

proximately 140 days, as compared to the turtle *T. scripta* which has enough stored lipids to support a standard metabolic rate at 28 C (0.09 cm³ O₂/g/h, N = 5; SE = 0.10; R. Fischer, unpubl. data) for approximately 55 days. The large amount of NPL transferred from egg to hatchling (PIC) in alligators has apparently been made to fuel the prolonged period when hatchlings have a negative energy balance.

The level of allocation to PIC is far from trivial, and in those reptiles examined, exceeds 50% of the egg lipids (Kramer and Bennett, 1981; Congdon et al., 1983a, b; Troyer, 1983; Wilhoft, 1986; Congdon, 1989; Congdon and Gibbons, 1989). Thus, the findings in this study along with the work done by Troyer (1983) on green iguanas may indicate that levels of PIC are determined by increases in fitness obtained by the female parent through investment in egg material, in excess of that needed for embryogenesis, that enhance survival of the neonate during the post-hatching period when energy balance is negative.

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Interspecific Aggression between *Anolis cristatellus* and *A. gundlachi*: Comparison of Sympatric and Allopatric Populations

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Interspecific territoriality occurs in a wide variety of organisms. At least some interspecific territoriality

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results from cases of mistaken identity (e.g., birds, Murray, 1981; fish, Kohda, 1981). In other cases, interspecific territoriality appears to be an adaptive response to interspecific competition. For example, Low (1971) found that the fish *Pomacentrus flavicauda* was territorial toward other algae-eaters, but not toward non-competitors (see also Myrberg and Thresher, 1974; Savard and Smith, 1987). Nishikawa (1985, 1987) found evidence for both mistaken identity and adaptive interspecific territoriality in two plethodontid salamanders.

The adaptive hypothesis implies that a species has evolved to recognize another species as a competitor and react aggressively toward it. By comparing populations that are sympatric and allopatric to a second species, one can infer whether interspecific aggressive behavior has evolved adaptively (Nishikawa, 1985, 1987). If aggression is an evolved, adaptive response to the presence of a second species, then individuals of the sympatric population should be more aggressive in interspecific interactions than are individuals from the allopatric population. Conversely, if the aggression results from mistaken identity, allopatric and sympatric individuals should display similar levels of aggression.

We used this approach to study interspecific aggression in the sibling species *Anolis cristatellus* and *A. gundlachi*. *Anolis gundlachi* is limited to the Luquillo Mountains in northeastern Puerto Rico, whereas *A. cristatellus* is widespread throughout Puerto Rico and nearby islands (Rivero, 1978). Where they occur sympatrically, *A. gundlachi* occurs in the shaded forest and *A. cristatellus* is limited to more open, sunnier areas. Although the two microhabitats are adjacent, *A. gundlachi* rarely is found in openings, and *A. cristatellus* only occasionally ventures into the forest (Rand, 1964; Schoener and Schoener, 1971). The species occur sympatrically at the forest edge, however, sometimes occupying the same tree at different times in the day (Schoener, 1970; Schoener and Schoener, 1971). Differences in thermal physiology are at least partially responsible for this distribution (Huey and Webster, 1976; Gorman and Hillman, 1977), but the abrupt transition suggests that interspecific territoriality might play a role as well. We conducted this study to determine if interspecific aggression occurs and, if so, to evaluate hypotheses about its cause.

We investigated whether *A. cristatellus* from the Luquillo Mountains (near the town of El Verde, Puerto Rico) and from southwestern Puerto Rico (near Parguera, Puerto Rico, >125 km from the nearest *A. gundlachi*) differed in aggressiveness toward *A. gundlachi*. To control for differences in aggressiveness between populations of *A. cristatellus*, we also staged intraspecific matches between *A. cristatellus* at each locality. *Anolis gundlachi* was always the stimulus animal in interspecific encounters. Behavioral evolution was only investigated in *A. cristatellus* because all populations of *A. gundlachi* are either sympatric with or geographically proximate to *A. cristatellus*.

Territorial encounters were staged by slowly moving a male lizard, tethered around the waist with dental floss (15–20 cm long to allow movement) and attached to a 2 m pole, onto a tree trunk approximately 1 m from a territorial male. The observer watched quietly from the other end of the pole and recorded all behavior over 30 min using a tape recorder.

Aggressiveness in a match was quantified using a

modification of an ethogram developed in laboratory trials (Ortiz and Jenssen, 1982). Points were awarded each time a particular behavior occurred; more points were awarded to those behaviors that indicate greater levels of aggressiveness. Points were awarded as follows: dewlap pulse, 1; head bob, 2; erect crest, 3; extended throat, 3; approach, 4; mouth open, 4; protruded tongue, 5; tail movement, 5; bite or attack, 6; jaw sparring, 6; and jaw-locking, 7 (see Ortiz and Jenssen [1982] for more detailed description). Behaviors that could not be detected reliably in the field (sagittal expansion, stretch posture, rocking, head roll), or that were prevented because the intruder could not escape (supplant, chase), were omitted. Points awarded for each behavior were modified slightly from Ortiz and Jenssen (1982) to prevent overemphasizing highly aggressive behavior. We scored only the behavior of the resident male to eliminate the effects of handling and reduced mobility of the intruder.

For the intraspecific encounters, individuals were collected just prior to the encounter. For the interspecific encounters, *A. gundlachi* was collected near the El Verde Field Station in the Luquillo Mountains. For the Luquillo Mountains matches, individuals of *A. gundlachi* were collected no more than 3 h before the match. However, for the Parguera matches it was necessary to collect *A. gundlachi* 24 h beforehand. Prior to the interspecific encounters, individuals of *A. gundlachi* were kept in plastic bags in an ice chest with a temperature below 34 C, its lethal upper temperature (Huey and Webster, 1976). No individual of either species was used more than once. Snout-vent length (SVL) of both animals was measured at the end of most of the El Verde encounters. Neither the intruder nor the resident was consistently larger in either set of trials; with one exception, the difference in SVL was <5 mm. All statistical comparisons were performed using a two-tailed Mann-Whitney U test.

Aggressive behavior occurred in most encounters. Although we did not quantify the behavior of the introduced lizards, they often displayed, postured, and sometimes even attacked the unconstrained resident. The intraspecific aggressiveness of *A. cristatellus* from the Luquillo Mountains ($N = 15$) and Parguera ($N = 8$) did not differ ($P > 0.20$; Fig. 1). At each locality, *A. cristatellus* was more aggressive toward conspecific lizards than toward *A. gundlachi* (Luquillo Mountains, $N = 15$, $P < 0.05$; Parguera, $N = 9$, $P < 0.02$). The aggressiveness of *A. cristatellus* toward *A. gundlachi* did not differ between sites ($P > 0.40$). Although intraspecific encounters tended to be more aggressive, high levels of aggression often occurred in interspecific matches (e.g., biting occurred in 87.0% of intraspecific and 70.8% of interspecific encounters).

Anolis cristatellus are highly aggressive toward *A. gundlachi*, but not as aggressive as they are toward conspecifics. *Anolis cristatellus* from populations sympatric and allopatric to *A. gundlachi* do not differ in their behaviors toward their sibling species. These results can be explained in several ways.

The high degree of interspecific aggression may be an artifact of the experimental design. Most interspecific interactions among anoles result in no more than head-bobbing and dewlap extension (e.g., Fitch, 1975; Henderson and Fitch, 1975; Talbot, 1979; Losos, 1985; Tokarz and Beck, 1987; but see below). Further, in a laboratory study, Ortiz and Jenssen (1982) noted

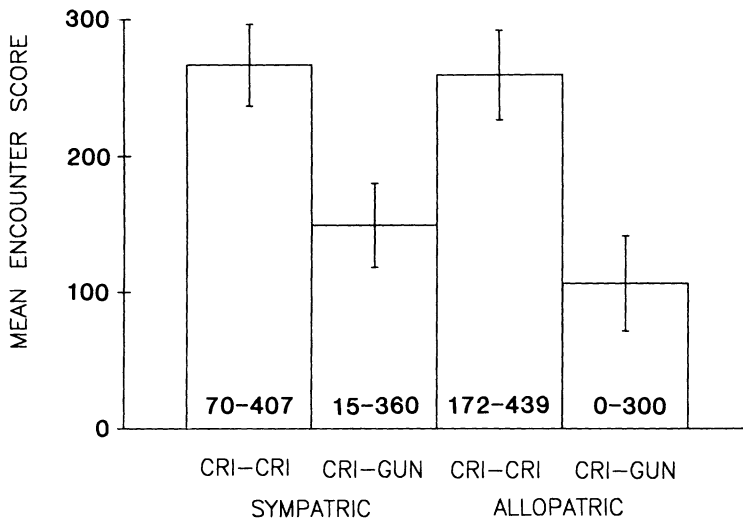


FIG. 1. Mean aggression scores (± 1 SE) in each of the four treatments. Numbers within each column are the range of scores in each treatment. Abbreviations: cri = *A. cristatellus*; gun = *A. gundlachi*.

little aggression between *A. cristatellus* and *A. gundlachi*. The cause of the discrepancy between our findings and those of Ortiz and Jenssen (1982) is not clear. Possibly, the laboratory animals were less responsive. On the other hand, resident males in nature may be highly aggressive to any lizard suddenly appearing a meter away within their territory. Unfortunately, our field schedule prevented conducting tests to determine whether *A. cristatellus* would react aggressively toward other species (e.g., *A. evermanni*).

Interspecific aggression occurs between a number of competing species of *Anolis* (Gorman, 1976; Ortiz and Jenssen, 1982; Jenssen et al., 1984). If aggression between sympatric *A. cristatellus* and *A. gundlachi* in the Luquillo Mountains is an adaptive response to the presence of a competing species, then the high degree of interspecific aggression by allopatric Parguera *A. cristatellus* requires explanation. Gene flow from the Luquillo Mountains might be responsible for the presence of this trait 125 km away from the nearest *A. gundlachi*. Levels of gene flow in some lizard species are inferred to be moderately high (e.g., Thompson and Sites, 1986; Moritz, 1987), though little data are available for *Anolis*. In the Dominican Republic, however, gene flow is not sufficient to prevent adaptive divergence of dewlap color in *A. caudalis* over a span of approximately 40 km (Webster and Burns, 1973).

Interspecific aggression may also result from mistaken identity. However, individuals of *Anolis cristatellus* are, on average, less aggressive toward *A. gundlachi* than they are toward conspecifics, which indicates that, at some point in an encounter, *A. cristatellus* identify *A. gundlachi* as non-conspecific. Sympatric anoles tend to differ in head-bobbing patterns (Garcea and Gorman, 1968; Jenssen and Gladson, 1984) and/or dewlap color (Echelle et al., 1971; Webster and Burns, 1973; Rand and Williams, 1970), particularly if they are morphologically similar. Experimental studies have confirmed that these signals are used in species recognition (Jenssen, 1970; Losos, 1985). The

head-bobbing patterns for *A. gundlachi* and *A. cristatellus* have not been reported. Body and iris coloration differ between the species, but differences in dewlap coloration are more subtle (Rivero, 1978; Ortiz and Jenssen, 1982). If *A. cristatellus* identifies non-conspecifics by coloration or bobbing pattern, however, considerably less aggression would have been expected in interspecific encounters. Most of the interspecific interactions involved high levels of aggression; biting occurred in 17 of 24 encounters. It is difficult to imagine what source of information (other than taste) a lizard could receive after encounters had escalated to the biting stage that would indicate that an opponent was non-conspecific.

A second possibility is that southwest Puerto Rican *A. cristatellus* mistake *A. gundlachi* for another species to which they respond aggressively. Near our study site, another sibling species, *A. cooki*, occurs and competes for resources with *A. cristatellus* (Jenssen et al., 1984). The two species exhibit high levels of interspecific aggression (Ortiz and Jenssen, 1982). Cues *A. cristatellus* uses to identify *A. cooki* need to be determined before we can determine whether it misidentifies *A. gundlachi* as *A. cooki*.

Neither the mistaken-identity nor the adaptation hypothesis satisfactorily explains the interspecific aggressiveness between *A. gundlachi* and *A. cristatellus*. More research is needed on the nature and extent of ecological and behavioral interactions between the species and the mechanisms by which other species are recognized and identified.

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