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**Structural Habitat and Ecological
Overlap of the Puerto Rican Lizards
Anolis cristatellus and *A. cooki*, with
Comments on the Long-term Survival
and Conservation of *A. cooki***

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Anolis cristatellus and *A. cooki* are morphologically and ecologically similar lizards native to the dry forest region of southwestern Puerto Rico. Both species are osteologically identical (Pregill, 1981) but can be separated by some morphological characters and karyotypic differences (Gorman et al., 1968; 1980; 1983). Both species are medium sized and are classified as trunk-ground ecomorphs (Williams, 1983), although they differ in their distribution, abundance, and biotic interactions.

While *A. cristatellus* is widespread and abundant throughout Puerto Rico, *A. cooki* is restricted to a limited number of coastal scrub habitat patches within 1 km of the coast in the extreme southwestern portion of the island (Marcellini et al., 1985; Jenssen, 1990). Although small allopatric populations of *A. cooki* have been documented (Jenssen et al., 1984; Marcellini et al., 1985), almost the entire distribution of this species overlaps that of *A. cristatellus*. *Anolis cooki* populations may be declining towards eventual extinction (Williams, 1972) and the survival of the species requires immediate and continual attention (Ortiz, 1990).

In sympatry, similar species should differ along at least one of their primary resource axes (structural habitat, thermal habitat, or prey size distribution) in order to coexist in stable equilibrium (Schoener and Schoener, 1971a; b). In response to competitive interactions, *Anolis* lizards alter selection of perches and perch positions (e.g., Jenssen, 1973; Schoener, 1975; Lister, 1976). Shifts in structural habitat among sympatric species have been documented in response to seasonal variation in food availability, reproductive condition (Lister, 1981), and the occurrence of direct competitors (Salzburg, 1984; Losos et al., 1993; Losos and Spiller, 1999). Jenssen et al. (1984) found that where *A. cristatellus* and *A. cooki* are allopatric, their structural habitats are not significantly different. However, lab-staged aggressive encounters between males of these species were intense and indicated that *A. cristatellus* was more dominant (Ortiz and Jenssen, 1982). The inference was that where the two species were sympatric, *A. cristatellus* could displace *A. cooki* to less desirable microhabitats. This prediction was supported by field observations and release experiments (Jenssen et al., 1984).

If *A. cooki* is in a tenuous existence, it is important to re-evaluate its habitat use in the presence of *A. cristatellus*, a direct and apparently superior competitor. My primary objectives were to (1) compare the structural habitats of both species in areas where they coincide in a highly fragmented dry forest landscape, and (2) assess the current status of *A. cooki* and the conservation implications of inter- and intraspecific interactions.

Lizards were surveyed during the summers of 1997 and 1998 in 12 forest fragments (four in each of the following three size categories: small [<1 ha], medium

[1-10 ha], and large [>10 ha]) and in a reference site (Guánica Commonwealth Forest) in the subtropical dry forest life zone (Holdridge, 1967) of southwestern Puerto Rico (Fig. 1). Guánica Forest is one of the best remaining examples of subtropical dry forest habitat and supports the richest dry forest lizard community on the island (Genet et al., 2001). At each site, 100 m transects of fixed area (total transect area: 415 m²) were randomly located throughout the study area. The number of transects was scaled according to the size class of each site (small: 2, medium: 4, large: 8, reference site: 8 transects each in four habitat types).

Lizards were surveyed at 5 m intervals along the length of each transect. At each interval, the following data were recorded for all *A. cristatellus* and *A. cooki* individuals within a 2.5 m radius of the transect sampling point: (1) species identification, (2) age/size class, (3) perch height, (4) perch diameter, and (5) perch species (identification of the tree species used as a perch). Individuals on the ground were also included, and it was noted whether they were located on litter or bare substrate. The species were distinguished in the field by estimating the ratio of tail length (TL) to snout-vent length (SVL) (Marcellini and Jenssen, 1983). Each individual was assigned to an age/size class upon visual estimation of SVL (Schwartz and Henderson, 1991). Individuals were periodically captured (every 10-15 individuals) and measured to ensure accurate visual estimation of TL and SVL and correct assignment to age/size class (93% accuracy based on caught and measured specimens, $n = 173$). Individuals with broken tails were noted ($n = 242$), but omitted from this study because it was difficult to identify them.

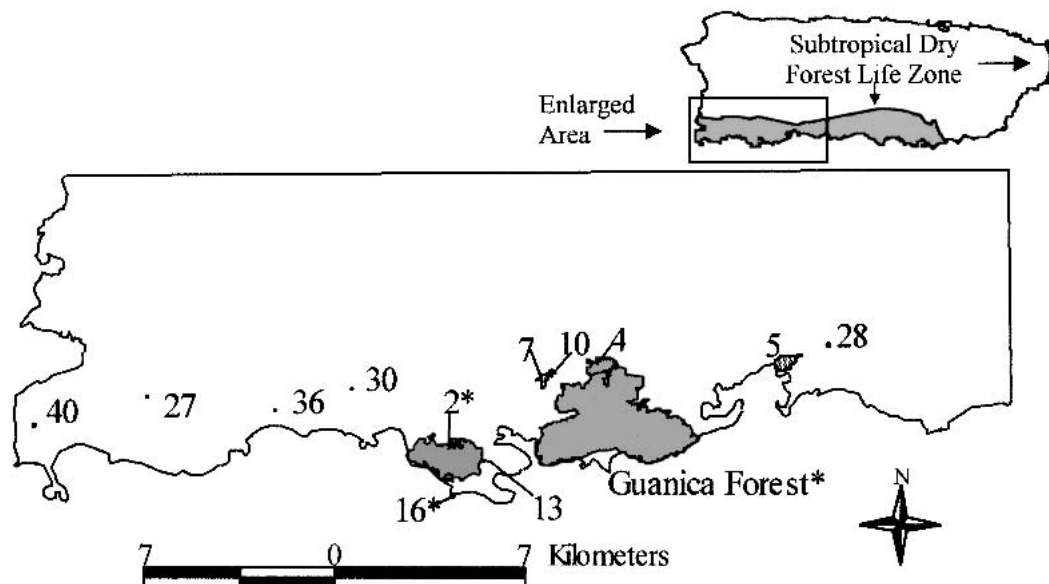


FIG. 1. Locations of study sites in southwestern Puerto Rico. Asterisks indicate sites where *A. cooki* was present; *A. cristatellus* was present at all study sites. Shaded areas in upper right portion of figure indicate dry forest habitat; shading in enlarged area indicates relative size of study sites.

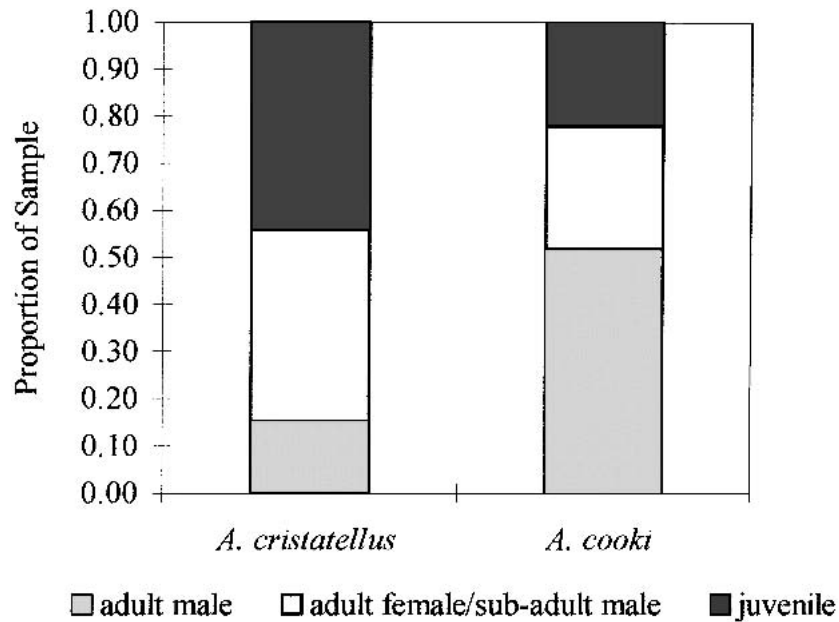


FIG. 2. Age distribution of *A. cristatellus* (N= 345 adult males, N= 936 adult females/sub-adult males, and N= 1132 juveniles) and *A. cooki* (N= 40 adult males, N= 20 adult females/sub-adult males, and N= 16 juveniles) in 1997-1998. Gray bars indicate adults males, open bars indicate females/sub-adult males, black bars indicate juveniles.

TABLE 1. Mean density estimates (std. error) of *A. cristatellus* and *A. cooki* at sympatric study sites (see Fig. 1 for locations).

	Site 16 (#/ha)	Site 2 (#/ha)	Guánica Forest coastal scrub forest (#/ha)
<i>Anolis cristatellus</i>			
Male	31.67 (20.85)	67.5 (21.63)	68.00 (27.15)
Female/sub-adult male	55.67 (7.67)	206.33 (62.93)	139.57 (43.02)
Juvenile	174.67 (31.67)	178.5 (34.72)	88.43 (51.36)
All age/size classes	262.00 (13.86)	452.33 (69.50)	296.00 (70.18)
<i>Anolis cooki</i>			
Male	127.00 (8.00)	36.00 (5.37)	20.00 (7.38)
Female/sub-adult Male	39.67 (20.92)	40.00 (5.06)	8.00 (5.06)
Juvenile	31.67 (31.67)	31.83 (15.87)	8.00 (5.06)
All age/size classes	198.33 (43.88)	107.83 (22.86)	36.00 (5.37)

The structural habitat (perch height and diameter) of *A. cristatellus* was evaluated where it was sympatric with *A. cooki* and where it was the only trunk-ground anole. No allopatric *A. cooki* populations were found. Perch height was estimated visually to the nearest 0.1 m using reference points on the observer's body; perch diameter was measured to the nearest 0.5 cm with calipers. Structural habitats and density estimates (individuals/ha based on transect counts) were analyzed to determine if inter- or intraspecific differences existed between species and/or age/size classes.

Statistical analyses were performed using SYSTAT

(version 5.0, Evanston, IL). Non-parametric statistics were utilized on untransformed data throughout; perch height, perch diameter, and density data did not meet the assumptions of normality for parametric tests, nor did transformation normalize the data distribution. Perch height data and density estimates from 1997 and 1998 were pooled for both species because there were no significant differences between years (Wilcoxon paired sample test, $P > 0.05$).

Anolis cooki was very rare in comparison with *A. cristatellus* (total individuals sampled 76 and 2413, respectively), thus underscoring the extreme rarity and

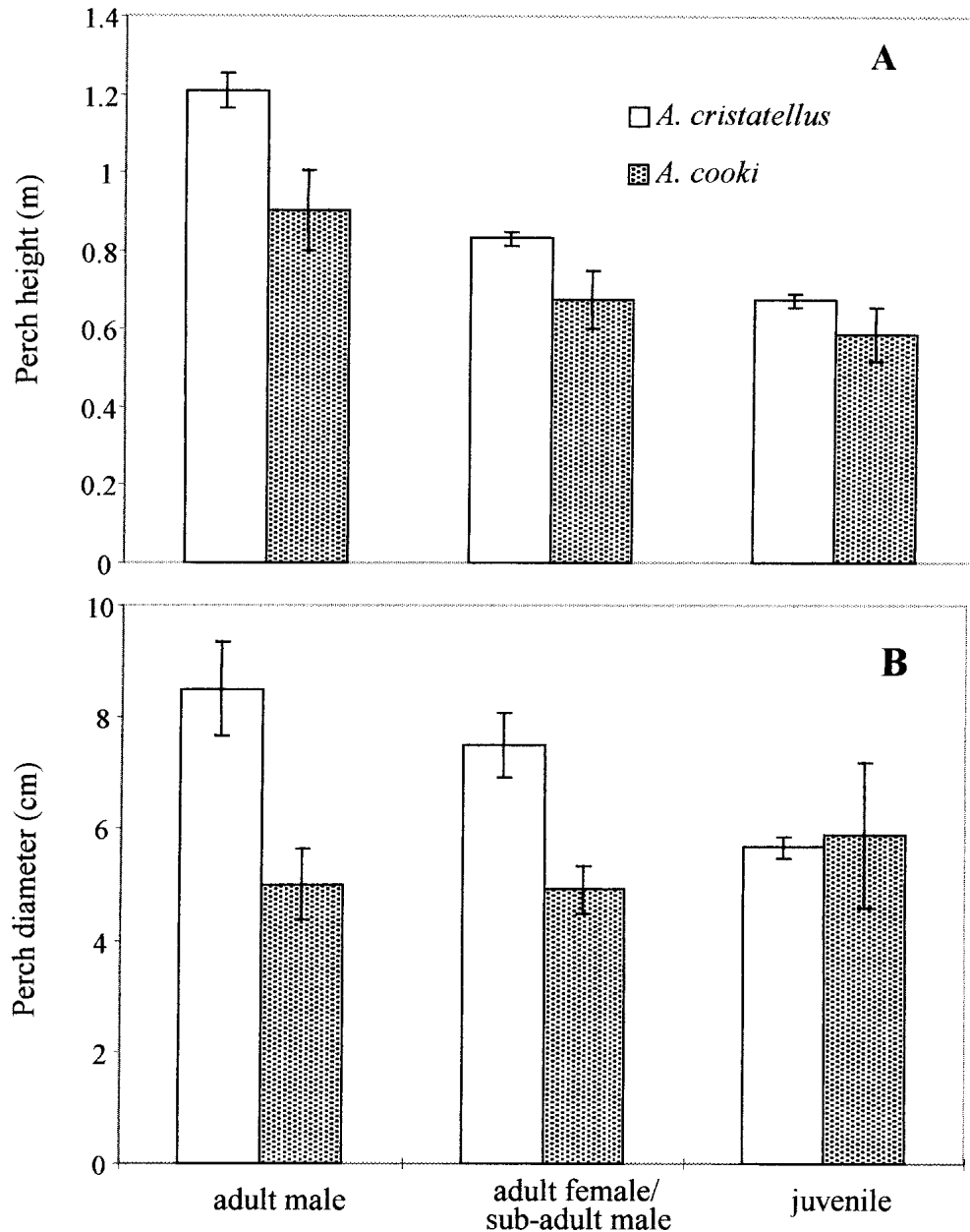


FIG. 3. A. Mean perch height and B. mean perch diameter for *A. cristatellus* and *A. cooki* age/size classes at all study sites. Error bars represent standard error of the mean.

vulnerability of its small populations. Most *A. cooki* were adults and subadult males (78%), with very few juveniles for recruitment and replacement (Fig. 2). In contrast, 44% of *A. cristatellus* were juveniles (Fig. 2). *Anolis cristatellus* was present in all forest fragments and habitat types within the reference site, while *A. cooki* was found in only two forest fragments (one medium and one large) and in two isolated areas near the

coast in Guánica Forest (Fig. 1). At sympatric sites, density estimates for *A. cooki* were lower than those for *A. cristatellus* (Table 1). Although total density was similar for both species at Site 16, density estimates for age/size classes indicated differences in the age distribution between the two species. *Anolis cristatellus* was much more abundant than *A. cooki* at Site 2 and in the coastal scrub forest of Guánica Forest.

In the 13 sites sampled there were several differences in structural habitat between species and among age/size classes within species. Adult male *A. cristatellus* perched significantly higher ($P = 0.011$) and on larger stems ($P = 0.034$) than adult male *A. cooki* (Figure 3, Mann-Whitney U Test). They also occupied larger stems than conspecific females and juveniles (Kruskal-Wallis ANOVA, $P < 0.05$); no such significant trends were apparent for *A. cooki* (Fig. 3). According to regression analyses, adult males of both species did not show a significant relationship between SVL and perch height, indicating that intraspecific competition among males is not significantly influencing perch selection (*A. cristatellus*: $n = 47$, $R^2 = 0.0207$, $P > 0.05$; *A. cooki*: $n = 39$, $R^2 = 0.681$, $P > 0.05$).

Allopatric *A. cristatellus* did not perch significantly higher than *A. cooki* (Mann-Whitney U Test, $P = 0.632$) but they selected significantly larger stems than when they occurred with *A. cooki* (Mann-Whitney U Test, $P = 0.001$). In sympatric sites there were no significant differences in structural habitat between species in any of the age/size classes (Fig. 4, Mann-Whitney U Test, $P > 0.05$). Differences in the structural habitats were not statistically significant when evaluated only under sympatric conditions in coastal scrub habitats, although there appeared to be a trend of lower perches for *A. cooki* adult males (Fig. 4).

Although *A. cooki* occupies relatively large and complex perch sites in sympatry with *A. cristatellus*, its abundance and age distribution do not indicate a state of stable equilibrium with its congeneric competitor.

The age distribution of *A. cooki* was biased towards adults, with minimal juvenile recruitment, while the age distribution of *A. cristatellus* appeared stable and indicative of adequate replacement. The age distributions of both species suggest that juvenile survival and recruitment differ markedly. If *A. cooki* is not reproducing and recruiting juveniles at a rate adequate to replace current populations, then the species appears to be on a trajectory towards natural extinction. The population dynamics and extremely restricted and patchy distribution of *A. cooki* has made it a species of special concern for management and conservation officials in southwestern Puerto Rico (Ortiz, 1990; M. Canals Mora, pers. comm.).

Anolis cristatellus and *A. cooki* occupy similar niches and are virtual ecological equivalents. Males of both species generally perched higher than females, and intraspecific differences in perch diameter were only seen for *A. cristatellus*. The ability to shift and modify structural habitats in response to competitive interactions has been documented for anoles in many areas throughout the West Indies and the southeastern United States (e.g., Jenssen, 1973; Schoener, 1975; Lister, 1976). My results indicate that there were no differences in perch height between species, but that *A. cooki* used smaller perches than *A. cristatellus*. However, perch selection may also be a function of the available perches in the coastal scrub habitats to which *A. cooki* is restricted. In Guánica Forest, coastal scrub forest is less complex and has fewer large stems compared to deciduous and semi-evergreen forest (Lugo et al. 1978).

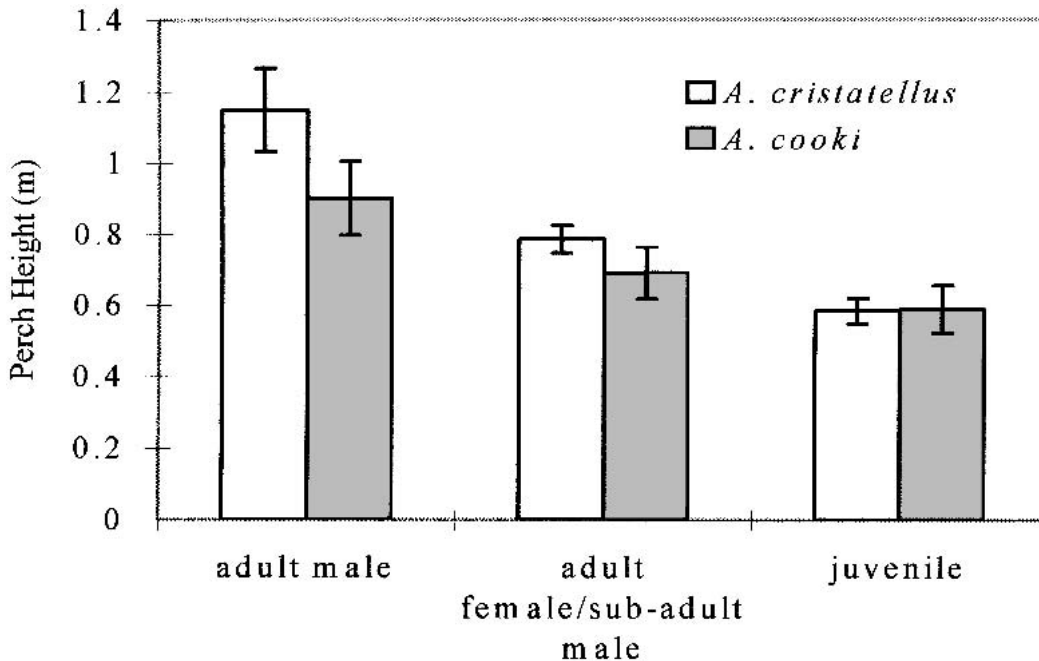


FIG. 4. Mean (\pm std. error) perch height for *A. cristatellus* ($N = 289$) and *A. cooki* ($N = 76$) where they occurred in sympatry (sites 2, 16, and Guánica Forest). Within age/size classes, differences between species were not significant (Mann-Whitney U Test, $P > 0.05$).

A significant relationship between adult male SVL and perch height would indicate intraspecific competition among males, with larger males predominating in larger and more complex habitats. Jenssen et al. (1984) found a significant positive relationship between SVL and the relative complexity and height of microhabitat for adult males of *A. cristatellus* and *A. cooki* in allopatric habitats, but only for *A. cristatellus* when sympatric with *A. cooki*. The lack of a significant relationship here between adult male size and perch height in either species, as well as the lack of a significant difference in perch height between the two species, indicates extensive structural habitat overlap and the potential for interspecific competitive interactions that may influence community dynamics.

Anolis cristatellus is the dominant species and superior competitor where it coexists with *A. cooki* (Jenssen et al., 1984). It is also thriving throughout its range while *A. cooki* struggles to persist within its restricted distribution. In my study, individuals of *A. cooki* also seemed to be under physiological stress, as they were weak and more easily caught than *A. cristatellus*. Habitat degradation and fragmentation in the dry forest region may also be contributing to the tenuous existence of *A. cooki*, perhaps limiting its range to areas of sympatry with *A. cristatellus*.

Given the highly fragmented landscape of the dry forest region of Puerto Rico and the patchy distribution of *A. cooki*, my results suggest that this species' range is shrinking and that it deserves immediate conservation attention. The outlook for this species has certainly not improved over the last few decades and its long-term persistence is questionable. Continual monitoring is critical to the long-term survival of *Anolis cooki*.

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LITERATURE CITED

- Genet, K. S., J. A. Genet, T. M. Burton, and P. G. Murphy. 2001. The lizard community of a subtropical dry forest: Guánica Forest, Puerto Rico. *Trop. Ecol.* 42: 97-109
- Gorman, G. C., R. Thomas, and L. Atkins. 1968. Intra- and interspecific chromosome variation in the lizard *Anolis cristatellus* and its close relatives. *Breviora* 293:1-13
- Gorman, G. C., D. G. Buth, M. Soulé, and S. Y. Yang. 1980. The relationships of *Anolis cristatellus* species group: electrophoretic analysis. *J. Herpetol.* 14: 269-278
- Gorman, G. C., D. G. Buth, M. Soulé, and S. Y. Yang. 1983. The relationships of the Puerto Rican *Anolis*: electrophoretic and karyotypic studies. *In*: G. J. Anders, et al. (eds.). *Advances in Herpetology and Evolutionary Biology: Essays in Honor of E. E. Williams*, pp. 626-642, Museum of Comparative Zoology, Harvard University, Cambridge, MA.
- Holdridge, L. R. 1967. *Life Zone Ecology*. Tropical Science Center, San Jose, Costa Rica
- Jenssen, T. A. 1973. Shifts in the structural habitat of *Anolis opalinus* due to congeneric competition. *Ecology* 54: 863-869
- Jenssen, T. A. 1990. *Anolis cooki* Grant: Cook's anole. *Catalogue of American Amphibians and Reptiles* No. 488:1-2
- Jenssen, T. A., D. L. Marcellini, C. A. Pague, and L. A. Jenssen. 1984. Competitive interference between the Puerto Rican lizards, *Anolis cooki* and *A. cristatellus*. *Copeia* 1984: 853-862
- Lister, B. C. 1976. The nature of niche expansion in West Indian *Anolis* lizards. I. Ecological consequences of reduced competition. *Evolution* 30: 659-676
- Lister, B. C. 1981. Seasonal relationships of rainforest anoles. *Ecology* 62: 1548-1560
- Losos, J. B. and D. A. Spiller. 1999. Differential colonization success and asymmetrical interactions between two lizard species. *Ecology* 80: 252-258
- Losos, J. B., J. C. Marks, and T. W. Schoener. 1993. Habitat use and ecological interactions of an introduced and native species of *Anolis* lizard on Grand Cayman, with a review of outcomes of anole introductions. *Oecologia* 95:525-532
- Lugo, A. E., J. A. Gonzalez-Liboy, B. Cintrón, and K. Dugger. 1978. Structure, productivity, and transpiration of a subtropical dry forest in Puerto Rico. *Biotropica* 10: 278-291
- Marcellini, D. L. and T. A. Jenssen. 1983. A character for differentiating the sympatric lizards *Anolis cooki* and *Anolis cristatellus*. *Herpetol. Rev.* 14: 113-114
- Marcellini, D. L., T. A. Jenssen, and C. A. Pague. 1985. Distribution of the lizard *Anolis cooki*, with comments on its possible future extinction. *Herpetol. Rev.* 16: 99-102
- Ortiz, P. R. 1990. Status and distribution of *Anolis cooki* (Reptilia; Sauria; Iguanidae). *Acta Científica* 4: 157-159
- Ortiz, P. R. and T. A. Jenssen. 1982. Interspecific aggression between lizard competitors, *Anolis cooki* and *Anolis cristatellus*. *Zeit. Tierpsych.* 60: 227-238
- Pregill, G. 1981. Late Pleistocene herpetofaunas from Puerto Rico. University of Kansas Museum of Natural History Misc. Publication. 71: 1-72
- Salzburg, M. A. 1984. *Anolis sagrei* and *Anolis cristatellus* in southern Florida: a case study in interspecific competition. *Ecology* 65: 14-19
- Schoener, T. W. 1975. Presence and absence of habitat shift in some widespread lizard species. *Ecol. Mon.* 45: 233-249
- Schoener, T. W. and A. Schoener. 1971a. Structural habitats of West Indian *Anolis* lizards. I. Jamaican lowlands. *Breviora* 368: 1-53
- Schoener, T. W. and A. Schoener. 1971b. Structural

- habitats of West Indian *Anolis* lizards. II. Puerto Rican uplands. *Breviora* 375: 1-39
- Schwartz, A. and R. W. Henderson. 1991. Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history. University of Florida Press, Gainesville, FL. 720 pp.
- Williams, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. *In*: T. Dobzhansky, M. Hecht, and W. Steere (eds.). *Evolutionary Biology*, 6. Appleton-Century Crofts, pp. 47-89. New York, NY.
- Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. *In*: R. B. Huey et al. (eds.). *Lizard ecology: studies of a model organism*, pp. 326-370. Harvard University Press, Cambridge, MA.