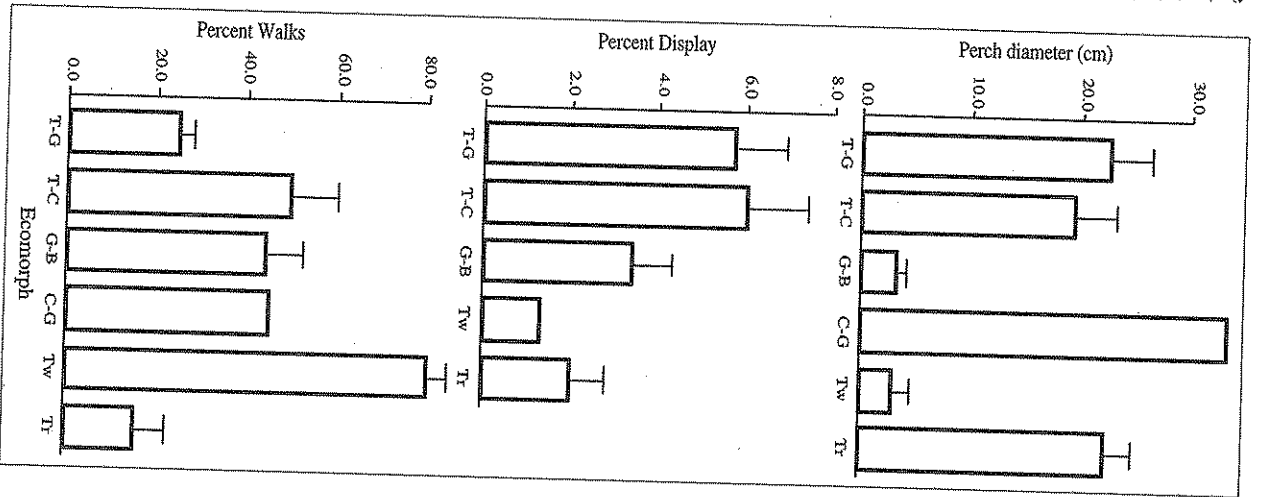


24 *A. angusticeps* were found on trunks or on the ground and the majority of individuals were observed oriented parallel with the perch occupied. Both sexes of *A. angusticeps* were found relatively high in the canopy and did not differ significantly in this measure (Table 2; ANOVA, $F_{1,22} = 0.22$, $P > 0.50$). Both sexes were found on relatively narrow perches, with males tending to perch on broader supports than females (Table 2; ANOVA, $F_{1,22} = 5.40$, $P < 0.05$). Male and female *A. angusticeps* both walked as their primary means of locomotion and did not differ significantly in this behavior (Table 2; ANOVA, $F_{1,22} = 1.06$, $P > 0.25$). Male *A. angusticeps* spent more time displaying than females (ANOVA, $F_{1,22} = 3.09$, $P < 0.05$, one-tailed test due to the *a priori* expectation that males would display more than females).

The habitat, locomotor, and display characteristics of *Anolis angusticeps* are similar to other twig anoles and differed strikingly from most other anole ecomorphs (Tables 1 and 2, Figure 2). The other twig anoles for which locomotor and display behavior data are available (*A. valencienni* and *A. insulinus*) also use narrow supports, walk frequently, and display infrequently relative to other ecomorphs (Table 1, Figure 2). The ecomorph most distinctive from the twig anoles are the trunk-ground anoles. Trunk-ground anoles use broad supports, move primarily by running, and spend about four times as much time displaying as twig anoles. In contrast, grass-bush anoles are much more similar to twig anoles. Grass-bush anoles also use narrow supports, move about 44% of the time by walking, and display only about twice as much as twig anoles. The remaining ecomorphs (trunk-crown, crown-giant, trunk) exhibit habitat, locomotor, and display characteristics intermediate between these extremes.

Figure 2. Mean (± 1 SD) perch diameter, percentage of time displaying, and percentage of walks for West Indian *Anolis* (see Appendix 2 for list of species included in ecological and behavioral comparisons). Ecomorphs are indicated as in Table 1. No standard error bars are provided for the crown-giant ecomorph type because only one species is included. No standard error bars are indicated on the twig ecomorph type for the percent display comparison because the error was too small to be seen on the plot.



Values for ecological and behavioral characteristics of some ecomorphs should be given greater consideration than others due to uneven sample sizes (e.g., six trunk-crown anoles and one crown-giant anole).

DISCUSSION

In all respects, *Anolis angusticeps* appears to be a twig anole; it is similar morphologically to other twig anoles, uses narrow perches, tends to move by walking slowly, and displays infrequently. These data show that, at least on South Bimini, this species uses a habitat and behaves like a twig anole. Although no quantitative habitat or behavioral data are available for *A. angusticeps* from Cuba, Cuban individuals are morphologically similar to Bahamian *A. angusticeps*.

How, then, can we explain the reported differences in habitat use of *Anolis angusticeps* on Cuba and the Bahamas (Collette 1961; Ruhlal 1964; Hardy 1967; Schoener 1968; Schwartz and Thomas 1969)? One possibility is that, for some reason, *A. angusticeps* evolved a twig morphology on Cuba even though it does not use a typical twig habitat. A more likely possibility is that workers on Cuba (Collette 1961; Ruhlal 1964; Hardy 1967; Schwartz and Thomas 1969) did not detect *A. angusticeps* in its twig habitat. This is not unlikely, as *A. angusticeps* is likely to be much more obvious when they use substrates such as tree trunks or rocks rather than twigs. Indeed, several authors have noted that *A. angusticeps* is a difficult species to find (Barbour 1937; Oliver 1948; Schoener 1968). For example, Oliver (1948) did not discover *A. angusticeps* on South Bimini until the end of a month long trip, missing this species in its natural habitat despite the fact that this species is not uncommon on the island (Schoener 1968; D. J. Jrschick and J. B. Losos, personal observation). Therefore, detailed searching on available habitat in Cuba may reveal whether *A. angusticeps* uses a habitat similar to that used by the species on South Bimini Island.

Ecology-morphology Correlations

Correlations between ecology and morphology have long been considered as evidence that species have

evolved adaptations for their microhabitats (Karr and James 1975; Ricklefs and Travis 1980, but see Wiens and Rotenberry 1980; Wiens 1984). Previous studies of *Anolis* lizards from Costa Rica, Hispaniola, Puerto Rico, and Jamaica have documented strong correlations between habitat use and morphology (Moermond 1979a; Pounds 1988; Losos 1990a). The most striking of these correlations exists between the preferred perch diameter and limb dimensions of *Anolis* species; species that use broad surfaces possess long hindlimbs whereas species using narrow perches possess shorter hindlimbs. The data presented here are consistent with this correlation; *A. angusticeps* is typically found on narrow perches and possesses short hindlimbs.

This correlation between limb length and perch diameter in *Anolis* lizards is consistent with biomechanical models (Carnall 1985). On broad surfaces, where there is little risk of losing balance, *Anolis* species have maximized their ability to run quickly and jump farther by evolving long legs which enhance maximal running and jumping ability (Emerson 1985; Hildebrand 1985; Losos 1990a, 1990c). In contrast, on narrow surfaces anoles have evolved short legs to prevent toppling while moving. Although a correlation has been documented in three twig anoles (*A. valencienni*, *A. angusticeps*, and *A. insulinus*), quantitative ecological and morphological data are unavailable for others considered to be twig anoles (e.g., *A. placidus*, *A. sheplani*, *A. darlingtoni*, and *A. fowleri* of Hispaniola). We recommend quantitative assessment of microhabitat and morphology of these species to determine whether they also use narrow supports and possess short limbs.

Locomotor Behavior and Performance

The habitat matrix model predicts that species will evolve locomotor behavior appropriate for their microhabitats (Moermond 1979a, 1979b; Flegle and Mittermeier 1980; Robinson and Holmes 1982; Pounds 1988; Losos 1990b). Previous studies have interpreted the behavior of slow walking as a means to avoid losing balance while moving on narrow surfaces (Pounds 1988; Losos 1990b). The use of

narrow supports and slow movements of *Anolis angusticeps* supports this generalization. In contrast, anoles that use supports in which loss of balance is less of a concern (e.g., trunk-ground and trunk-crown anoles that use broad supports) move primarily by rapid movements that might be more difficult on narrow supports.

The microhabitat of twig anoles may also exert a strong influence on their locomotor capabilities. Laboratory tests of locomotor capabilities indicate that whereas the twig anole *Anolis valencienni* moves with little difficulty on narrow surfaces, it exhibits poor sprinting and jumping capabilities on broad surfaces relative to other, similarly-sized anoles (Losos and Sinervo 1989; Losos 1990a, 1990c). These limited maximal locomotor capabilities of *A. valencienni* result, in part, from the short limbs of this anole which, in turn, may have evolved to allow slow, steady movements on narrow supports (Losos and Sinervo 1989; Losos 1990a). These findings demonstrate that the evolution of morphological characteristics appropriate for movement on specific surfaces involves trade-offs. Further tests of the locomotor capabilities of *A. angusticeps* may reveal if this species, by evolving a morphology and locomotor behavior appropriate for walking on narrow surfaces, exhibits reduced maximal sprinting and jumping capabilities on broad supports.

Display Behavior

The microhabitat of twig anoles may exert a strong influence on their escape behavior and display behavior. Because lizards run quickly on narrow supports only with difficulty (D. J. Irschick, personal observation), the ability of anoles using such surfaces to escape predators (e.g., snakes) rapidly may be compromised. Furthermore, twig anoles possess limited maximal running and jumping capabilities, making running and jumping quickly an especially inefficient mode of escape (Losos and Sinervo 1989; Losos 1990a, 1990c). An alternative method of avoiding predators is to be highly inconspicuous and, when detected, to elude capture by hiding. Possibly as a consequence of the above factors, twig anoles have opted for this second approach. All twig

anolis known to date are highly cryptic and, when disturbed, slowly move out of sight (Schoener 1968; Williams and Rand 1969; Hicks and Trivers 1983; D. J. Irschick and J. B. Losos, personal observation). If twig anoles have evolved to be highly inconspicuous, then frequent displays might render them highly visible to predators. The need to avoid predation may thus explain, in part, why twig anoles examined to date display infrequently relative to other anole ecomorphs. Because anoles display to defend territories, infrequent displays might thus make active defense of a territory unfeasible. Although few data are available on territoriality in twig anoles, that at least one twig anole (*Anolis valencienni*) appears to be much less territorial than other anoles (Hicks and Trivers 1983) is in support of this hypothesis. One means of testing if display behavior is directly correlated with behavioral characteristics such as territorial behavior would be to examine whether anole ecomorphs which display frequently (e.g., trunk-ground anoles) are more territorial than ecomorphs which display less frequently (e.g., twig anoles).

Intersexual Differences in *Anolis angusticeps*

Intersexual differences in microhabitat use have been previously documented in *Anolis* lizards (Andrews 1971; Lister 1976). We observed a significant propensity for males to perch on broader supports than females. In a much more extensive study at the same locality, Schoener (1968) observed no significant intersexual differences in perch diameter in *A. angusticeps*. Due to his much larger data set, Schoener's data probably best reflects intersexual ecological relationships. We also observed that male *A. angusticeps* spent more time displaying than females. This difference in display behavior is consistent with data which indicate that male lizards are more likely to actively defend territories or attempt to attract mates than females (Stamps 1983).

SUMMARY

Few quantitative data exist on the behavior and ecology of twig anoles. Their cryptic habits make such studies especially difficult. Here we examined

whether an anole superficially similar to twig anoles, *Anolis angusticeps*, exhibits morphological, ecological, and behavioral characteristics similar to other twig anoles for which data are available. In particular, we predicted that, if *A. angusticeps* is a twig anole, it should be similar morphologically to other twig anoles, use narrow perches, move by walking slowly, and display infrequently. These predictions were confirmed. We recommend further studies investigating the morphological, ecological and behavioral characteristics of twig anoles to verify whether the above-mentioned characteristics are more broadly applicable.

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APPENDIX 1. National Museum of Natural History (USNM) specimen numbers for Cuban samples of *Anolis angusticeps* examined in this study. Data for Bahamian specimens of *A. angusticeps* are available upon request from the authors.

USNM 51847, Cape San Antonio, Cuba; USNM 54416, Santa Cruz River, Cuba; USNM 160915, Habana, Cuba; USNM 160920, Habana, Cuba; USNM 160921, Habana, Cuba; USNM 160922, Habana, Cuba; USNM 160924, Bosque de Habana, Cuba; USNM 160928, La Habana, Cuba; USNM 160937, La Habana, Cuba; USNM 337640, Matanzas, Playa Larga, Cuba; USNM 337641, Matanzas, Playa Larga, Cuba; USNM 337642, Matanzas, Playa Larga, Cuba; USNM 337644, Matanzas, Playa Larga, Cuba.

APPENDIX 2. *Anolis* species included in morphological (designated by an M), ecological (E), and behavioral (B) analyses, followed by the ecomorph designation and island of origin: HSP = Hispaniola, JA = Jamaica, PR = Puerto Rico. Sample sizes for ecological analyses are noted in parentheses (sample sizes for morphological and behavioral analyses are not provided).

Anolis sageri — Trunk-ground, JA (18) [M, E, B]; *A. lineatopus* — Trunk-ground, JA (18) [M, E, B]; *A. cookei* — Trunk-ground, PR [M]; *A. cristallus* — Trunk-ground, PR (28) [M, E, B]; *A. gundlachi* — Trunk-ground, PR (28) [M, E, B]; *A. cybotes* — Trunk-ground, HSP (71) [M, E, B]; *A. longitibialis* — Trunk-ground, HSP [M]; *A. marcanoi* — Trunk-ground, HSP [M]; *A. strabini* — Trunk-ground, HSP [M]; *A. grahami* — Trunk-crown, JA (18) [M, E, B]; *A. opalinus* — Trunk-crown, JA (18) [M, E, B]; *A. evermanni* — Trunk-crown, PR (28) [M, E, B]; *A. stratulus* — Trunk-crown, PR (28) [M, E, B]; *A. chlorocyanus* — Trunk-crown, HSP (86) [M, E, B]; *A. albigiger* — Trunk-crown, HSP (36) [M, E, B]; *A. coelestinus* — Trunk-crown, HSP (40) [M]; *A. singularis* — Trunk-crown, HSP [M]; *A. poroculus* — Trunk-crown, HSP [M]; *A. pulchellus* — Grass-bush, PR (28) [M, E, B]; *A. poncensis* — Grass-bush, PR (18) [M, E, B]; *A. krugi* — Grass-bush, PR (28) [M, E, B]; *A. olsoni* — Grass-bush, HSP (46) [M, E, B]; *A. semilineatus* — Grass-bush, HSP [M]; *A. behni* — Grass-bush, HSP [M]; *A. distichus* — Trunk, HSP (44) [M, E, B]; *A. christophi* — Trunk, HSP [E, B]; *A. brewsteri* — Trunk, HSP [E, B]; *A. valencienni* — Twig, JA (15) [M, E, B]; *A. occulus* — Twig, PR [M]; *A. insolitus* — Twig, HSP (4) [M, E, B]; *A. caviert* — Crown-giant, PR (5) [M]; *A. garnani* — Crown-giant, JA (18) [M, E, B]; *A. barrozoense* — Crown-giant, HSP (5) [M].

* No data for display behavior are available.

Resumen.—La lagartija policróida *Anolis angusticeps* es superficialmente similar a las lagartijas anolinas enanas que viven en ramitas, un ecomorfo que ha surgido independientemente varias veces en las Antillas. Examinamos la utilización del hábitat, conducta de locomoción y características morfológicas de *A. angusticeps* para determinar si éste exhibe características similares a las de otras lagartijas anolinas enanas que viven en ramitas. Nuestros resultados indican que en todos los aspectos *A. angusticeps* es una típica lagartija anolina enana que vive en ramitas. Como fue predicho, *A. angusticeps* se encuentra característicamente en perchas de dimensiones estrechas, camina lentamente, raras veces muestra alguna conducta, y es morfológicamente similar a otras lagartijas anolinas que viven en ramitas. La coloración críptica, movimientos lentos, y exhibición ineficaz de conductas de las lagartijas anolinas enanas que viven en ramitas apoyan la hipótesis de que estas lagartijas han evolucionado para ser inconspicuas. Las características crípticas de las lagartijas anolinas enanas que viven en ramitas pudieron haber surgido porque estas lagartijas utilizan un hábitat (perchas estrechas) en el cual escapar rápidamente puede ser difícil y por lo tanto han evolucionado para esconderse de depredadores potenciales.

Résumé.—Nous avons étudié la répartition de la faune herpétologique dans 31 îles de Exuma Cays Land and Sea Park (eclsp) aux Bahamas dans le cadre de quatre visites intensives effectuées entre 1990 et 1993. La faune herpétologique se compose de 15 espèces dont deux (peu-être quatre) ont été introduites. Trois modèles zoogéographiques fondamentaux sont mis en évidence par la faune herpétologique, c'est-à-dire par les espèces dont la répartition est soit ubiquiste, soit réservée aux îles centrales, soit répandue. On ne trouve qu'une seule espèce sur presque toutes les îles, trois sur les îles les plus grandes et les plus complexes sur le plan structural (îles centrales) et quatre sur une vaste gamme d'îles dont la taille varie de grande à petite. Trois espèces sont si rares que nous n'avons pas pu les classifier. Les deux autres espèces devaient probablement être plus répandues avant mais semblent aujourd'hui confinées à certains territoires. La taille de l'île explique à elle seule 42% de la variation au titre de la richesse des espèces. La taille de l'île centrale la plus proche et la distance entre l'île centrale la plus proche et les îles satellites n'influent nullement sur la diversité faunique. La répartition de la faune herpétologique de eclsp résulte vraisemblablement d'une série d'événements géologiques et historiques associés à des manifestations écologiques dynamiques permanentes. L'impact potentiel des prédateurs exotiques et des établissements humains ne saurait être sous-estimé pour expliquer le modèle zoogéographique actuel.



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