a match. A mean

AI was then calculated for each class of conspecific and interspecific

matches. The amount of time spent in actual behavioral interaction

was also recorded for each match and termed, "total duration" or

TD (Table 14). This last measurement was determined by adding the

duration of all the rounds in a match and the intervals during which

the lizards were alert to each other's movements. A mean total

duration for each class of participants was calculated.

Descriptive statistics (mean, standard deviation, coefficient of

variation, and standard error) were calculated for the AI and TD of

each class of subjects. The coefficient of correlation between AI

and TD was also computed. Statistical comparisons of aggression

indices between the various classes of interactions given below, were

made using the non-parametric Wilcoxon two-sample rank test. Because

each of the hypotheses predicted a higher aggression index for only

one of the classes, significance was determined with a one-tailed test.

The different classes of interactions run and their replications
(N) are as follows: conspecific cooki (12), conspecific cristatellus
(13), cooki vs. sympatric cristatellus (6), cooki vs. allopatric
cristatellus (10), cooki vs. evermanni (5), cooki vs. monensis (2),
cristatellus vs. evermanni (5), and cristatellus vs. gundlachi (2).

A total of 55 interactions involving 21 males of 5 species were
set up. These were performed within 2 months after the lizards were
collected. Most of the males were used more than once. Because prior
conditioning and experience play an important role in determining the
outcome of aggressive disputes (Parker, 1974), three conventions were
observed.

The first was to set up the interactions in a way that would help
to reduce the possible effect of experience. For this purpose the same
males were not used in consecutive interactions, and at least five
days elapsed before re-using a subject.

The second convention was to only match males of similar size,
because a difference in size would give an advantage to the biggest
male (Miller, 1964a, 1967). In all the interactions held, the size
ratio (SVL smallest/SVL largest) of the contenders was $0.94 \pm$ SE 0.006.

The third convention was to hold interspecific interactions prior
to conspecific interactions. It was hoped that this would assure
maximum aggression of the contenders while they were still "naive".

Results

To test whether conspecific interactions would be more intense than
interspecific interactions, all conspecific interactions were compared

with all the interspecific interactions. The mean conspecific AI
(357.6 $\pm$ 83.2) was significantly greater (P $\leq$ 0.05) than the congeneric
AI (136.1 $\pm$ SE 25.4) (Tables 14 and 15). For A. cristatellus, all
conspecific interactions were significantly higher than all its inter-
specific interactions. For A. cooki, conspecific interactions tended
to be higher than interspecific interactions, but the differences were
not statistically significant (0.1 $\leq$ P $\leq$ 0.2).

The second hypothesis was that interactions between syntopic
species would be more intense than between sympatric species with
different ecological requirements. The mean AI of A. cooki vs.
sympatric A. cristatellus (representing the syntopic situation) matches
were significantly higher (P $\leq$ 0.01) than the combined AI of the
matches between cristatellus and A. evermanni, and A. gundlachi.

The third hypothesis stated that interactions between sympatric
species with wide overlap in most dimensions of their niche (syntopic)
were more intense than those interactions between similar-appearing
species pairs. The mean AI of A. cooki vs. sympatric A. cristatellus
matches were significantly higher (P $\leq$ 0.01) than the combined mean
AI of the matches between A. cooki vs. A. monensis and A. cristatellus
vs. A. gundlachi.

Anolis cooki can apparently distinguish sympatric A. cristatellus
from allopatric A. cristatellus. The comparison of cooki vs. sympatric
cristatellus with cooki vs. allopatric cristatellus matches was
statistically significant (P $\leq$ 0.05), with the cooki vs. sympatric
cristatellus having the larger value (Fig. 10). Thus the third

hypothesis appears supported. Not tested, however, was the possibility

that allopatric A. cristatellus are not as aggressive as the sympatric

A. cristatellus.

The combined cooki vs. cristatellus matches were significantly

higher ($P \leq 0.01$) than all other interspecific matches in which the two

species were involved (Table 15). In all these cooki-cristatellus

matches A. cristatellus dominated A. cooki as evidenced by cristatellus

supplanting and chasing their cooki opponent.

Discussion

It has been a frequent assumption of past studies (Darwin, 1859;

Cole, 1960; Miller, 1967) that when competition manifests itself in

an aggressive form, it is most intense between individuals of the same

species. Yet this assumption has not been well supported by

experimental data. My results, however, provide empirical evidence

that conspecific interactions are more intense than interspecific

interactions for a sympatric pair of Anolis lizards.

It also seems likely that in interspecific interactions in Anolis

lizards, the degree of aggression towards other species is directly

related to the degree of resource overlap. This was supported by our

findings that the interactions between syntopic A. cooki and A.

cristatellus were significantly more intense than those of A.

cristatellus with A. evermanni and A. gundlachi.

When comparing resource overlap, one finds that A. gundlachi,

a cryptic species of A. cristatellus, replaces A. cristatellus

ecologically at high altitudes (Rand, 1964). Though primarily

upland and lowland forms, respectively, A. gundlachi and A. cristatellus
overlap broadly at middle elevations in Puerto Rico (Williams, 1972).
Where sympatric, A. gundlachi occur in deep forest habitats, while
A. cristatellus live in open habitats (Huey and Webster, 1976; Rand,
1964; Schoener and Schoener, 1971; Williams, 1972). Huey and Webster
(1976) reported overall differences in body temperature (BT) in these
two species, with A. gundlachi active at much lower BT than A.
cristatellus. Their preferred body temperatures (PBT) also differed
significantly. Thus, habitat differences between the two species are
very substantial suggesting little overlap in their resources. The
other species A. evermanni is another Puerto Rican anole of about the
same size as A. cristatellus and A. gundlachi, but is quite different
in appearance (green) and in its structural habitat. It is sympatric
with A. cristatellus at middle elevations, but is a trunk-crown species;
the overlap with A. cristatellus, a trunk-ground species, is minimal,
if any.

However, in the cooki-cristatellus situation there is wide resource
overlap. The high intensity of their interactions suggests that their
mutual aggression reflects proportionally the amount of overlap in
their resource requirements. Other studies have provided similar evi-
dence for other animal groups (Branch, 1975; Low, 1971; Orians and
Willson, 1964; Stimson, 1970, 1973).

My results also indicate that interspecific aggression between
A. cooki and A. cristatellus can not be explained as being misdirected
intraspecific behavior (Murray, 1971). If that had been the case, all
interactions between similar-appearing lizards (e.g. A. cristatellus

and A. gundlachi) should have been about the same. In fact, the
interactions between syntopic A. cooki and A. cristatellus were
significantly more intense than those between A. cristatellus and
A. gundlachi and A. cooki and A. monensis (which are similar even in
aspects of their display behavior) (Fig. 10).

The significant difference found between A. cooki's interactions
with sympatric cristatellus and its interactions with allopatric A.
cristatellus suggests that subtle behavioral elements that are found in
one species must be recognized by the other, or that allopatric
cristatellus is less aggressive than sympatric cristatellus.

Because so few cases of active competitive interference have
been documented from naturally occurring populations, one must conclude
that most ecologists have never observed a competitive system during
its initial phase of flux, where behavior is in the process of pushing
the ecological interaction to some point of equilibrium (e.g. niche
divergence or competitive exclusion). Indeed, many ecologists are
skeptical of competitive theory altogether. My laboratory suggests
that the cooki-cristatellus aggressive interactions are as nearly
intense as the species' congeneric encounters. This is strong evidence
that A. cooki and A. cristatellus do exhibit marked interspecific ter-
ritoriality in the field and that they are competing for perch sites.
Considering A. cristatellus was dominant over A. cooki in all their
lab-held interactions suggest that in the field A. cristatellus might
be pushing A. cooki into less favorable habitat. If this is true,
the dynamic relationship between A. cooki and A. cristatellus

populations is still unstable, and with it the fate of A. cooki.

What is eminently obvious at this point is the need for a thorough

field study of the behavioral dynamics between A. cooki and sympatric

A. cristatellus, and documentation that competitive interference is

indeed taking place.

SUMMARY

The present study is the first study to document the behavioral
repertoire of some Puerto Rican anoles (<u>Anolis cooki</u>, <u>A.</u> <u>cristatellus</u>,
and <u>A.</u> <u>monensis</u>) and the intensity of their agressive interactions
with conspecifics and other congeners (<u>A.</u> <u>evermanni</u>, and <u>A.</u> <u>gundlachi</u>).
The species involved in the study were collected during January 5-8
of 1978 and 1979, at the Salt Plant area of Cabo Rojo in southwestern
P.R. and at El Yunque, Luquillo. The research included a display
behavior analysis and lab-staged intra and interspecific aggressive
interactions.

Display Behavior Analysis

1. <u>Anolis</u> <u>cooki</u> display repertoire consisted of one head bob pattern
   that is used in several social contexts: assertion, courtship
   and challenge. It was composed of five head bobs arranged in a
   "one small-two big-two smaller" pattern, accompanied by non-
   stereotyped dewlap movements during the challenge context. The
   display was strongly stereotyped in its temporal sequencing and
   total duration.

2. <u>Anolis</u> <u>cristatellus</u> display repertoire consisted of two distinct
   head bob patterns (Type A and Type B). The Type A (signature)
   was used mainly during assertion and courtship while the Type B
   was used exclusively during the challenge context.
   The Type A core display consisted of three similarly spaced head
   bobs strongly stereotyped in their temporal sequencing and total
   duration.

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The Type B core display consisted of four head bobs whose most prominent feature was a conspicuous pause after the second head bob. Thus, the arrangement of the bobs give the impression of a "two big-one small-one smaller" pattern. Some of the head bob units were strongly stereotyped, others, of short duration, were variable. Most of the variability in these units was found when comparing between lizards.

A sample of A. cristatellus from an allopatric population revealed the same two patterns, although an analysis of their temporal aspects indicated significant differences from the sympatric population.

3. Anolis monensis display repertoire consisted of one head bob pattern used in several contexts. It was composed of five head bobs very similar in arrangement to the A. cooki display. with the exception of two inter-bob pauses in the pattern, the display was highly stereotyped.

4. A survey of all the modifiers used by the species in their social interactions revealed that most modifiers were shared by all the species in this study. The vertical tail movements sometimes associated with the Type B display is absent in A. evermanni. The hierarchical manner in which they were used suggested that the increasing arousal of the displayer during prolonged agonistic encounters was indicated.

Aggressive Interactions

1. The level of aggression in conspecific interactions of A. cooki and

of _A_. _cristatellus_ was higher than the level of aggression in their congeneric interactions.

2. _Anolis_ _cooki_ and _A_. _cristatellus_ interacted intensely with each other in the lab-held matches suggesting interspecific territoriality between the two anoles probably occurs in the field.

3. The intense interactions of _A_. _cooki_ and _A_. _cristatellus_ were not explained by Murray's (1971) mistaken identity argument, as was indicated by their low intensity interactions with "similar-appearance" congeners.

4. The interspecific aggression between _A_. _cooki_ and _A_. _cristatellus_ was suggested as a function of their wide overlap in resource requirements.

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APPENDIX
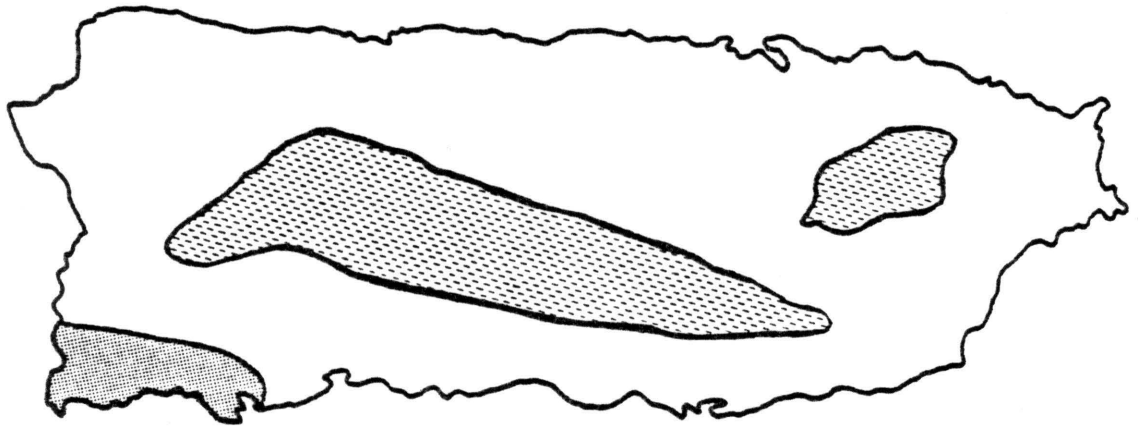
Fig. 1. Geographic distribution of the Puerto Rican anoles in this
study. Dotted area indicates sympatric region for A.
cristatellus and A. cooki. Broken-lines indicate the range
of A. evermanni and A. gundlachi.
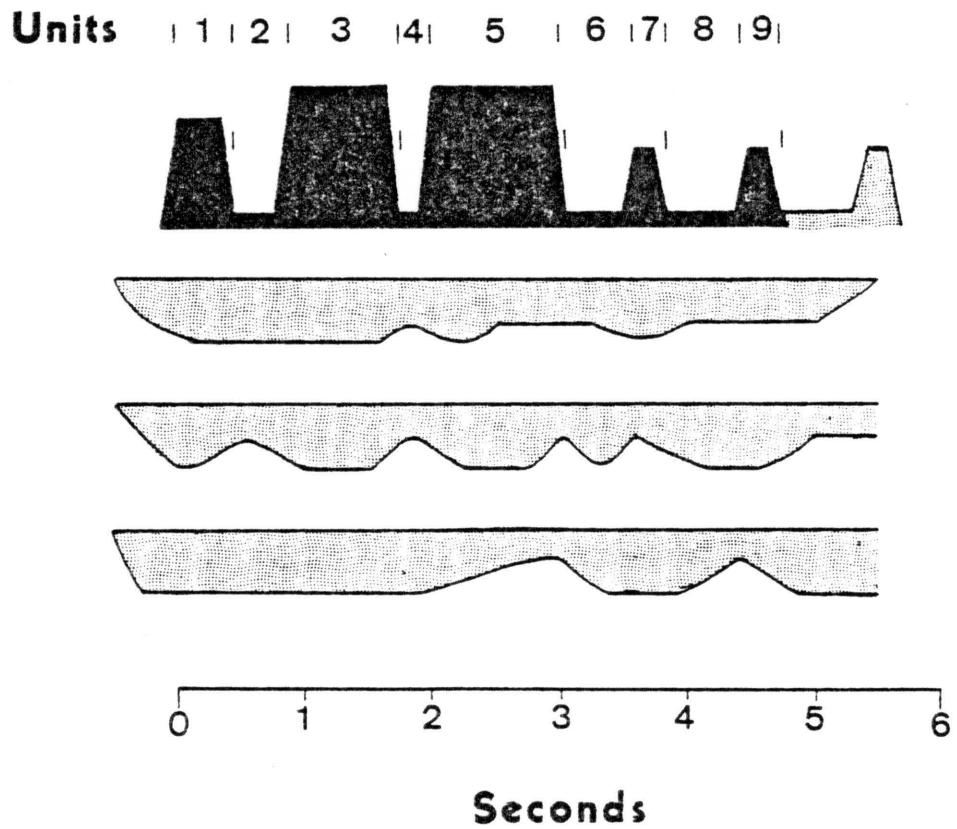
Fig. 2. Generalized DAP graph of _Anolis cooki_ display. Dotted areas indicate display components not always present. Dewlap movements provided are some of the possible patterns performed. Upper part of this figure (in black) denote head movements, lower three denote dewlap movements.
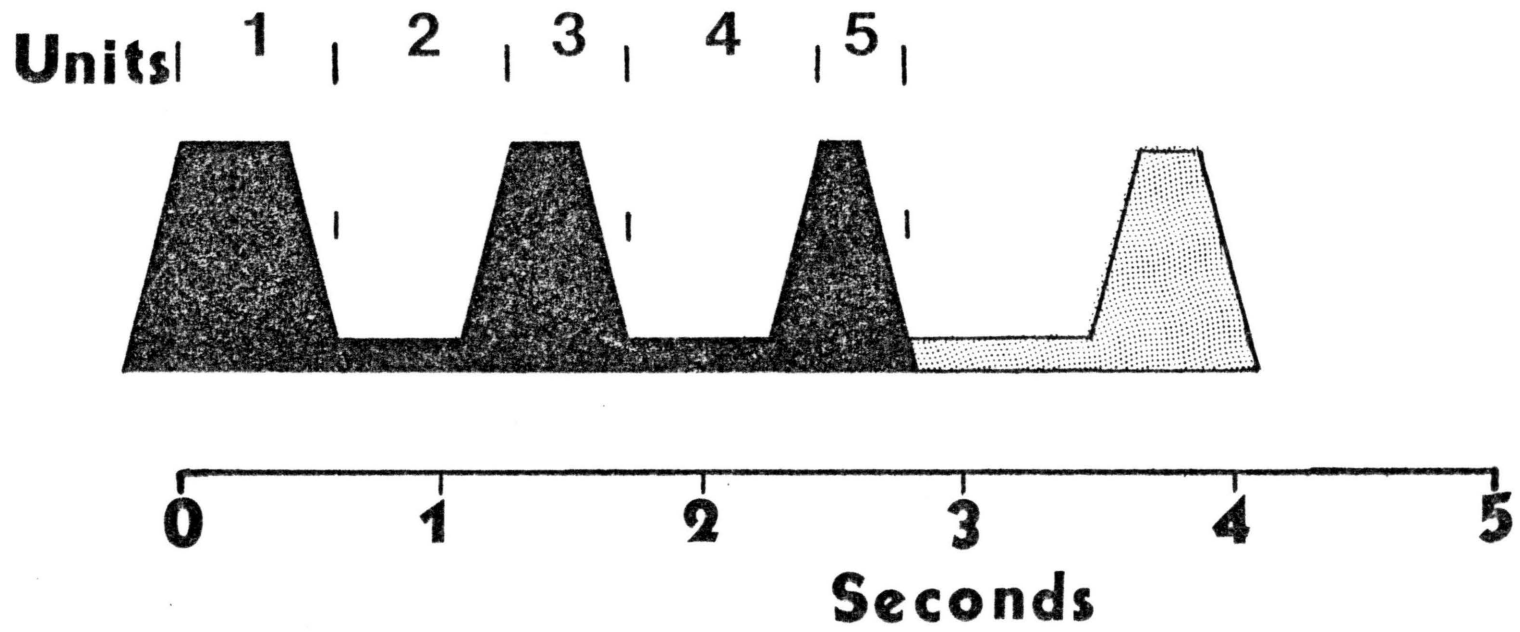
Fig. 3. Generalized DAP graph of _Anolis cristatellus_ signature (Type A) display.
Dotted areas indicated display components not always present.
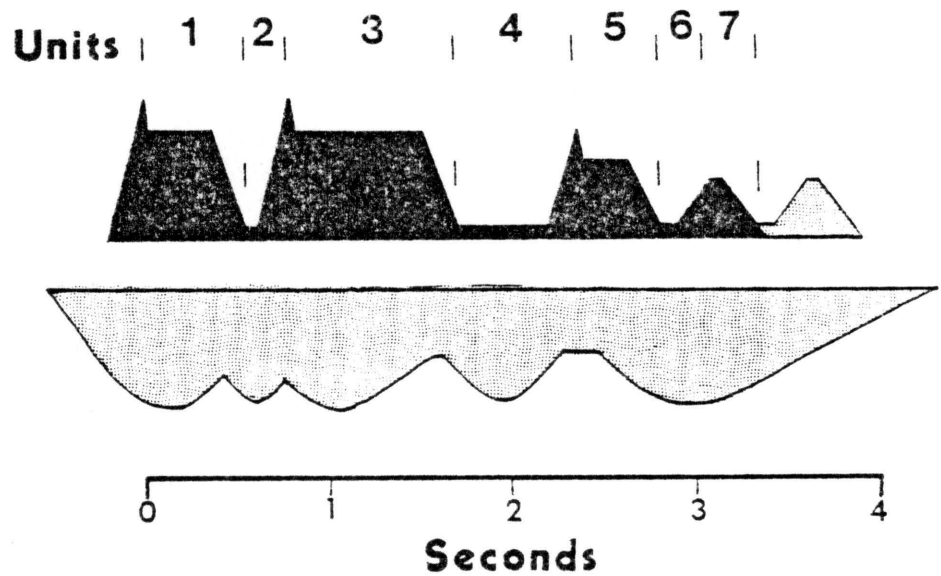
Fig. 4. Generalized DAP graph of <u>Anolis</u> <u>cristatellus</u> agonistic
(Type B) display. Dotted areas indicated display com-
ponents not always present. One of the dewlap movements
(lower drawing) observed is also provided. Upper drawing
(in black) denotes head movements.
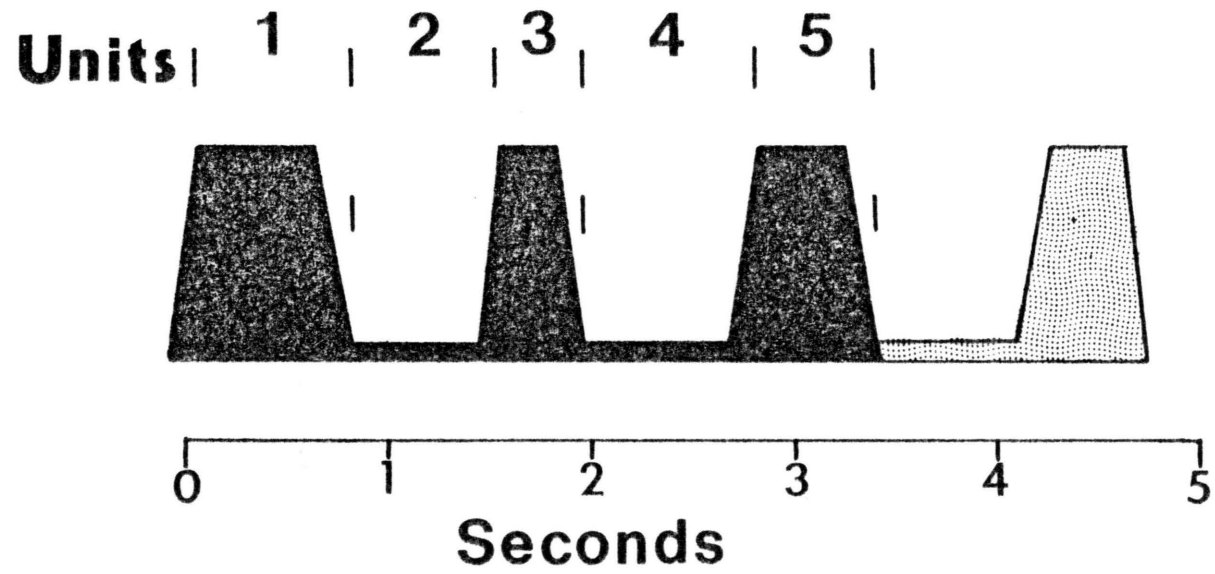
Fig. 5. Generalized DAP graph of allopatric <u>A</u>. <u>cristatellus</u> signature (Type A) display. Dotted areas denote display components not always present.
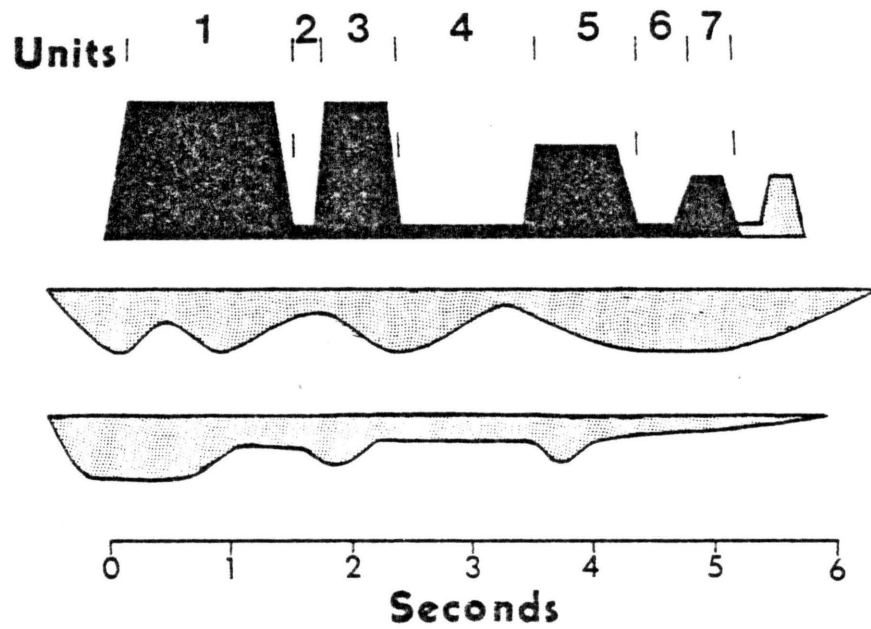
Fig. 6. Generalized DAP graph of allopatric <u>A</u>. <u>cristatellus</u>
Type B (agonistic) display. Upper portion of the
diagram (in black) represent head bobbing movements,
lower portion denote some of the possible dewlap
movements.
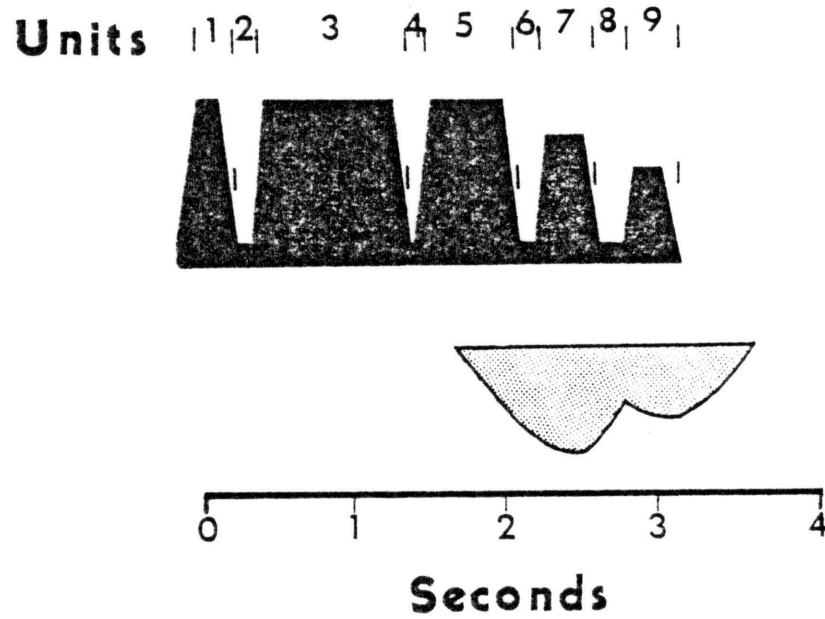
Fig. 7. Generalized DAP graph of <u>Anolis</u> <u>monensis</u> display. Dotted areas denotes display components not always present. Upper drawing (in black) indicate head movements, lower (dotted) indicate dewlap movements.
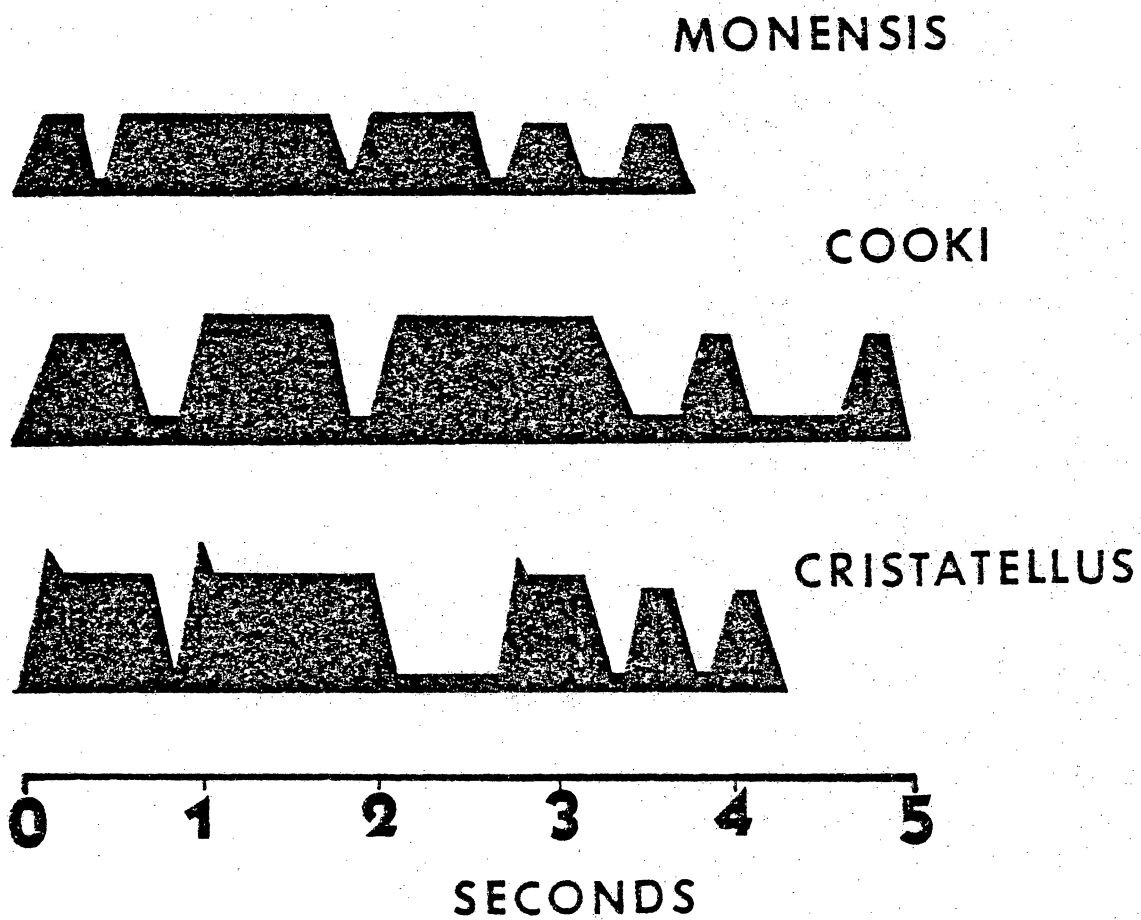
Fig. 8. Generalized DAP graphs of some of the members of the
   cristatellus species group.
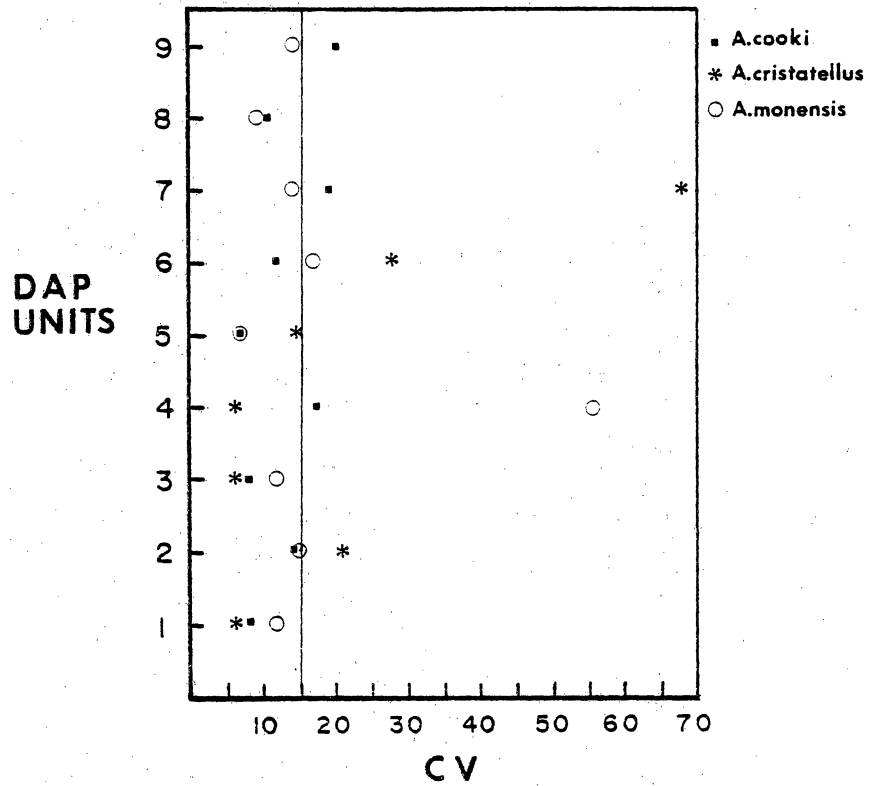
Fig. 9. Relative stereotypy of the units of A. cooki
and A. monensis signature display, and
A. cristatellus Type B display. Units
lying to the left of the line (CV ≤ 15)
are considered strongly stereotyped.
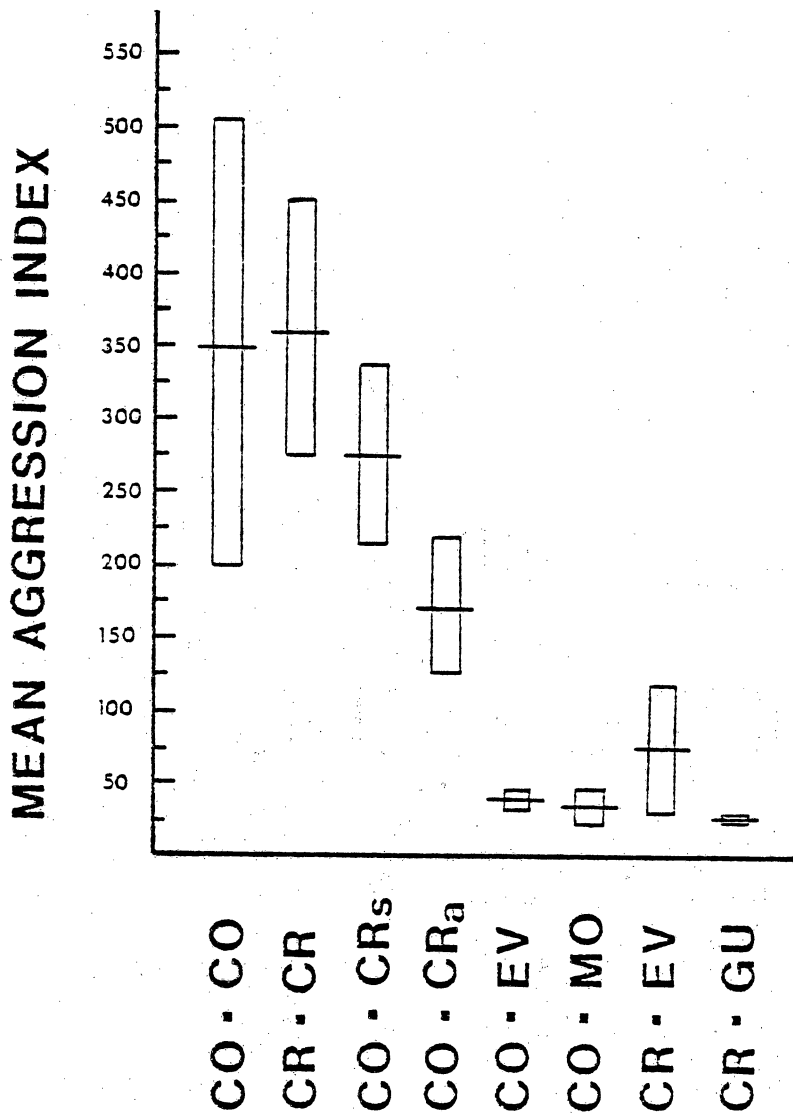
Fig. 10. Mean aggression index for the different types of interactions
performed in the lab. Horizontal line represents the mean and the
ends of the bar represent the standard error of the mean. CO - CO =
conspecific cooki, CR - CR = Conspecific cristatellus, CO - CR$_s$ =
cooki vs. sympatric cristatellus, CO - CR$_a$ = cooki vs. allopatric
cristatellus, CO - EV = cooki vs. evermanni, CO - MO = cooki vs.
monensis, CR - EV = cristatellus vs. evermanni, and CR - GU =
cristatellus vs. gundlachi.

TABLE 1

Mean duration in seconds of the units of <u>Anolis cooki</u> display, with their coefficient of variation (CV), standard error (SE), and 95% confidence limits of the mean (L_1 L_2)

Unit	Mean	CV	SE	L_1	L_2
1	0.49	8.4	.006	0.48	.50
2	0.36	13.6	.006	0.35	.38
3	1.03	8.2	.011	1.02	1.06
4	0.17	17.5	.004	0.17	.19
5	1.16	6.5	.010	1.14	1.18
6	0.45	11.5	.006	0.44	0.46
7	0.21	19.4	.005	0.20	0.22
8	0.64	10.5	.008	0.62	0.65
9	0.17	19.8	.004	0.16	0.18
Total Duration (Units 1-9)	4.70	3.5	.002	4.65	4.74

TABLE 2

Proportionment of variance found within and among males resulting from single classification analyses of variance applied to unit durations of 11 units of 56 Anolis cooki displays.

Unit	Source of variation	% Proportionment (unit duration)
1	within	18.4
	among	81.6
2	within	30.0
	among	70.0
3	within	9.3
	among	90.7
4	within	46.3
	among	53.7
5	within	16.0
	among	84.0
6	within	39.5
	among	60.5
7	within	92.8
	among	7.2
8	within	25.7
	among	74.3
9	within	74.8
	among	25.2
Total Duration (Units 1-9)	within	10.4
	among	89.6

Table 3

Mean duration in seconds of the units of 85 $\underline{A}$. <u>cristatellus</u>
signature display (Type A), with their coefficient of variation
(CV) standard error (SE), and 95% confidence limits of the mean
(L_1 L_2)

Unit	Mean	CV	SE	L_1	L_2
1	0.61	10.4	0.007	0.60	0.62
2	0.71	6.9	0.005	0.70	0.73
3	0.38	10.9	0.004	0.37	0.38
4	0.84	9.0	0.008	0.82	0.85
5	0.23	13.2	0.003	0.23	0.24

Total Duration
(Units 1-5)

| | 2.76 | 3.8 | 0.012 | 2.73 | 2.77 |

TABLE 4

Proportionment of variance found within and among
males resulting from single classification analyses of
variance applied to unit durations of the units of 85
signature displays (Type A) of A. cristatellus.

Unit	Source of variation	% Proportionment
1	within	30.0
	among	70.0
2	within	38.0
	among	62.0
3	within	36.3
	among	63.7
4	within	45.4
	among	54.6
5	within	39.1
	among	60.9
Total Duration (Units 1-5)	within	14.0
	among	86.0

Table 5

Mean duration in seconds of the units of
67 A. _cristatellus_ agonistic displays (Type B)
with their coefficient of variation (CV),
standard error (SE), and 95% confidence limits
of the mean (L_1, L_2)

Unit	Mean	CV	SE	L_1	L_2
1	0.72	6.6	0.006	0.71	0.73
2	0.15	20.7	0.003	0.14	0.16
3	1.08.	5.5	0.007	1.07	1.10
4	0.76	6.4	0.006	0.75	0.77
5	0.43	14.5	0.007	0.41	0.44
6	0.10	28.2	0.003	0.09	0.11
7	0.16	67.8	0.013	0.14	0.18
Total Duration (Units 1-7)	3.39	4.7	0.019	3.35	3.43

TABLE 6

Proportionment of variance found within and among males resulting for single classification analyses of variance applied to unit duration of the units of 67 agonistic displays (Type B) of A. cristatellus

Unit	Source of variation	% Proportionment
1	within	18.6
	among	81.4
2	within	50.8
	among	49.2
3	within	30.9
	among	69.1
4	within	33.1
	among	66.9
5	within	85.4
	among	14.6
6	within	81.8
	among	18.2
7	within	47.8
	among	52.2
Total Duration (Units 1-7)	within	53.8
	among	46.2

Table 7

Mean duration in seconds of the units of
allopatric cristatellus signature (Type A)
display, their coefficient of variation (CV),
standard error (SE), and 95% confidence limits
of the mean (L_1 L_2).

Unit	Mean	CV	SE	L_1	L_2
1	0.84	9.7	0.018	0.80	0.88
2	0.86	4.8	0.009	0.84	0.88
3	0.28	8.1	0.005	0.27	0.29
4	1.02	4.8	0.011	1.00	1.04
5	0.41	8.2	0.007	0.40	0.42
Total Duration (Units 1-5)	3.41	3.4	0.023	3.36	3.46

TABLE 8

Proportionment of variance found within and among males resulting from sigle classification analyses of variance applied to unit durations of all the units of A. cristatellus signature display.

Unit	Source of variation	% Proportionment (Unit durations)
1	within	41.2
	among	58.8
2	within	70.1
	among	29.9
3	within	64.0
	among	36.0
4	within	18.6
	among	81.4
5	within	77.8
	among	22.2
Total Duration (Units 1-5)	within	13.7
	among	86.3

Table 9

Mean duration in seconds of the units of
allopatric cristatellus agonistic display, their
coefficient of variation (CV), standard error
(SE), and 95% confidence limits of the mean
(L_1, L_2).

Unit	Mean	CV	SE	L_1	L_2
1	1.42	21.7	0.09	1.22	1.63
2	0.19	20.9	0.01	0.16	0.21
3	0.69	14.9	0.03	0.62	0.75
4	1.04	9.5	0.02	0.97	1.10
5	0.91	6.3	0.01	0.87	0.94
6	0.48	6.0	0.008	0.46	0.50
7	0.40	28.3	0.03	0.33	0.48

Total Duration
(Units 1-7)

	5.14	6.8	0.10	4.90	5.30

Table 10

Proportionment of variance found within
and among males resulting from single class-
ification analysis of variance applied to
unit durations of all the units of allopatric
<u>cristatellus</u> agonistic display.

Unit	Source of variation	% Proportionment (unit duration)
1	within	17.2
	among	82.8
2	within	72.3
	among	27.7
3	within	54.7
	among	45.3
4	within	4.1
	among	95.9
5	within	1.9
	among	98.1
6	within	0.2
	among	99.8
7.	within	4.5
	among	95.5
Total Duration (Units 1-7)	within	40.1
	among	59.9

Table 11

Mean duration in seconds of the units of
Anolis monensis display, their coefficient of
variation (CV), standard error (SE), and con-
fidence limits of the mean (L_1, L_2).

Unit	Mean	CV	SE	L_1	L_2
1	0.24	11.6	0.014	0.20	0.27
2	0.18	15.1	0.014	0.14	0.22
3	1.06	11.5	0.050	0.92	1.19
4	0.09	55.6	0.020	0.03	0.14
5	0.61	6.5	0.017	0.56	0.66
6	0.19	16.1	0.014	0.15	0.22
7	0.32	14.4	0.020	0.27	0.38
8	0.27	9.3	0.010	0.24	0.29
9	0.28	14.2	0.017	0.23	0.32
Display Duration (Units 1-9)	3.20	5.4	0.080	2.98	3.42

Table 12

Weighing scale of modifiers and actions, used to
calculate an Agression Index for an interaction.

Modifiers/Actions/Displays	Point Value
Dewlap pulses	1
Crest erected	3
Extended throat	3
Type A DAP	2
Sides flattened	4
Rounded eyes	4
Head rolls	5
Introductory rocking	6
Type B DAP	7
Approach	8
Mouth opened	8
Protruded tongue	8
Stretch Posture	9
Tail movements	9
Attack	10
Jaw sparring	10
Jaw locking	11
Supplant	12
Chase	13

TABLE 13

Data collected during conspecific and
interspecific (congereric) paired encounters.

Match No. _____
Lizards Involved

   A: ID _____ SVL _____ Wt. _____
   B: ID _____ SVL _____ Wt. _____

Round No. _____   Duration _____

A	Lizard	B
____	Crest erect	____
____	Extended throat	____
____	Rounded eyes	____
____	Mouth opened	____
____	Sides flattened	____
____	Tongue out	____
____	Stretch Posture	____
____	Head rolls	____
____	Dewlap pulses	____
____	Tail movements	____
____	Rocking introduction	____
____	Approach	____
____	Supplant	____
____	Chase	____
____	Attack	____
____	Jaw Sparring	____
____	Jaw Locking	____
	Display Types	
____	A	____
____	B	____

These data were recorded for each round of a
match. After 60 minutes, data from all the
rounds were used to calculate the Aggression
Index for the match

Table 14

List of individual conspecific matches, their total duration (TD) and their aggression index (AI). Mean ($\bar{x}$), standard error (SE) and the correlation coefficient (Corr. C.) for TD, and AI are given for all the matches in a class.

Class	Match no.	TD (min.)	AI (Point Value)
A. _A. cristatellus_	7	35.1	208
	8	13.0	186
	9	47.0	594
	10	57.6	726
	11	35.3	302
	12	39.9	845
	13	41.1	797
	14	44.7	584
	15	8.9	3
	16	8.9	182
	17	21.9	127
	18	25.9	53
	19	23.8	98
	N = 13	$\bar{x} \pm$ SE = 31.0 $\pm$ 4.4	$\bar{x} \pm$ SE = 361.9 $\pm$ 87.3

Correlation Coefficient: 0.81

B. _A. cooki_	20	27.3	355
	21	51.1	606
	22	14.9	324
	23	56.0	1886
	24	12.3	87
	25	19.0	76
	26	14.6	208
	27	18.6	219
	28	33.0	327
	29	7.3	24
	30	13.0	111
	31	.5	12
	N = 12	$\bar{x} \pm$ SE = 22.3 $\pm$ 5.1	$\bar{x} \pm$ SE = 352.9 $\pm$ 154

Corr. C. = 0.83

A + B	N = 25	26.8 $\pm$ 3.3	357.6 $\pm$ 83.2

Corr. C. = 0.78

Table 15

List of individual interspecific matches, their total duration (TD), and aggression index (AI). Mean ($\bar{x}$), standard error (SE) and the correlation coefficient (Corr. C.) are given for all the matches in a class.

Class		Match no.	TD	AI	
A.	A. cooki	1	55.1	517	
	vs	2	20.0	149	
	A. cristatellus (symp)	3	14.8	212	
		4	31.3	171	
		5	53.7	311	
		6	29.6	300	
		N	$\bar{x}$+SE	$\bar{x}$+SE	Corr. C.
		6	34.1+7.5	276.7+60.4	0.79
B.	A. cooki	30	26.0	157	
	vs	31	8.2	46	
	A. cristatellus (allop)	32	14.5	224	
		33	37.4	483	
		34	30.8	141	
		35	24.1	78	
		36	15.5	134	
		37	9.0	73	
		38	2.8	48	
		39	27.0	333	
		10	19.5+3.7	171.7+46.8	0.72
C.	A. cristatellus	40	21.9	45	
	vs	41	1.0	46	
	A. evermanni	42	15.8	20	
		43	8.2	68	
		44	5.0	33	
		5	10.4+4.2	73.8+44.2	0.91
D.	A. cooki	45	4.1	45	
	vs	46	5.5	46	
	A. evermanni	47	2.5	20	
		48	17.1	68	
		49	5.5	33	
		5	6.9+2.9	42.4+8.9	0.87
E.	A. cooki	50	6.4	27	
	vs	51	6.9	44	
	A. monensis	2	6.7+0.35	35.5+12	1.0
F.	A. cristatellus	52	21.5	26	
	vs	53	15.9	27	
	A. gundlachi	2	18.9+3.8	26.5+0.71	1.0
	ALL	30	17.9+2.6	136.1+25.4	

BEHAVIORAL COMPARISON OF ANOLINE COMPETITORS:
ANOLIS COOKI AND ANOLIS CRISTATELLUS
(REPTILIA: SAURIA: IQUANIDAE)

by

Peter R. Ortiz

(ABSTRACT)

The behavioral repertoire of the Puerto Rican anoles, Anolis cooki,

A. cristatellus and A. monensis was studied in the laboratory. The

display of A. cooki and A. monensis revealed great similarities;

consisting of one head bob pattern highly stereotyped in its temporal

sequencing and total duration, sometimes accompanied by non-stereotyped

dewlap movements. A. cristatellus display behavior consisted of two

distinct head bob patterns (Type A and Type B). The A display is

strongly stereotyped and used in the assertion and courtship contexts,

while B display is less stereotyped and appeared only in the challenge

context.

Similar display modifiers used during aggressive interactions were

found in A. cooki, A. cristatellus, A. monensis and two other Puerto

Rican anoles, A. evermanni and A. gundlachi. In all these species

the modifiers were progressively added during prolonged aggressive

encounters and seemed to indicate the increasing arousal of the

combatants.

A grading scale was designed to measure the level of aggression in

conspecific and congeneric interactions. It was based on the different

behaviors that the lizards used during their agonistic encounters.

The scale assigned a numerical value to each behavior according to

their order of appearance in the sequence of behaviors performed in

the encounter. Thus, a numerical value was derived for the level

of aggression exhibited in each interaction, and that was called

the "aggression index" (AI). The AI of A. cooki and A. cristatellus

conspecific interactions was significantly higher than the AI of their

congeneric interactions. The high AI of the cooki-cristatellus

interactions was not explained by Murray's (1971) "mistaken identity

argument", but as a function of their wide overlap in resource

requirements.