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Interspecific Aggression between Lizard Competitors, *Anolis cooki* and *Anolis cristatellus*

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With 2 figures

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Abstract

Aggressive encounters were staged between two species of Puerto Rican lizards (*Anolis cooki* and *Anolis cristatellus*) which share the same microhabitat (synoptic). The intensity of these interspecific matches was as great as their respective conspecific matches. When the two species interacted with either "look alike" congeners (*A. cooki* with *A. momentis* and *A. cristatellus* with *A. gundlachi*) or with the quite different appearing *A. evermanni*, aggressive intensity was only 1/6 that of the *cooki-cristatellus* encounters. It seems that *A. cooki* and *A. cristatellus* recognize each other as competitors; it was improbable that this interspecific aggression was caused by the two species misidentifying each other as conspecifics. Because *A. cristatellus* eventually dominated *A. cooki* during staged encounters, it is predicted *A. cristatellus* should ecologically displace *A. cooki* in their synoptic zones of contact.

Introduction

In complex anoline communities where sympatric congeners are common, interspecific competition seems to have resulted in niche divergence. The most well-studied niche dimensions which reflect congenetic segregation are "structural niche" (divergence in perch height and diameter, as proposed by RAND 1964), "climatic niche" (divergence in preferred body temperature, as proposed by RUBAL 1961), and food resource (divergence in distribution of ingested prey size or taxa, as proposed by SCHOENER 1967, 1968). Low overlap along one or more of these niche variables suggests that resource partitioning has evolved to reduce interspecific competition. However, there are very few

data from any vertebrate group which document the actual competitive behavior between naturally occurring species preceding niche divergence (MORSE 1974). As a consequence, most examples of niche shifts in areas of congenetic sympatry are interpreted as having been induced by competitive exploitation rather than by competitive interference (COLWELL and FUENTES 1975).

SCHOENER (1977) states that little is known about interference competition in reptiles at the levels of either individuals or populations and far less is known at the interspecific level. Examples at this last level are scarce (e.g. FERGUSON 1971; JENSSEN 1973; MONTANUCCI 1974; RAND 1961, 1967). It is generally accepted that intraspecific interactions are more intense than those between species. However, the relative intensity of intraspecific versus interspecific patterns of aggression has not been established (MORSE 1980: 254).

The present study quantitatively documents the intensity of conspecific and congenetic aggression in two competing species of Puerto Rican *Anolis* lizards (*A. cooki* and *A. cristatellus*) and some of their allopatric and sympatric but not syntopic (allotopic) congeners. In this paper we address the following three hypotheses regarding interspecific aggression.

1. Aggressive interactions are more intense between conspecifics than between individuals of different species. Theoretically, the overlap in any niche dimension is greatest among members of the same species. Thus, it is expected that the most acute competitive interference (i.e., agonistic encounters) will be between conspecifics. In this regard, recent food habits data have related degree of aggression between different species to the degree of dietary overlap (BRANCH 1975; EBERSOLE 1977; LOW 1971; STIMSON 1970, 1973).

2. Interactions are more intense during encounters between syntopic and ecologically similar congeners than between those which do not share the same microhabitat. It is expected that the more nearly alike the ecological requirements of two species, the greater will be the interspecific interaction (MILLER 1967). STAMPS' (1977) model on conspecific aggression may be applicable to interspecific aggression. She found that the more overlap conspecifics have in certain resources (e.g., food, mates), the more agonistic behavior is exhibited. This suggests that congeners will exhibit more interspecific aggression when a greater overlap in shared resources exists. For syntopic species of recent contact and similar requirements, the intensity of interaction should be particularly high. This may occur because insufficient time has passed for the species to diverge along critical niche dimensions (ORRANS and WILLSON 1964).

3. The intensity of the interspecific interactions is not a function of similarity in appearance between species pairs. Instances of sharp interspecific interactions have led to a controversy. Interspecific territoriality has been interpreted as misdirected intraspecific territoriality (e.g. BECKER 1977; CODY 1969, 1974; MURRAY 1971) or as positive recognition of non-conspecific competitors (e.g. CATCHPOLE 1978; LOW 1971; MYRBERG and THRESHER 1974; THRESHER 1976). Our study examines these alternatives.

Materials and Methods

Subjects

We used adult males of five Puerto Rican species (Table 1), but focused primarily on *A. cooki* and *A. cristatellus*. The latter two species exhibit conspicuous interspecific territoriality. They are moderately large (55–70 mm SVL) and of similar size, conditions which SCHÖENER (1975) found likely to enhance the intensity of competition. They are also of similar appearance, only recently being recognized as separate species (GORMAN et al. 1968). *Anolis cooki* is restricted to a small xeric habitat in southwestern Puerto Rico, where at places it is syntopic with the more widespread *A. cristatellus*. In their areas of sympatry, *A. cooki* tends to occupy a slightly more open microhabitat (WILLIAMS 1972), but both species share broadly overlapping climatic and structural niche dimensions (HUEY and WESTER 1976; LISTER 1976; JENSEN, JENSEN and MARCELLINI, unpubl. data). Furthermore, physical fighting (i.e., biting) frequently occurs between these congeners as observed in the field during intruder-release experiments (JENSEN, JENSEN and MARCELLINI, unpubl. data).

Table 1: Morphological comparisons of *Anolis cooki* (CO), *Anolis cristatellus* (CR), *Anolis monensis* (MO), *Anolis gundlachi* (GU), and *Anolis evermanni* (EV)

Trait	CO	CR	MO	GU	EV
Adult male SVL	55–65 mm	60–70 mm	50–60 mm	60–70 mm	60–70 mm
Presence of a caudal fin	yes	yes	yes	yes	no
General body morphology	moderately stout	stout	moderately stout	stout	moderately stout
General body color	mottled grey to dark brown	mottled grey to dark brown	mottled light brown to dark brown	heavily mottled brown to sooty black	green
Dewlap color**	dull orange to orangish red	yellow to dull orange	yellow to dull orange	deep yellow to dull orange	yellow

* Varies within individuals; ** Varies between individuals.

The other three anoline species of our study were selected to complement the *cooki*-*cristatellus* comparison. *Anolis monensis*, the only *Anolis* species found on Mona Island off the western shore of Puerto Rico, is the closest relative of *A. cooki* and is very similar in appearance to *A. cooki*. *Anolis gundlachi* is a sibling species of *A. cristatellus*, but is allopatric to *A. cristatellus* by virtue of a cooler climatic niche (HARTZ et al. 1979; HUEY and WESTER 1976; RAND 1964; SCHÖENER and SCHÖENER 1971; WILLIAMS 1972). *Anolis evermanni*, which is similar in size with the other four species, is quite different in appearance. It is green instead of having the mottled brown body patterns of the other anoles of this study. *Anolis evermanni* is allopatric to *A. cooki* and allopatric to *A. cristatellus*, having a divergent structural niche in areas of sympatry with *A. cristatellus* (RAND 1964; SCHÖENER and SCHÖENER 1971; WILLIAMS 1972).

Although more animals were collected, the population of males in our lab at V.P.I. and S.U. stabilized at 7 *A. cooki* (CO) from Cabo Rojo; 5 *A. cristatellus* (CR) from Cabo Rojo, one *A. monensis* (MO) from Mona Island, 4 *A. gundlachi* (GU) from El Yungue, and 4 *A. evermanni* (EV) from El Yungue. Each lizard was toe clipped and its snout-vent length (SVL) and body weight recorded.

Males were housed singly in 1.2 × 0.6 × 0.7 m enclosures, along with two to four conspecific adult females per cage. These holding cages contained stumps, branches, and artificial

foliage. The lizards were watered and fed crickets and *Tenebrio* larvae daily. The lab was kept at approximately 24°C, with cages having their fluorescent lights set on a 12L-12D cycle, centered at 13:00 h.

Experiments

7 classes of encounters were staged between pairs of male conspecifics and congeners. The classes of pairings and their replications (N) were: CO-CO (12), CR-CR (13), CO-CR (6), CO-MO (2), CO-EV (5), CR-GU (2), and CR-EV (5). A total of 45 interactions involving 21 males were analyzed. The males were tested within two months of their capture, and all were in good health.

The above interactions occurred in a 0.6 × 1.3 × 2 m enclosure, having a central removable partition. Simulated habitat was arranged most densely at the ends of the enclosure; tiered branches were positioned along the length of the back wall, ending on the substrate at the partition. With the partition present, a male was placed in each end of the enclosure. After at least 24 h, the partition was removed. Introducing the subjects to each other in this manner eliminated handling effects and produced a "resident-resident" relationship to enhance territorial behavior.

Paired interactions, termed "matches", were 60 min long, and consisted of a variable number of subject-determined "rounds" (i.e., intervals when subjects were overtly interacting), interspersed by periods of inactivity. The duration of each round and the occurrence of various behaviors performed by each subject per round were recorded from a blind, using a stopwatch, timer, and tape recorder.

Quantification of the aggressive intensity was accomplished by first making an ethogram of aggressive behavior for all species (ORTIZ 1979; summarized in Table 2). With the exception of the species-unique head bob displays, all species shared the same repertoire of agonistic-related behaviors. Observations on our species (ORTIZ 1979) and on other anoles (HOVER and JENSEN 1976; JENSEN 1978, 1979) indicate that the agonistic behaviors are used in a progressive manner. Some behaviors predictably appear early in encounters, while others are performed progressively later during prolonged encounters. Based on their approximate order of appearance, the various behaviors were scored with a weighted scale (Table 2).

To score a match, the point values for all behaviors performed by each subject during a match were summed; this total formed a subject's "aggression index" (AIX) for a match. The and actions used to calculate the aggression index (AIX) for a match

Display / modifiers / actions	Point value
Dewlap pulse	1
Head bob display	2
Erected crest	3
Extended throat	3
Sagittal expansion	4
Orbed eyes	4
Head roll	5
Rocking	6
Approach	8
Opened mouth	8
Protruded tongue	9
Stretch posture	9
Tail movements	10
Attack	10
Jaw sparring	11
Jaw locking	11
Suppliant	12
Chase	13

greater the AIX, the more aggressive behavior a subject contributed during a match. A mean AIX was calculated for each class of conspecific and congenetic matches. In addition, "total amount of time spent in overt interaction was summed for each match and was termed, "total duration" (TD). The greater the TD value, the more time a pair interacted during the 60-min match. Mean TD values were also calculated for each class of matches. Statistical comparisons were made among the class scores for both AIX and TD data sets using the nonparametric Mann-Whitney U test (SIEGEL 1956).

Due to the limited size of the laboratory population, most males were used more than once, but not more than three times. Three conventions were employed to decrease the chance of prior experience affecting the outcome of the subsequent aggressive disputes. The first was to pit at least five days between trials if a male was to be re-used. The second was to match only similar sized subjects; in all matches the size ratio of contenders (SVL smaller subject/SVL larger subject) was $0.94 \pm SE 0.006$ mm. The last convention was to run interspecific matches before pairing subjects with conspecifics.

Ethogram

The agonistic behaviors were divided into four general categories. The first was the species-unique head bob displays which were used by the observed species in a similar manner during aggressive encounters. The second was a group of postures that at times accompanied the head bob displays ("static display modifiers", sensu JENSSEN 1977, 1978), but which could be performed independently of the head bob displays. The third was a group of movements that at times accompanied the head bob displays ("dynamic display modifiers", sensu JENSSEN 1977, 1978), but which also could appear independently of the head bob displays. The fourth contains aggressive behaviors not directly associated with the head bob displays which we termed "actions" (e.g., chasing, biting). With two exceptions (stretch posture by *A. cooki* and absence of tail arching by *A. evermanni*), each of the observed static modifiers, dynamic modifiers, and actions was shared by the five species, suggesting their value for interspecific communication.

Below are short descriptions of the modifiers and actions. Within each of these categories, the behaviors are ordered from those most likely to be performed early in an encounter to those given during intense conventional displaying or escalated fighting.

Static Display Modifiers

Erected crest. The erectile crest is a dorsal fold of skin projecting up from the neck and usually along the length of the body. For *A. cooki*, *A. monensis*, *A. cristatellus*, and *A. gundlachi* the crest is quite pronounced; for *A. evermanni* it is minuscule. The crest erection is a prolonged response, apparently being under autonomic control.

Extended throat. This modifier is produced by the extension of the hyoid apparatus. Like the erected crest, it gives the lizard an enlarged appearance when viewed laterally.

Sagittal expansion. This modifier is effected by lateral compression of the rib cage. When viewed laterally, sagittal expansion also increases the apparent size of the lizard.

Orbed eyes. This modifier consists of widely opened eyelids and at times dilated pupils.

Opened mouth. In this posture the mouth is held partially opened, but never widely gaped. It may represent an intention behavior to bite.

Protruded tongue. The pointed end of the tongue is pushed forward beyond the anterior margin of the lips in this modifier.

Stretch posture. When viewed laterally, the lizard has its head and body aligned so that the vertebral column is approximately straight. Superficially the lizard appears to be stretching since it achieves maximum SVL in this posture. This posture was seen only in *A. cooki*.

Dynamic Display Modifiers

Dewlap pulse. This is an extension and retraction of the dewlap. When associated with head bobbing, dewlap pulses are performed at the beginning and/or end of a head bob display. They vary in numbers of repetitions and usually occur when a subject first detects its adversary.

Head roll. This is simply a raising and lowering of the head, usually performed just before the stereotyped head bob display. Amplitude of the head roll can vary, with exaggerated movements giving the impression of bowing.

Rocking. This modifier begins from a four-legged stance. The forelimbs are flexed and extended, producing an alternating anterior-posterior component to the body motion as well as a vertical component. This rocking movement was usually observed just before the head bob display. It was observed in all five species, but was most conspicuously performed by *A. cooki*.

Tail Movements. Tail movements were of two types: an upward arching of the tail with the tip held high and laterally moved tail wags. The latter graded from twitches to full swinging arcs. The tail wags were the most frequently performed, usually occurring independently of the head bob displays. The arched tail movement was an exception to the other modifiers in that it was only executed by those species of the *cristatellus* species group (WILLIAMS 1976), *A. cristatellus*, *A. gundlachi*, *A. cooki*, and *A. monensis*.

Actions

Approach. This is simply the approach of one or both lizards towards each other, but with no attempt to bite.

Attack: This is a rapid approach to within at least a body length of an opponent, with intent to bite or actually delivering a bite.

Jaw sparring. This occurs when the two males orient head-to-head, with mouths partially open. They alternate in a series of ritualized attempts to bite the jaw or rostrum of the opponent. One male swings its head toward the side of its opponent's head, while the other male parries the move by first evading the thrust and then countering with a cheek-to-cheek push. If this contact is substantial, one of the males may lose its grip on the perch.

Jaw locking. This occurs when both males lock jaws; one male bites the other's jaw, while the second male grips the first male's rostrum. When jaw locking occurs, it almost always follows jaw sparring. Jaw locking establishes dominance in those encounters which continue to escalated fighting.

Supplant. In this action one lizard moves to an occupied site and displaces the second lizard, but does not follow the supplanted individual. This is a criterion of established dominance.

Chase. This occurs when one lizard consistently follows another throughout the enclosure, driving the second lizard off of every perch it takes. This is a pronounced criterion of established dominance.

Results and Discussion

Hypothesis 1: Conspecific males interact more intensely than congenetic males. This hypothesis was supported (Fig. 1). The mean for pooled AIX values from conspecific matches (CO-CO and CR-CR) was 2.5 times greater than the mean AIX for pooled congenetic matches (CO-CR, CO-EV, CO-MO, CR-EV, and CR-GU); these mean values were $358 \pm SE 81.5$ and $113 \pm SE 28.7$, respectively, and they were significantly different ($p < 0.05$).

The exception to this hypothesis was the strong aggressive behavior occurring between *A. cooki* and *A. cristatellus*. The mean AIX for the CO-CR matches was $277 \pm SE 60.4$ (Fig. 1). When the CO-CR data were tested against the pooled conspecific matches (CO-CO and CR-CR), there was no significant difference ($p = 0.44$).

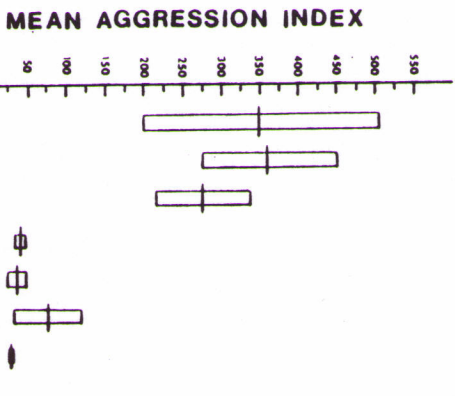


Fig. 1: Mean aggression index (AIX) for paired encounters of CO-CO (conspecific *cooki*), CR-CR (conspecific *cristatellus*), CO-CR (*cooki* vs. *cristatellus*), CO-EV (*cooki* vs. *evermanni*), CO-MO (*cooki* vs. *monensis*), CR-EV (*cristatellus* vs. *evermanni*), and CR-GU (*cristatellus* vs. *gundlachi*). The horizontal lines indicate mean AIX values and the ends of the bars represent the standard error of the mean.

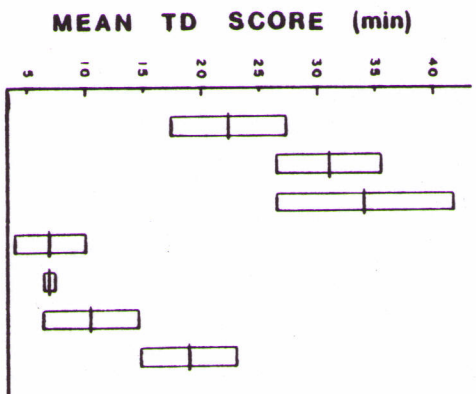


Fig. 2: Mean total duration (TD) of all rounds of a match from classes of paired encounters. See Fig. 1 legend for key to symbols.

Hypothesis 2: Syntopic and ecologically similar congeners interact more intensely than allopatric or allotopic congeners. This relationship was strongly supported. The syntopic competitors *A. cooki* and *A. cristatellus* interacted 5.5 times more aggressively than when these species were matched against the other non-syntopic congenetic species (Fig. 1). There was a highly significant difference ($p < 0.01$) when comparing the AIX data for CO-CR matches ($277 \pm SE 60.4$) with the pooled data from CO-EV, CO-MO, CR-EV, and CR-GU matches ($50 \pm SE 6.4$).

The second hypothesis continued to hold for solely sympatric species as well. *Anolis cristatellus* is syntopic with *A. cooki* in southwestern Puerto Rico and is allotopic with *A. evermanni* and *A. gundlachi* at higher elevations (e.g., in the Sierra de Luquillo). The mean AIX score for CO-CR matches ($277 \pm SE 60.4$) was significantly greater ($p < 0.01$) than the AIX mean for pooled CR-EV and CR-GU matches ($60 \pm SE 10.5$).

Being syntopic, however, does not necessarily dictate that congeners will exhibit intense competitive interference. For example, TALBOT (1979) observed almost no agonistic exchange between the similarly sized *Anolis humilis* and *Anolis limifrons* in areas where they were syntopic. The lack of evidence for interference competition in the *humilis-limifrons* study would suggest that the two species have diverged along some critical resource dimension to permit co-existence. Conversely, it may be hypothesized that the *cooki-cristatellus* contact is a recent phenomenon in which no mechanism for stable co-existence has yet evolved.

Hypothesis 3: Congeneric male aggression is not a function of similarity of species appearance. The data did not indicate that interspecific aggression

is caused or influenced by mistaken identity. *Anolis cooki* and *A. cristatellus*, the two species which interacted with almost the same intensity as conspecifics, were each matched against a "look-alike" congener (CO-MO and CR-GU) and against the distinctly different appearing *A. evermanni* (CO-EV and CR-EV). The mean AIX for pooled "look-alike" matches was $31 \pm SE 4.3$; the corresponding mean for the pooled CO-EV and CR-EV matches was $58 \pm SE 7.5$ (Fig. 1).

There was very little aggressive behavior exhibited between *A. cooki* and its closest relative, the allopatric *A. monensis* from Mona Island; likewise, *A. cristatellus* interacted very little with its allopatric sibling congener, *A. gundlachi*. In fact these two pairs of similar appearing congeners showed less agonistic responses than when *A. cooki* and *A. cristatellus* were each paired with the green colored *A. evermanni*. It is concluded that the high level of aggression evoked during the *cooki-cristatellus* encounters is not merely intraspecific aggression being elicited because each species is mis-identifying the other as a conspecific. Instead, the syntopic *A. cooki* and *A. cristatellus* are most likely recognizing each other as an immediate interspecific competitor.

The TD data (Fig. 2) were positively correlated with the AIX results (Pearson correlation coefficient: $N=45$, $r=0.75$, $p < 0.001$). In general, those classes of matches which elicited the most aggressive behavior also had the longest periods of total duration. It is noteworthy that the most prolonged encounters occurred in the *cooki-cristatellus* matches (Fig. 2, CO-CR).

The only obvious exception from the TD-AIX correlation was the CR-GU matches. Even though very little aggressive behavior was elicited (Fig. 1), these two congeners nevertheless oriented toward each other and occasionally exchanged low value signals for about a third of their hour-long matches.

The final observations involve the *cooki-cristatellus* matches. Since these were the only congeneric matches which reached escalated encounters, it is significant that *A. cristatellus* eventually dominated all matches. Both species contributed heavily to the AIX scores during the early rounds. However, *A. cristatellus* eventually exhibited chasing and supplanting which confirmed its domination over *A. cooki*. It was also the high values carried by these *cristatellus*-initiated supplantings and chases which permitted *A. cristatellus* to outscore *A. cooki*; *A. cristatellus* generated 67% of the CO-CR AIX mean (Table 3). The implication of these data for the field situation is that male *A. cristatellus* should displace *A. cooki* males from areas of mutually preferred microhabitat.

Table 3: % of total AIX points contributed to interspecific matches by *Anolis cooki* and *Anolis cristatellus*. Species abbreviations are as in Table 1

Principal species	Opposing species				
	CO	CR	MO	GU	EV
<i>cooki</i>	-	33 %	77 %	-	68 %
<i>cristatellus</i>	67 %	-	-	92 %	55 %

Summary

This study quantifies the intensity of agonistic interactions within and among an assemblage of Puerto Rican *Anolis* lizards. Aggressive behavior occurring during controlled lab-staged encounters was scored to yield a quantitative aggressive index (AIX) and total duration (TD) of overt interactions. It was found that two syntopic species, *A. cooki* and *A. cristatellus*, interacted as intensely interspecifically as when they were paired with their respective conspecifics. This level of interspecific aggression was 5.5 times as intense as when the two species were paired with either "look alike" congeners (*A. cooki* vs. *A. monensis* and *A. cristatellus* vs. *A. gundlachi*) or with the much different appearing *A. evermanni*. These data indicate that *A. cooki* and *A. cristatellus* males are capable of marked interspecific territoriality in the field, and that their agonistic response to each other is not based on mistaking one another as conspecifics. Furthermore, *A. cooki* was eventually dominated by similar sized *A. cristatellus* in all *cooki-cristatellus* matches, suggesting that in the field *A. cristatellus* will displace *A. cooki* from areas of microhabitat overlap.

Zusammenfassung

Diese Untersuchung quantifiziert agonistische Auseinandersetzungen (innerterritoriale und zwischenartliche) mehrerer *Anolis*-Arten aus Puerto Rico. Die aggressiven Verhaltensweisen in Käfigexperimenten wurden nach Intensität (Aggressive Index = AIX) und Gesamtdauer (Total Duration = TD) aufgeschlüsselt. Die syntropischen Arten *A. cooki* und *A. cristatellus* beeinflussen sich gegenseitig ebenso wie unter Artgenossen. Ihre zwischenartlichen Kämpfe waren 5,5mal intensiver als Kämpfe zwischen anderen *Anolis*-Arten (z. B. *A. cooki* gegen *A. monensis* und *A. cristatellus* gegen *A. gundlachi*), sowie zwischen diesen vorgenannten Arten und der anders aussehenden Art *A. evermanni*. Das zeigt, daß Männchen von *A. cooki* und *A. cristatellus* im Freiland tatsächlich ein starkes gegenseitiges Revierverhalten haben und sich nicht einfach verwechseln. Da *A. cooki* im Laufe der Experimente gleich große *A. cristatellus* besiegte, wird diese Art wohl in Biotopen, wo beide vorkommen, verdrängt.

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