



**Mortality Rates of Insular Anolis Lizards: A Systematic Effect of Island Area?**

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## NOTES AND COMMENTS

MORTALITY RATES OF INSULAR *ANOLIS* LIZARDS: A SYSTEMATIC EFFECT OF ISLAND AREA?

Wright (1979, 1981) proposed that competition occurs between insectivorous birds and lizards of the genus *Anolis*. This proposal was based on three lines of evidence. (1) Extensive diet overlap occurs between anoles and insectivorous birds. (2) Many anoles are food limited. (3) There are reciprocal changes in the abundances of anoles and insectivorous birds in sclerophyll scrub in the West Indies and on islands in Gatun Lake, Panama. In both archipelagoes, insectivorous birds are most abundant on large islands where anoles are relatively rare and anoles are most abundant on small islands where insectivorous birds are relatively rare (Wright 1979, 1981). Differential extinction rates could generate this pattern. Extinction rates are inversely related to island area (MacArthur and Wilson 1967), and the extinction rates of birds are greater than the extinction rates of lizards (Williams 1969; Ricklefs and Cox 1972; Terborgh and Faaborg 1973; Case 1975). Wright (1979, 1981) hypothesized that (1) resident anoles experience competitive release upon the extinction of avian insectivores and (2) this occurs more frequently on small than on large islands. As a result, anoles should be more abundant on small islands and insectivorous birds more abundant on large islands, exactly as observed.

Waide and Reagan (1983) object to this hypothesis. They do so, however, without testing the original hypothesis and without presenting new data. Rather, Waide and Reagan (1983) marshal evidence from the literature and raise an alternative hypothesis which they also fail to test. We believe that their literature review is incomplete; but, before documenting this, we will provide a test of their alternative hypothesis.

Waide and Reagan hypothesize that release from predation allows increased abundances of anoles on small islands. Their rationale follows. Within an archipelago, the number of species of predators will usually be greater on large islands than on small islands. Therefore, release from predation may occur on small islands, and an inverse relation between prey (i.e., anole) abundance and island area may result. Waide and Reagan proceed to document a positive relation between island area and the number of species of potential anole predators in the West Indies. However, they do not relate this gradient to predation rates experienced by anoles. We will test the hypothesis that anoles experience lower predation rates on smaller islands which support fewer species of predators.

To do so, we monitored populations of *Anolis limifrons* at seven sites on islands

in Gatun Lake, Panama, and at one site on the adjacent mainland. These sites support very different numbers of anole predators. There is a 20-fold range in both the number of species of potential avian predators and the summed abundances of these avian predators (table 1). The number of mammalian predators also varies. For instance, the mainland and Barro Colorado Island support three diurnal mammals which prey upon anoles (*Nasua narica*, *Eira barbara*, and *Cebus capucinus*), Juan Gallegos and Puma support coatis (*N. narica*) only and the smaller islands completely lack diurnal mammals which prey upon anoles. Snakes, large insects, and nocturnal mammals also prey on *A. limifrons*. The distributions of these predators are not known, but the relation between species density and island area is invariably positive (e.g., MacArthur and Wilson 1967) so species number is undoubtedly greater on the mainland and the larger islands than on the very small islands. In sum, the study sites provide a steep gradient in the species richness of anole predators and a suitable testing ground for the hypothesis that *A. limifrons* experiences lower predation rates on smaller islands.

Predation on anoles is rarely observed. Therefore, we will use three indirect methods to infer predation rates. First, predation contributes to mortality rates. We will examine anole mortality rates at each site. Second, anoles autotomize their tails to escape predators. We will examine the proportion of individuals with autotomized tails. This index is often directly related to the density of predators (Rand 1954; Shaffer 1978; Ballinger 1979; Schall and Pianka 1980). On occasion, however, this is not true (Schoener 1979; Schoener and Schoener 1980b). Schoener (1979) suggests a reason: Predator efficiency may vary so that the proportion of animals which escape after being attacked by a predator varies. If this is true, the relationship between predation rates and the proportion of animals with autotomized tails is no longer straightforward (Schoener 1979). However, if predation is the only source of mortality, predator efficiency and the intensity of predation can be inferred from mortality rates and the proportion of individuals with damaged tails (Schoener 1979). This will provide our third index of predation rates.

To estimate mortality rates, we established 30 m × 30 m quadrats at each site. We monitored the populations of *A. limifrons* delimited by these quadrats between August 1980, and November 1981. During this period, we captured, marked, and released 2,170 animals. We used the Jolly-Seber model (Jolly 1965) to estimate mortality rates for sexually mature individuals which are territorial (table 1). Mortality rates did not vary seasonally (also see Andrews et al. 1983). Therefore, we calculated an overall mortality rate for each site (Jolly, in press). Further methodological details will be published elsewhere (S.J. Wright et al., in prep.).

We performed rank correlations to test the null hypothesis that the intensity of predation is independent of island area. The null hypothesis could not be rejected for any of the three indices of predation rates. For mortality rates,  $r_s = 0.18$  ( $P > .50$ ). For the proportion of individuals with autotomized tails,  $r_s = 0.23$  ( $P > .50$ ); and, for Schoener's index of predation intensity,  $r_s = 0.23$  ( $P > .50$ ). The data are inconsistent with the predation hypothesis advanced by Waide and Reagan. *Anolis limifrons* does not experience lower predation rates on smaller islands in Gatun Lake even though these islands support fewer species of predators. Differ-

TABLE 1  
SITE CHARACTERISTICS, TAIL-INJURY FREQUENCIES, SURVIVORSHIP, AND ESTIMATED PREDATION RATES FOR *Anolis limifrons*

SITE	AREA (ha)	DISTANCE TO MAINLAND (m)	POTENTIAL AVIAN PREDATORS*		TAIL-INJURY FREQUENCY (sample size)†	MORTALITY RATE (per day)	PREDATION INTENSITY‡
			No. of Species	Summed Abundance			
Pipeline Rd. ....	mainland		65	.46	.286 (77)	.013 ± .006	.0183
BCI .....	1,500	250	34	.35	.303 (75)	.015 ± .002	.0217
Juan Gallegos .....	659	775	12	.23	.131 (161)	.006 ± .002	.0072
Puma .....	77	2,100	6	.09	.146 (177)	.011 ± .002	.0130
Lion Hill (site 2) .....	51	3,500	6	.09	.195 (107)	.010 ± .003	.0125
Lion Hill (site 1) .....	51	3,500	6	.09	.136 (54)	.011 ± .004	.0129
Tigre .....	33	2,750	3	...	.163 (106)	.011 ± .003	.0133
Pantera .....	15	2,575	3	.02	.244 (102)	.013 ± .002	.0173

\* Birds which might prey upon *A. limifrons*. Only permanent residents which weigh between 20 g and 600 g and are omnivorous, insectivorous, or raptorial are included. Frugivores and species which forage exclusively in the canopy or in second growth are excluded. Abundances are the number of individuals of these species captured per day of operation of mist nets. See Wright (1979) for details.

† Proportion of adults (> 39 mm snout-vent length) with injured tails when first captured. Subsequent recaptures of the same individual are not considered. Sample size also applies to mortality and predation rates. Sample size does not include recaptures.

‡ Predation intensity equals  $-\ln(S)/(I - D)$ , where  $S$  equals one minus the mortality rate, and  $I$  equals tail-injury frequency (Schoener 1979). The units are days<sup>-1</sup>.

ences in predation rates cannot explain the gradient in anole abundance which Wright (1979) observed for this same archipelago.

This result should not be surprising. The relationship between the number of species of predators and their efficiency is complex. The addition of a new predator may increase or decrease the efficiency with which the predator guild consumes its prey depending upon the ecological relations among the predators (Case et al. 1979). For instance, the thrasher *Margarops fuscatus* is a potent anole predator (Waide and Reagan 1983) and is six times more abundant on Mona, a small West Indian island, than on Puerto Rico (Terborgh and Faaborg 1973). As a result, anoles may experience higher predation rates on Mona even though Mona supports fewer species of predators than does Puerto Rico. Still, in the absence of systematic data on predation rates, we cannot conclude that predation rates are independent of island area in the West Indies, the system examined most closely by Waide and Reagan. However, other considerations suggest that predation on West Indian anoles does not have the paramount importance assumed by Waide and Reagan.

The predation hypothesis advanced by Waide and Reagan assumes that the abundances of anoles are limited by predators, at least on large islands. If this were not true, release from predation would not lead to greater abundances on smaller islands. Waide and Reagan provide no evidence that anole abundances are predator limited in the West Indies. In fact, they overlook several studies which indicate that predation is relatively unimportant for West Indian anoles. Lister (1981) found that mortality rates of West Indian anoles are lower than mortality rates of Central American anoles. Andrews (1979) made the same observation and argued forcefully that West Indian anoles are relatively predator free and, as a result, are food limited.

Many other studies indicate that West Indian anoles are food limited. Very briefly, experimental manipulations of food supply show that food is limited during at least part of the year for *A. cristatellus* on Puerto Rico (Licht 1974), *A. acutus* on St. Croix (Rose 1982), *A. lineatopus* on Jamaica (Rand 1967), and *A. aeneus* on Grenada (Stamps and Tanaka 1981a, 1981b). Numerous comparative studies also conclude that West Indian anoles are food limited (e.g., Andrews 1976, 1979; Roughgarden and Fuentes 1977; Stamps 1977; Schoener and Schoener 1978a, 1980a; Lister 1981). Finally, three lines of evidence suggest that limited food supplies have influenced West Indian anoles through evolutionary time: (1) Ratios of body size are large for sympatric West Indian anoles. This minimizes diet overlap (Schoener 1970). (2) Behavior and morphology of widespread anoles vary between islands. Where widespread species overlap with congeners, divergence frequently occurs (Schoener 1970; Lister 1976a, 1976b). (3) Life history traits of West Indian anoles are characteristic of species which are food limited and relatively predator free (Andrews 1979). Limited food supplies are not necessarily inconsistent with the assumption that predators limit anole abundances. This is especially true since food supplies may only be limited on a seasonal basis in the West Indies (Lister 1981; Stamps and Tanaka 1981b). Still, the overwhelming evidence that West Indian anoles are food limited indicates that predation may not have the paramount importance assumed by Waide and Reagan. Waide and

Reagan (1983) do not consider the possibility that West Indian anoles are food limited.

In addition to proposing their alternative predation hypothesis, Waide and Reagan raise two further objections to Wright (1981). First, they observe that: "Patterns observed in sclerophyll scrub [in the West Indies] cannot be generalized to other island habitats" (p. 133). We agree. However, Waide and Reagan (1983) believe that the extinction-mediated competition hypothesis is weakened if patterns observed in sclerophyll scrub are not precisely repeated in other habitats. We disagree. Waide and Reagan (1983, p. 136) reason that extinction is an "island-wide phenomenon." Therefore, anoles should experience competitive release "in all habitats formerly occupied" (p. 136) by an extinct avian insectivore. However, many avian insectivores do not occur in all habitats on an island. This is especially true for the Greater Antilles (Terborgh and Faaborg 1980) and the larger islands of the Lesser Antilles which support rain forest (Terborgh et al. 1978). On these islands, many of the avian inhabitants of rain forest (the other habitat considered by Waide and Reagan) are found only in rain forest. The extinction of one of these species should not affect inhabitants of sclerophyll scrub even though they share the same island. Therefore, we expect the proposed competitive interaction between birds and anoles to produce different outcomes in rain forest and sclerophyll scrub. This should be especially true if the avifaunas of the two habitats are "subject to separate immigration-extinction equilibria" as suggested by Terborgh and Faaborg (1980, p. 189).

The final objection raised by Waide and Reagan (1983) is that the evidence for diet overlap between anoles and insectivorous birds is suspect. Wright (1981) incorrectly reported mean prey size ranges taken from Schoener (1968) and Schoener and Gorman (1968) as mean prey sizes. Hence, prey size distributions of anoles and insectivorous birds must be reexamined.

Waide and Reagan (1983) claim that anoles take smaller prey than insectivorous birds. This is certainly not true in Central America. In lowland rain forest in central Panama, the Kentucky warbler (*Oporornis formosus*) and *A. limifrons* forage in the lower levels of the vegetation and primarily on the forest floor. Mean prey size for the Kentucky warbler (3.08 mm,  $N = 114$ , Morton 1980) is smaller than mean prey size for juveniles (4.77 mm,  $N = 35$ ), females (6.11 mm,  $N = 60$ ), and males (5.45 mm,  $N = 65$ ) of *A. limifrons* (also see Sexton et al. 1972). Experimental manipulation of arthropod abundance indicates that food is limited for *A. limifrons* in the dry season when Kentucky warblers are present (S.J. Wright and C.J. Campbell, in prep.). At Finca la Selva, Costa Rica, mean prey sizes for several small-bodied insectivorous birds (6 residents, 1 migrant) vary between 2.61 mm and 7.73 mm (T. W. Sherry, personal communication). Also, at Finca la Selva, mean prey sizes taken by males and females of two small-bodied anoles, *A. humilis* and *A. limifrons*, vary between 6.8 mm and 8.7 mm (Talbot 1979). Again, small-bodied insectivorous birds take smaller prey than do syntopic, small-bodied anoles.

Prey size distributions of West Indian anoles and birds cannot be compared because prey size data are not available for West Indian birds. However, prey size distributions of West Indian anoles can be compared with prey size distributions of ecologically similar North and Central American birds. Using this approach,

Waide and Reagan (1983) claim that West Indian anoles take smaller prey than do insectivorous birds. Waide and Reagan (1983) cite a small portion of the available data on the prey of West Indian anoles and they conclude: "When both sexes and all size classes are taken into account, at least 80% of the prey taken by six species of anole are less than 2 mm in length" (p. 136). This misrepresents the potential for diet overlap between West Indian birds and anoles in three ways. First, their sources (Schoener [1968] and Schoener and Gorman [1968]) include seven, not six, species of *Anolis*. Waide and Reagan (1983) omit *A. richardi*. *Anolis richardi* is the largest of the seven species and takes the largest arthropod prey. Second, three of the six species included by Waide and Reagan (*A. sagrei*, *A. angusticeps*, *A. distichus* on Bimini) are smaller than any of the species studied by Wright (1981). This is important because larger anoles take larger prey (fig. 1). Therefore Waide and Reagan's subsample of the prey-size data available for *Anolis* does not accurately represent the diets of the anoles studied by Wright (1981).

Our most important objection to Waide and Reagan's representation of the diets of West Indian anoles concerns the contribution of tiny prey items to the diet. Although many tiny items may be present, they usually make a minor contribution to the total weight or volume of prey consumed. This is true because the weights of arthropods scale as the second or third power of length (Schoener 1980). The energetic reward gained from one large prey item outweighs the rewards of several smaller items. Therefore, to determine which prey items make the largest contribution to the diet, it is standard procedure to examine distributions of prey weight or prey volume among prey length categories (e.g., Roughgarden 1972; Stamps 1977; Lister 1981). Instead, Waide and Reagan (1983) examine the distribution of prey individuals among prey length categories. As a result, the bulk of prey weight or prey volume (i.e., the bulk of the diet) comes from much larger items than reported by Waide and Reagan (1983). For adult males, mean prey lengths for distributions of prey weight and prey volume are greater than 6 mm with just one exception (fig. 1). For adult females of nine species, the same means are 7.6 mm, 10.1 mm, 7.9 mm, 4.3 mm, 2.8 mm, 6.3 mm, 8.0 mm, 11.4 mm, and 8.9 mm (Schoener 1967, 1968; Schoener and Gorman 1968; Andrews 1979); and, for juveniles of six species, the same means are 3.9 mm, 3.5 mm, 3.9 mm, 4.3 mm, 2.4 mm, and 3.4 mm (Schoener 1967, 1968; Andrews 1979). These prey size distributions broadly overlap prey sizes taken by insectivorous birds in North and Central America (Hespenheide 1971, 1973; Morton 1980; T. W. Sherry, personal communication). We infer that there is overlap between the sizes of the arthropod prey taken by West Indian birds and anoles.

In summary, the data do not support the positions expressed by Waide and Reagan (1983). Their predation hypothesis cannot explain the gradient in anole abundance observed by Wright (1979) because the intensity of predation experienced by *A. limifrons* on the same islands does not vary systematically with island area. This does not mean that predation on *A. limifrons* is unimportant. On the contrary, *A. limifrons* experiences high predation rates. However, the intensity of predation does not vary directly with island area as required by the predation hypothesis. Predation rates have not been examined systematically for West Indian anoles. The fact that many West Indian anoles are food limited (references cited above) and the observation that predation is relatively unimportant for

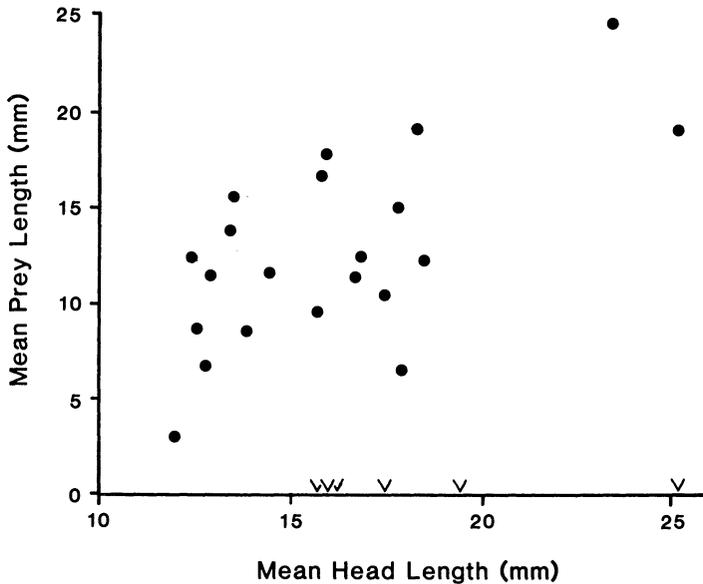


FIG. 1.—Relation between mean prey length and mean head length for adult male anoles. Mean for prey length refers to distributions of prey volume (or prey weight) and not to distributions of prey individuals. Each point = a separate island population; 12 islands and 15 species are included. Relation between head length and prey length is significant ( $r = 0.65$ ,  $P < .01$ ). Arrows along the abscissa = head lengths of populations studied by Wright (1981). Sources of data: Andrews (1979), Lister (1976, 1981), Roughgarden (1972), Schoener (1967, 1968), and Schoener and Gorman (1968).

several West Indian anoles (Andrews 1979; Lister 1981) suggest that predators do not control anole abundances as assumed by Waide and Reagan. Finally, there is broad overlap in the size (see above) and taxonomic distributions (Wright 1979, 1981) of the arthropod prey consumed by the birds and anoles studied by Wright (1979, 1981). We conclude that the extinction-mediated competition hypothesis remains the most plausible explanation of the patterns observed by Wright (1979, 1981). Perturbation experiments are now underway in Panama to test this hypothesis.

#### ADDENDUM

Waide and Reagan (1983, p. 136) cite Schoener and Gorman (1968) as the source of prey size distributions of six anole species. In fact, Schoener and Gorman only studied three species. In manuscript, Waide and Reagan cited both Schoener (1968) and Schoener and Gorman (1968). We have assumed that Waide and Reagan accidentally omitted the reference to Schoener (1968).

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