

Competitive Interference between the Puerto Rican Lizards, *Anolis cooki* and *A. cristatellus*

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Anolis cooki and *Anolis cristatellus* are sympatric lizards engaged in intense interspecific competition. We have identified and analyzed a critical area of competitive interference by measuring various niche dimensions and behavioral interactions under natural conditions. Four study areas of similar habitat composition were established within 5 km of each other: one allopatric for *A. cooki*, one allopatric for *A. cristatellus* and two sympatric areas. The variables of cloacal temperatures, perch height, perch diameter and habitat type were compared between lizards in and among the study areas. No significant differences in the variables were found between the sexes of a species or between species on the allopatric areas, nor were there differences between sympatric and allopatric *A. cristatellus*. Sympatric *A. cooki* males and females, however, exhibited a significant divergence from their allopatric counterparts by utilizing standing dead vegetation and small bushes rather than larger and more complex microhabitat. This shift was most likely in response to competitive interference from *A. cristatellus*.

Except for sympatric *A. cooki*, adult males in both the allopatric and sympatric conditions showed a significant and positive correlation between snout-vent lengths and the relative complexity and height of their immediate microhabitat. This suggests that there is intraspecific competition among males, with the larger conspecific males controlling the taller and more complex habitat. Thus when the sympatric male *A. cooki* occupy small types of microhabitat, they are only likely to encounter the smaller size classes of *A. cristatellus* males.

Intruder-release experiments showed that encounters between male *A. cooki* and *A. cristatellus* were very aggressive, similar in intensity to conspecific interactions. Less than one out of two times were resident *A. cooki* able to evict *A. cristatellus* intruders of similar size. Thus by occupying smaller habitat types, sympatric *A. cooki* appears to decrease the likelihood of interacting with large *A. cristatellus*, against whom they would have little chance of holding a disputed territory. From current evidence, *A. cooki* is under competitive pressure from the more ubiquitous *A. cristatellus* and has no apparent refugium.

SCHOENER (1977) has noted that little is known about interference competition among reptiles at either the individual or population level, and even less is known at the interspecific level. Part of the problem is that there have been so few instances found where species are still engaged in intense behavioral interactions. This period of open contention is probably of short duration, and most likely occurs during initial interspecific contact before divergence or exclusion has taken place. In this paper we present a unique two-species system in which the lizards, *Anolis cooki* and *A. cristatellus*, demonstrate vigorous interspecific aggression. By examining the nature of these behavioral interactions and measuring various niche dimen-

sions under natural conditions, we have identified and analyzed a critical area of competitive interference.

A. cooki and *A. cristatellus* are medium sized anoles which are osteologically indistinguishable (Pregill, 1981) and of very similar overt appearance, being only recently recognized as separate species (Gorman, Thomas and Atkins, 1968). Both can be classified as "trunk-ground" anoles (*sensu* Rand and Williams, 1969), but they have very different distributions. *A. cooki* is restricted to a small area in the lowlands of extreme southwestern Puerto Rico, whereas *A. cristatellus* is found island-wide from sea level to mid-elevations in forest and open habitats (Heatwole, 1976; Williams, 1972). Almost the

entire distribution of *A. cooki* (Cabo Rojo peninsula in the west, in and about the Reserva Forestal de Guanica in the east, and the islet of Caya de Muertos) is sympatric with *A. cristatellus*. Observers have speculated that the two species are not in a state of stable equilibrium. Its diminutive range literally backed up to the ocean, *A. cooki* may well be slipping toward extinction (Williams, 1972). Our observations could have added significance establishing a vantage point in time from which the process of natural extinction may be viewed.

MATERIALS AND METHODS

Our study was conducted on the peninsular area of Cabo Rojo during August and Sept., 1980 and Jan., 1982. We established four study sites which shared a similar vegetational configuration: one allopatric for *A. cooki*, one allopatric for *A. cristatellus* and two sympatric areas (Fig. 1). Data from the two sympatric areas were pooled.

The sites were sandy areas sparsely covered with short grasses and low succulents (e.g., *Suriana maritima*). Spaced within this habitat were clumps of bushy vegetation (e.g., *Colubrina arborescens*, *Coccoloba uvifera*), trees of various ages (e.g., *Canella winteriana*, *Acacia* spp., *Avicennia nitida*, *Laguncularia racemosa*, *Conocarpus erectus*) and occasional fence posts and standing dead vegetation.

A vegetation analysis was made of each site to compare the microhabitat available to the lizards. As the plant species per se did not appear to be an important criterion for perch selection by the lizards, we characterized the sites according to vegetational physiognomy. Six classes of microhabitat structure, called "habitat types," were used: 1) fence posts or dead snags, 2) low shrubs (≤ 2 m high), 3) large shrubs (> 2 m high), 4) small trees (≤ 5 m high), 5) large trees (> 5 m high), and 6) open ground (bare soil or low ground cover). The first five classes were used in statistical analyses and were treated as continuous variables because they approximate a progression of increasing height and habitat complexity.

A stratified random design was used in which a longitudinal transect was laid down the length of each study site. The transect was divided into 10 m segments; within each segment a randomly determined point was used to run secondary transects across the width of the study site at a right angle to the longitudinal transect. These

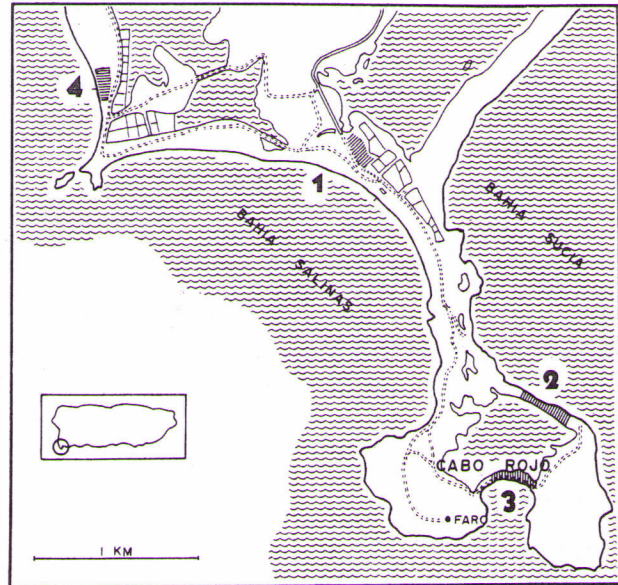


Fig. 1. The peninsula of Cabo Rojo, Puerto Rico. Two sympatric (1, 2), one allopatric *Anolis cooki* (3) and one allopatric *A. cristatellus* (4) study sites (shaded areas), dirt roads (dashed lines) and drying ponds of a local salt works (irregular polygons) are depicted.

secondary transects were paced and the linear distances which intercepted each habitat type were recorded. The number of transects, the total length of the transects, and the approximate area of each study site are as follows: allopatric *A. cooki*—26,793 m, and 7,930 m²; sympatric—19,1089 m, 10,890 m²; and allopatric *A. cristatellus*—12,843 m, 8,430 m². Using the proportions of habitat types on each transect, we calculated the variance of each available habitat type within and among study areas.

To obtain habitat data for the lizards, all clumps of vegetation (habitat types 1–5) were methodically searched, with an attempt to catch all lizards within a vegetation clump. Collection was primarily by noosing, but occasionally hand capture was employed for some smaller lizards. The following data were recorded for each captured lizard: 1) study site, 2) date, 3) time, 4) species, 5) sex, 6) snout-vent length (SVL), 7) body weight (nearest 0.01 g), 8) tail length, 9) perch height (nearest 0.1 m), 10) perch diameter (nearest 0.5 cm), 11) habitat type and 12) cloacal temperature (nearest 0.1 C). Cloacal temperatures were determined immediately upon capture using a Schultheis thermometer, and body weights were taken using an Ohaus Dial-A-Gram balance. Lizards were given a paint mark and returned as soon as possible to the point of capture.

TABLE 1. MEAN AND STANDARD DEVIATION OF THE MEAN FOR HABITAT TYPE PERCENTAGE FROM ALLOPATRIC *A. cooki* (ACO), SYMPATRIC (CO-CR) AND ALLOPATRIC *A. cristatellus* (ACR) STUDY AREAS. The proportion of each habitat type was compared among study areas for significant differences, using the Student-Newman-Keuls test after the data underwent arcsin transformation. Sample size (N) represents number of transects.

Habitat type	ACO (N = 26)		CO-CR (N = 19)		ACR (N = 12)
1	2.7 ± 10.99		4.1 ± 5.76		1.1 ± 2.30
			*		
2	16.4 ± 11.87	*	35.8 ± 24.50		43.2 ± 21.36
			*		
3	29.3 ± 20.13		30.8 ± 19.95	*	11.6 ± 11.80
			*		
4	33.2 ± 25.30	*	11.4 ± 9.82		14.4 ± 12.50
5	19.4 ± 21.31		16.9 ± 26.80		28.7 ± 15.08

* Significant difference, $P < 0.05$.

Twenty intruder-release trials were conducted in which a male *A. cristatellus* of known SVL was released into the territory of a male *A. cooki*. The intruder was released, without handling, from an opaque jar onto a prominent branch or trunk within the plant complex used by the resident. The release site was always 1–3 m from the resident. The observer then retreated to watch the resulting interaction through binoculars, and to record the observations into a tape recorder. Duration for each trial was subject determined, and ended when one lizard was either expelled from the territory or showed consistent escape behavior, or when both lizards exhibited extended non-aggressive co-existence. After each encounter the *A. cooki* resident was caught to record his SVL. When releases were made on the allopatric *A. cooki* study site, the intruding *A. cristatellus* were recaptured and each returned to its original territory. All trials involved different subjects.

The kinds of data recorded for the intruder-release trials were: 1) study area, 2) resident's habitat type, 3) SVLs of lizard pairs, 4) duration of encounter, 5) a record of the various behaviors performed by each lizard during a release, and 6) the eventual dominant of the encounter (if any) as determined by continued harassment and displacement. An encounter could be scored as "co-existence" if the lizards retreated from one another for more than 10 min with no further interaction. The intensity of the encounter was derived by using a modified version of the aggression index employed by Ortiz and Jense-

sen (1982: Table 2). We ranked the intensity of the encounters into four categories according to the most aggressive behaviors performed. These categories were: 1) "low-level ritualized aggression" which proceeded no further than dewlap pulsing and stereotyped head bob displays, 2) "moderate-level ritualized aggression" which included the previous behaviors plus postural changes (e.g., erect crest, sagittal expansion), indicating mounting arousal, 3) "high-level ritualized aggression" which included the previous behaviors plus close approaches and high arousal behaviors such as opened mouths and 4) "escalated fighting," involving physical contact.

Quantitative analyses were performed on an IBM 3081 computer using two software packages (Statistical Analysis System, Barr et al., 1979; Biomedical Computer Programs, Dixon, 1975).

RESULTS

Study area.—The same microhabitat types in similar proportions were available to the lizards on the three study sites. Bare ground or areas containing only low ground cover (non-anole substrate) composed 40, 41 and 35% of the allopatric *A. cooki* (ACO), sympatric (CO-CR) and allopatric *A. cristatellus* (ACR) study sites, respectively. The remaining habitat was partitioned between five types of habitat. From one transect to the next, the proportion of each habitat type varied considerably within a given

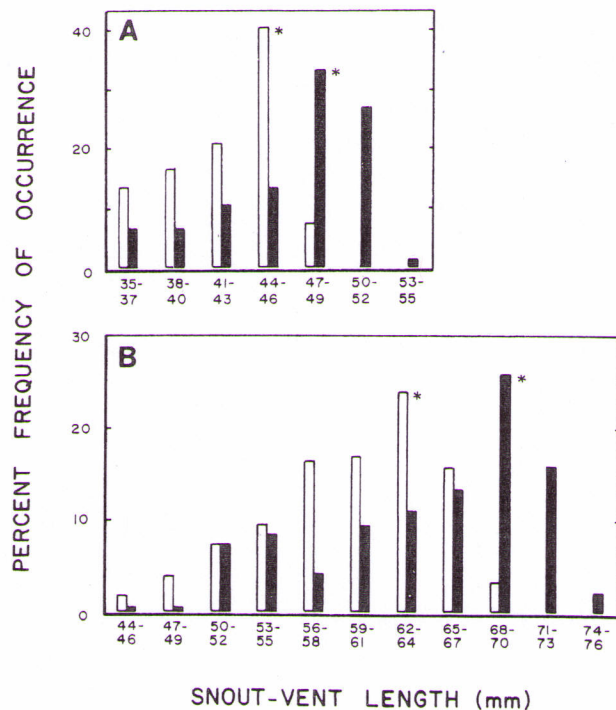


Fig. 2. A) Frequency distribution for 66 *Anolis cooki* (open bars) and 74 *A. cristatellus* (black bars) adult females. Mean SVL and body weight for most common size class (asterisk) are: *A. cooki*—44.9 mm, 2.41 g; *A. cristatellus*—48.4 mm, 3.09 g.

B) Frequency distribution for 146 *A. cooki* (open bars) and 162 *A. cristatellus* (black bars) adult males. Mean SVL and body weight for most common size class (asterisk) are: *A. cooki*—63.1 mm, 6.76 g; *A. cristatellus*—68.8 mm, 9.05 g.

study area (Table 1), with coefficients of variation (SD/mean \times 100) ranging from 49–403%.

The ACO and ACR areas were about equally divided between bushy plant growth (47 and 57%, respectively) and trees (51 and 43%, respectively). The sympatric area tended to have more of its plant growth in small and large bushes (69%) than in small and large trees (25%). When statistically comparing the proportion of any one habitat type between the study areas, six of the possible 15 comparisons were significantly different (Table 1).

Morphological characteristics.—Both *A. cooki* and *A. cristatellus* are sexually size dimorphic (Fig. 2). Using the most frequent adult size class, *A. cooki* and *A. cristatellus* males are 1.4 times as long and about three times as heavy as their respective females. *Anolis cristatellus* tends to be larger than *A. cooki* (Fig. 2), and for a given SVL, *A. cristatellus* is heavier than *A. cooki*. Moderate to large sized male *A. cristatellus* averaged about

10% heavier than male *A. cooki* of equal length, as did female *A. cristatellus* when compared with female *A. cooki* of equal length. The mean weight of male *A. cristatellus* for their most common size class was 30% greater than that of the most common size class of *A. cooki* males. The same interspecific comparison between females showed *A. cristatellus* to be 28% heavier than *A. cooki*.

Climatic habitat.—Based on hourly intervals, there were no significant differences (Mann-Whitney U test) in cloacal temperatures between *A. cooki* (N = 201) and *A. cristatellus* (N = 216) when comparing between sites of allopatry or when comparing within the sympatric sites for the Jan. and Aug. data. While the cloacal temperatures of *A. cooki* averaged 0.3 C higher for any given hour than those of *A. cristatellus*, maximum values for hourly samples ranged equally high for *A. cristatellus* (up to 36.4 C).

Structural habitat.—On their allopatric study areas, there were no significant intraspecific differences between males and females of either *A. cooki* or *A. cristatellus* with regard to perch height, perch diameter and habitat type, and there were no significant interspecific differences when comparing these habitat variables between the species on their allopatric areas (Mann-Whitney U Test; Fig. 3). This similar interspecific pattern of microhabitat utilization existed in spite of significant differences in the availability of habitat types 2, 3 and 4 (Table 1). Furthermore, male and female *A. cristatellus* maintained the same perch characteristics when comparing between their allopatric and sympatric areas. This was not the case, however, for *A. cooki*. On the sympatric area, *A. cooki* males and females were perching on significantly thinner vegetation of smaller growth form than allopatric *A. cooki*. Although sympatric and allopatric *A. cooki* males perched about 0.75 m above the ground, the sympatric *A. cooki* females were occupying significantly lower perch sites than their counterparts on the allopatric area (Mann-Whitney U Test; Fig. 3a).

The distribution of habitat types utilized by male and female *A. cristatellus* did not change much when comparing the allopatric and sympatric conditions (Fig. 4). In contrast to the *A. cristatellus* data, the histograms of Fig. 4 for *A. cooki* show that there was a dramatic shift in habitat utilization for both sexes when comparing allopatric and sympatric areas. The sym-

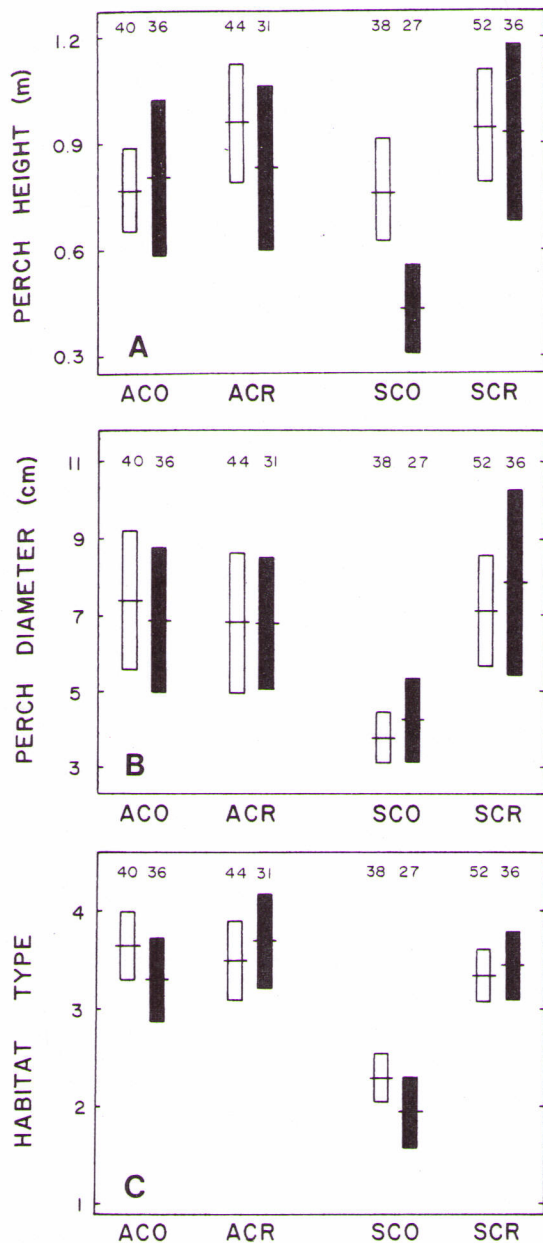


Fig. 3. A) Descriptive statistics for perch height data based on Jan. samples for adult allopatric *Anolis cooki* (ACO), allopatric *A. cristatellus* (ACR), sympatric *A. cooki* (SCO) and sympatric *A. cristatellus* (SCR). Male data are represented by open bars and females by black bars. Horizontal lines give means and ends of bars are 95% confidence limits of means. Sample sizes appear over bars.

B) Descriptive statistics for perch diameter data based on Jan. samples.

C) Descriptive statistics for habitat type data based on Jan. samples, where 1 = dead snags and fence posts, 2 = small bushes, 3 = large bushes and 4 = small trees.

patric *A. cooki* distributions are skewed strongly toward dead snags and small bushes.

Discriminant analysis.—A stepwise discriminant analysis (Biomedical Computer Programs, P7M)

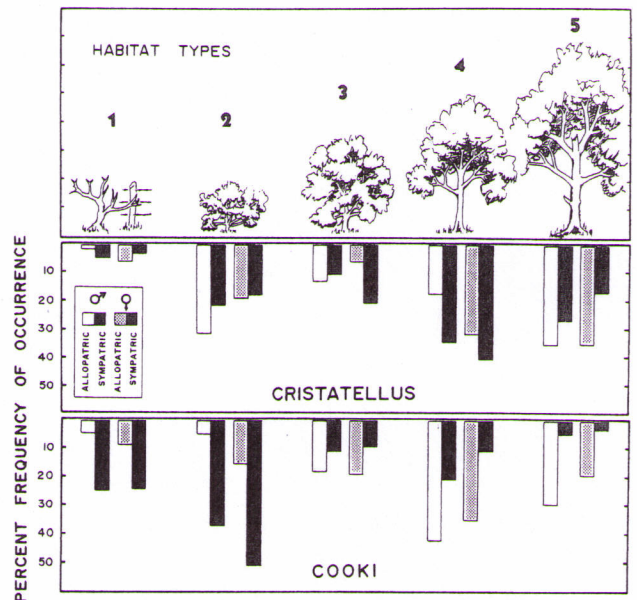


Fig. 4. Frequency distribution among habitat types for 340 adult *Anolis cooki* and 282 adult *A. cristatellus* based on Aug. and Jan. samples. Open and stippled bars give male and female allopatric data, respectively, and black bars show sympatric values for each sex.

was run using four variables (cloacal temperature, perch height, perch diameter and habitat type) to distinguish relative niche differences among eight groups of lizards: allopatric *A. cooki* males and females (ACOM, ACOF), allopatric *A. cristatellus* males and females (ACRM, ACRF), sympatric *A. cooki* males and females (SCOM, SCOF) and sympatric *A. cristatellus* males and females (SCRM, SCRF). The program evaluated how much each of the four variables explained the observed differences among the eight lizard groups, and presented the differences as a spatial relationship (Fig. 5). To check the adequacy of the discriminant functions, the program used the discriminating variables to classify each of the observations to see how many of them could be correctly classified into their original group designation.

Habitat type was the single best discriminating variable, and the variable, cloacal temperature, best improved the discrimination in combination with habitat type. Perch height and perch diameter did not significantly contribute any further to the discrimination and were not used by the program. The two canonical variables (discriminant functions) of Fig. 5, incorporating habitat type and cloacal temperature, explained 69 and 31% of the group separation, respectively (eigenvalues = .258, .115; canonical correlations = .453, .321, respectively).

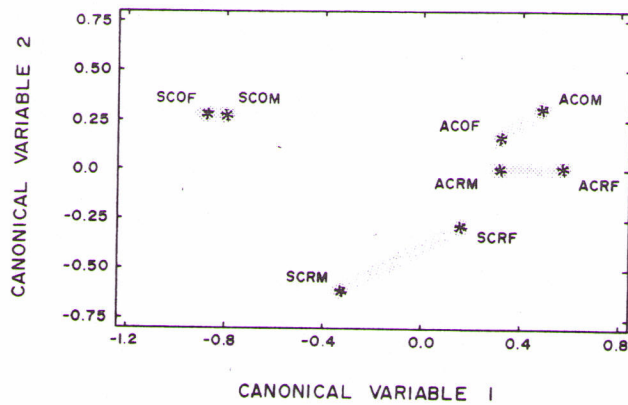


Fig. 5. Graphic presentation of stepwise discriminant analysis using January data for cloacal temperatures, perch height, perch diameter, and habitat type from allopatric *Anolis cooki* males and females (ACOM, ACOF), allopatric *A. cristatellus* males and females (ACRM, ACRF), sympatric *A. cooki* males and females (SCOM, SCOF) and sympatric *A. cristatellus* males and females (SCRM, SCRf). Stars denote mean group centroids for each of the eight lizard groups.

For each lizard group, a centroid was calculated which represented the lizard group mean for the two discriminating functions. Figure 5 shows that all the allopatric centroids were tightly clustered, and the F-matrix (Table 2) found no significant differences between any pair of allopatric group means (centroids). The most divergent centroids were those of sympatric *A. cooki* males and females. They were not significantly different from each other, but both differed significantly from all other group mean comparisons (Table 2).

Even though most of the sympatric group means significantly differed from the allopatric group means (Table 2), all eight group distributions, nevertheless, broadly overlapped one

another, indicating that no one class of lizards was ecologically distinct from any of the others. This overlap was reflected by the poor discrimination among groups, where the program was only able to correctly classify an average of 22% of the observations. When the sexes were pooled, the resulting classification matrix correctly classified 31% of the allopatric *A. cooki*, 35% of the allopatric *A. cristatellus*, 37% of the sympatric *A. cristatellus* and 67% of the sympatric *A. cooki*. The two fold success rate in classifying the last group reflects its uniqueness from the other lizard groups; this is graphically depicted in Figure 5 by the noticeable displacement of sympatric *A. cooki* away from the other lizard groups.

Habitat type.—Because habitat type was the single best variable for showing divergence, overlap between the eight lizard groups was determined using habitat type as a niche dimension. Overlap was calculated from an index used by Schoener (1968):

$$D = 1 - \frac{1}{2} \sum_{i=1}^n |P_{x,i} - P_{y,i}|$$

where $P_{x,i}$ and $P_{y,i}$ are frequencies for classes x and y , respectively, for the i th category. The index, D , ranges from zero (no overlap) to one (complete overlap).

The results show that the greatest overlap occurred between male and female conspecifics within study areas; these four indices averaged .86 (.80–.89). Overlap values did not decrease much when comparing within and among the sexes of allopatric with sympatric *A. cristatellus*

TABLE 2. F VALUES RESULTING FROM MANOVA APPROXIMATE F-TESTS COMPARING THE MEAN VECTORS OF EACH PAIR OF LIZARD GROUPS (DEGREES OF FREEDOM = 2,255; * = $P < .05$, ** = $P < .01$) ALLOPATRIC (A) AND SYMPATRIC (S) *Anolis cooki* (CO) AND *A. cristatellus* (CR) MALES (M) AND FEMALES (F).

Lizard groups	Lizard groups						
	ACOM	ACOF	ACRM	ACRF	SCOM	SCOF	SCRM
ACOF	0.37						
ACRM	1.15	0.26					
ACRF	1.24	1.00	0.66				
SCOM	12.93**	8.78**	10.93**	14.33**			
SCOF	13.25**	9.46**	11.58**	14.93**			
SCRM	14.84**	9.39**	8.78**	9.52**	0.12		
SCRf	3.52*	1.67	0.89	1.55	8.34**	9.92**	
						9.27**	3.10*

($\bar{x} = .78$; .68–.85), or when comparing within and among the sexes of allopatric *A. cooki* with sympatric *A. cristatellus* ($\bar{x} = .79$; .75–.84). However, a marked drop in indice values were found when sympatric *A. cooki* sexes were compared with sympatric *A. cristatellus* sexes ($\bar{x} = .54$; .49–.59); and especially when comparing allopatric *A. cooki* sexes with its sympatric conspecific sexes ($\bar{x} = .44$; .42–.49). The overlap values emphasize how similar the structural habitat preference is between allopatric *A. cooki* and *A. cristatellus*, and how much *A. cooki* diverges from its allopatric condition when sympatric with *A. cristatellus*.

Habitat type was also examined for covariance with perch height, perch diameter, and SVL (Spearman correlation procedure, SAS, Barr et al., 1979). Perch height was positively and significantly correlated with habitat type for six of the eight lizard groups (male and female allopatric *A. cooki* were the exceptions). This indicates that the lizards tend to perch in the upper portion of their available microhabitat: the larger the vegetational configuration, the higher the absolute perch height.

Perch diameter was also positively correlated with habitat type (except for male and female sympatric *A. cooki*). Thus when associated with larger sizes vegetation, the lizards tended to select the trunk or main branches. The failure of sympatric *A. cooki* to show this correlation may reflect their displacement into thin-branched, low vegetation.

SVL was also positively correlated with habitat type for some classes of lizards. Although the results for the four female groups were all non-significant, they were significant for most male groups ($P = .05$, .0002, .0005, .47 for ACOM, ACRM, SCRM, SCOM, respectively). Only sympatric *A. cooki* males failed to show a significant and positive relationship between SVL and habitat type; again, this is possibly the result of all male size classes of *A. cooki* being associated primarily with small habitat types.

Intruder-release experiment.—In the 20 experimental trials male *A. cristatellus* ($\bar{x} = 65.9 \pm \text{SE } 0.7$ mm SVL) were released singly into territories of male *A. cooki* ($\bar{x} = 65.3 \pm \text{SE } 0.5$ mm SVL). Thirteen of the intruders were slightly larger than the residents by an average of 2.9 mm SVL (SE 0.5), and in seven trials they were smaller by an average of 4.2 mm SVL (SE 0.7). All interactions resulted in considerable aggression, with each trial scoring 3 or 4 ($\bar{x} = 3.7 \pm$

SE 0.1) on our aggressive ranking system. In half of the trials, the introductions stabilized to co-existence, where neither lizard evicted the other. In the other 10 trials, *A. cooki* evicted the *A. cristatellus* intruder nine times, while relinquishing its territory once. *A. cooki* was the smaller lizard in seven of the nine successful defenses. Overall, the success rate of *A. cooki* driving off *A. cristatellus* was 45%.

In the 15 trials where the interaction reached escalated fighting (score of 4), only one involved jaw locking, a tactic which would put the lighter *A. cooki* at a disadvantage. Although jaw locking is commonly observed in conspecific male fighting, *A. cooki* seemed to avoid this maneuver when interacting with *A. cristatellus*. Instead, *A. cooki* frequently performed lunging-biting attacks without prolonged mouth holds in encounters with *A. cristatellus*. The one trial where jaw locking occurred, the heavier *A. cristatellus* threw the *A. cooki* out of a tree three times, while each time retaining his own hold on the perch.

It is likely that experience may affect interactions between *A. cooki* and *A. cristatellus*. The study site allopatric for *A. cooki* was the only place where interspecific jaw sparring and jaw locking occurred. One or both of these behaviors were seen in three of the five trials conducted on the allopatric *A. cooki* study site. The durations of the allopatric encounters were also significantly longer than those on the sympatric sites ($\bar{x} = 38.2 \pm \text{SE } 10.6$ min vs $\bar{x} = 12.8 \pm \text{SE } 2.5$ min, respectively; Mann-Whitney U test, $P < 0.05$).

All of the released *A. cristatellus* provoked a high level of aggressive response from resident *A. cooki*. Only 25% of the introductions fell short of escalated fighting, but even in these there was intense displaying in which the lizards approached within several body lengths of each other and postured aggressively with mouths open and tongues out.

DISCUSSION

In complex anoline faunas, the occurrence of interspecific competition seems likely. On close inspection, however, it has been found that anoles diverge along a number of niche dimensions. Some basic examples are climatic habitat (differing mean body temperature as proposed by Ruibal, 1961), structural habitat (differing perch height and diameter as proposed by Rand, 1964), and food resource (differing prey size with covarying lizard mouth and body size as

proposed by Schoener, 1968). These concepts have been widely applied (Schoener, 1977).

Typically, one or more of these measured niche variables have been found to overlap minimally when comparing sympatric congeners, suggesting that the species are partitioning the habitat, resulting in decreased interspecific competition. In areas where sympatry has been longstanding, discrete differences are observed in one or more niche variables. Schoener (1975) proposed the following niche hierarchy of effectiveness for limiting competitive interactions: sympatric anoles diverging in their climatic habitat are least likely to compete; species in the same climatic habitat diverge in their structural habitat; species in the same climatic and structural habitat diverge in body size and eat prey of different sizes. Given no distinct divergences in the above niche dimensions, maximum competitive interactions can be expected, especially if it is for space (Schoener, 1982).

Taking the above factors in turn, let us analyze the present situation for *A. cooki* and its sympatric congener, *A. cristatellus*. Their climatic habitats (as measured by body temperatures) are not distinctly different. Although Lister (1976) found significantly different cloacal temperatures (C) between sympatric *A. cooki* and *A. cristatellus* near Guanica in Feb. (\bar{x} = 32.7, CO; 30.6, CR), our data for the same diurnal interval (1100–1400) at Cabo Rojo in January averaged 32.2 C (CO) and 31.2 C (CR), and were not significantly different. Furthermore, for any given hourly interval, there were no significant differences between allopatric *A. cooki* and allopatric *A. cristatellus*, nor between these species on the sympatric area. Likewise, Huey and Webster (1976) reported no significant differences in 528 cloacal temperatures of *A. cooki* and *A. cristatellus* on various sympatric sites in July.

Structural habitat utilization did not differ on the allopatric areas. Both sexes within each species as well as among species showed no significant differences in perch height, perch diameter, or habitat type. Only on the sympatric study site was one species, *A. cooki*, found to occupy a different range of habitat types from its allopatric pattern, having shifted predominantly to small, simple vegetational configurations. These latter habitat types were available on both allopatric sites, yet both species exhibited little preference for them. Since the Cabo Rojo *A. cooki* represent a single population, it is improbable that the divergence in habitat type

by *A. cooki* when sympatric with *A. cristatellus* reflects a novel preference, but more likely it is the result of current competitive interference.

Body length was similar between the species, a condition which would enhance the intensity of competition (Schoener, 1975). The SVL ratio of *A. cristatellus* to *A. cooki* for males and females were both less than 1.1. Schoener (1970) also reported no evidence of divergence in body or head size between the species when comparing among allopatric and sympatric areas. These facts led Williams (1972) to suspect that the ecological contact of the two species has been relatively recent.

Coupled with the above inference for competitive exclusion are behavioral data that *A. cooki* and *A. cristatellus* are engaged in interspecific territoriality. Ortiz and Jenssen (1982) have shown in lab-staged encounters that males of these species were as aggressive interspecifically as they were in conspecific matches. The aggressive intensity between *A. cooki* and *A. cristatellus* was 5.5 times greater than that measured 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*. In all their matches, *A. cristatellus* eventually dominated *A. cooki*.

In the field, our intruder-release experiment verified the intensity of the lab-staged *A. cooki* vs *A. cristatellus* interactions. We also found that even though *A. cooki* were subordinated by *A. cristatellus* in all lab-held matches, *A. cooki* did manage to expel 45% of the *A. cristatellus* intruders in the field encounters. However, to retain a quality territory in the face of periodic challenges by *A. cristatellus*, this success rate is not particularly high, especially when considering that we attempted to match SVLs of the intruder and the resident. Given the size and weight distributions of the two species, there is a strong likelihood that a resident *A. cooki* would be over-matched by many potential *A. cristatellus* intruders. By retreating to smaller habitat types, *A. cooki* increases its competitive advantage since our data show the larger *A. cristatellus* do not frequent the smaller habitat types (see also Kiester et al., 1975). Thus, the *A. cristatellus* intruding into the small clumps of vegetation occupied by sympatric *A. cooki* would tend to be small adult males which had been pushed into the smaller habitat types by larger males of their species.

The next factor to consider is whether *A. cooki*

has special adaptations to maintain a refugium in its sympatric condition with *A. cristatellus*. The smaller habitat types provide less extensive shade than the large bushes and trees; hence ambient temperatures tend to be slightly higher. However, *A. cooki* does not appear to be better adapted to xeric conditions than the locally adapted/acclimated *A. cristatellus*. Huey and Webster (1976) found that *A. cooki* and *A. cristatellus* both had the same critical thermal maximum (38.9 C) and similar preferred body temperatures (30.6 C for *A. cooki* and 29.6 C for *A. cristatellus*); both of these preferred temperatures are exceeded during most of the day. In a comparative study of 11 species of *Anolis*, Hillman and Gorman (1977) showed that *A. cooki* and *A. cristatellus* from Cabo Rojo had some of the lowest water loss rates and highest critical activity points of the group. Of interest is that the Cabo Rojo *A. cristatellus* survived much better during extended desiccation than conspecifics from a mesic region, showing its obvious adaptation or acclimation to the Cabo Rojo climate. If the xeric habitat of ancestral *A. cooki* was a barrier that minimized contact with potential competitors, it is not currently effective against populations of Cabo Rojo *A. cristatellus*.

Past studies dealing with sympatric congeners foresaw the promise of uncovering the mode of interspecific competition, only to find little or no direct interspecific effects (e.g., Talbot, 1979; Tinkle, 1982); it appears that most of these systems have developed mechanisms for stable coexistence. The situation between *A. cooki* and *A. cristatellus*, however, appears to be in a dynamic phase, and fits the "shared-preference" model of habitat selection theory (see review of Pimm and Pimm, 1982). In this case one species is dominant and can physically exclude the subordinate species from the mutually preferred habitat patch; coexistence balances on the subordinate's ability to be more efficient in that part of the habitat matrix from which the dominant finds it unprofitable to exclude the subordinate. Whether *A. cooki* can persist in its sympatric association with *A. cristatellus* will decide the outcome of this natural experiment. Based on present data, we concur with Williams (1972) that the existence of *A. cooki* is tenuous and may be a model of a species about to submerge.

ACKNOWLEDGMENTS

We are indebted to Peter Ortiz (Department of Natural Resources, Puerto Rico) for his in-

valuable help making logistical arrangements and assistance in the field; Sean Furniss (US Fish and Wildlife Refuge manager, Boqueron, Puerto Rico) for his aid in locating housing and storing equipment; Carter Johnson for suggesting the vegetation analysis methods; and Gary Nunn who assisted with the computer analyses. We are also grateful to Robin Andrews, Ernest Williams and Raymond Huey for their valuable critiques of the manuscript. Financial assistance was provided by a grant from the Friends of the National Zoo, Washington, DC; an Education Foundation grant from Virginia Polytechnic Institute and State University; and the Department of Natural Resources, Scientific Research Area, Puerto Rico.

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Copeia, 1984(4), pp. 862-868

Incubation, Larval Growth, and Embryonic and Larval Survivorship of Smallmouth Salamanders (*Ambystoma texanum*) in Streams

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Selected aspects of the biology of premetamorphic stages of stream-breeding *A. texanum* were studied for four years in central Kentucky. Incubation periods varied from 29 to 82 days and were inversely related to the seasonal time of oviposition. Embryonic survivorship to hatching was 80% (1980) and 84% (1981). Mortality was greatest in eggs deposited at the beginning of the breeding season. Most embryos hatched during a two to three week period in April, and metamorphosis occurred 7 to 9 weeks later at 0.59 (1980), 0.57 (1981), and 0.73 (1982) g. Growth until the first observance of metamorphs was exponential. Annual survivorship until the first observance of metamorphs was 6% or less. Age-specific mortality was more or less constant through the mid-larval period, but tended to increase thereafter. Stream drying, flooding and predation were important sources of larval mortality.

THE physical and chemical properties of lentic and lotic habitats are very different (Hynes, 1970) and aquatic-breeding urodeles have evolved different adaptive strategies in response to these environments (Valentine and Dennis, 1964; Salthe, 1969; Salthe and Mecham, 1974). Pond strategists typically attach masses of small, heavily-pigmented eggs to vegetation or detritus. The larvae have balancers, prominent gills and dorsal fins, delayed limb development, rapid growth potentials and short

larval periods. In contrast, stream strategists have smaller clutches and larger, unpigmented eggs that are attached singly to the undersides of objects. The larvae have reduced gills and dorsal fins, slower growth potentials, and, in many instances, longer larval periods. Hatchlings lack balancers and have functional limbs. These patterns are only general and numerous exceptions exist (Salthe and Mecham, 1974).

Most aquatic-breeding urodeles are either strict pond or strict stream breeders. A few