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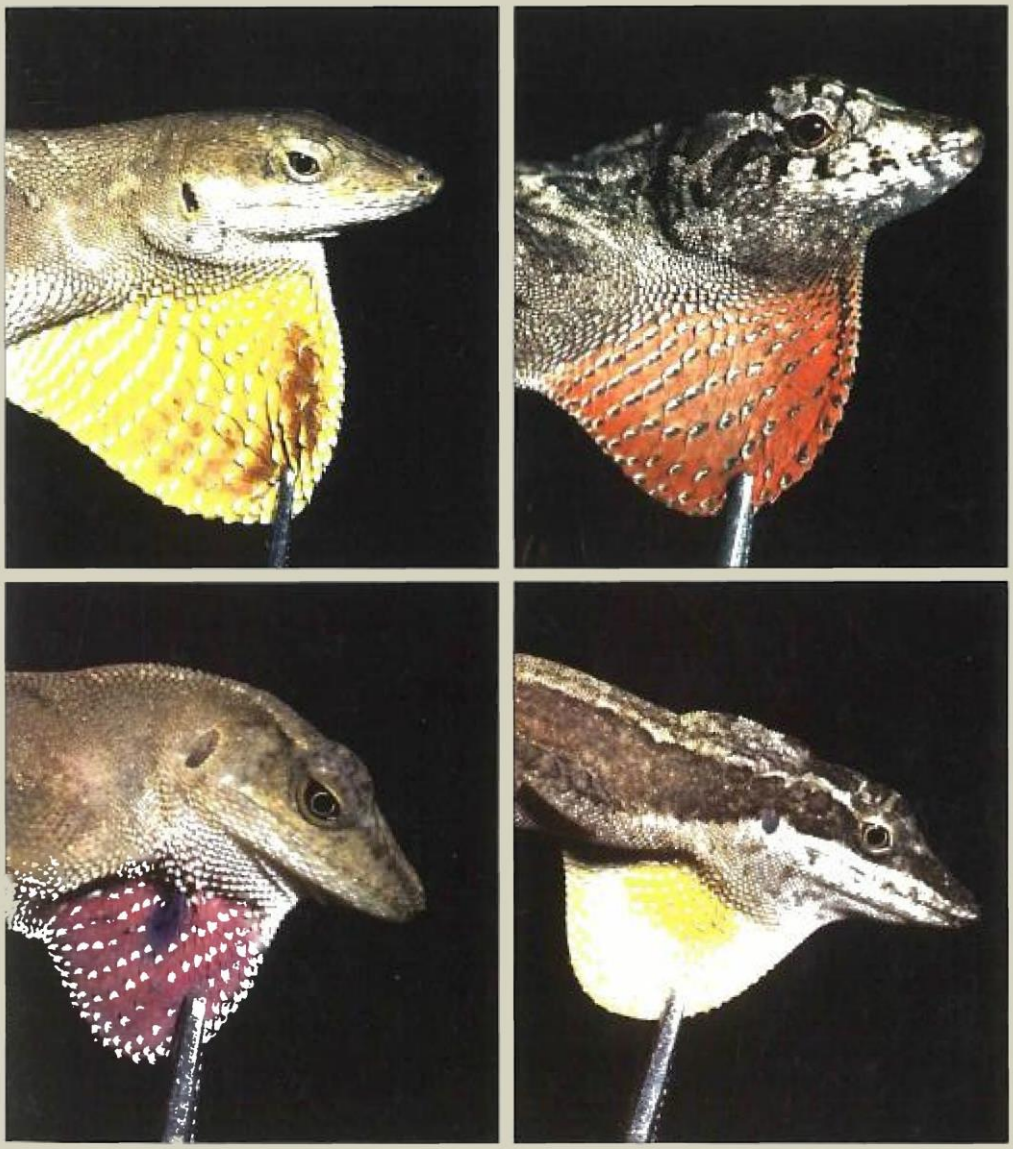

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Natural history observations of sympatric *Norops* (Beta *Anolis*) in a subtropical mainland community

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ABSTRACT – During an approximately four week period the natural history of a mainland forest community of *Norops* (Beta *Anolis*) was studied in Belize. Five species were observed to occur sympatrically (*N. uniformis*, *N. lemurinus*, *N. rodriguezii*, *N. tropidonotus* and *N. capito*). These taxa are all traditionally placed in the *A. auratus* series as originally recognized by Etheridge (1960). Until recently the majority of field research concerned with anoles has focused on species in the Caribbean islands, with mainland communities having generally received far less attention. The primary aim of this paper is to help redress this imbalance by describing the morphology, habitat and behaviour of species in a hitherto unstudied mainland community.

ANOLIS is a large clade of Neotropical lizards that is renowned for the tremendous amount of variation displayed by its members in colour, shape, size, ecological affinity and behaviour (e.g. Schoener, 1968; Williams, 1969; Losos, 1994). This diversity typically permits anoline communities to be composed of several often closely related species that successfully co-exist in the same ecosystem, presenting numerous opportunities for behavioural observations of species interactions, geographical comparisons and experimental manipulations. Consequently, communities of *Anolis* are widely utilized by biologists as experimental models to address some of the most complex questions in both ecological and evolutionary biology (Nicholson, 2002).

This genus is widely distributed across the New World tropics and subtropics with species found throughout the Caribbean islands, southeastern United States and mainland Americas from Mexico to South America (Etheridge, 1960). However, scientific research has not been equally divided between these localities. For decades, Caribbean communities have been the focus of numerous in-depth studies investigating an impressive array of concepts ranging from resource partitioning and community structure to phylogenetic relationships and speciation (e.g. Schoener, 1968; Williams, 1983; Losos, 1994; Leal *et al.*, 1998). As a result, an abundance of information is available regarding the morphology, behaviour, habitat and general natural history of island populations. In contrast, the mainland *Anolis* communities have generally received far less attention (but see Stuart, 1956; Fitch, 1975; Pounds, 1988), leaving a multitude of questions unanswered. Recently several papers have been published concentrating on mainland *Anolis* (e.g. Irschick *et al.*, 1997; Mancrini *et al.*, 2003; Nicholson, 2002), comparing findings to those in the Caribbean in order to redress the imbalance. In this paper I follow this example by providing natural history observations of a mainland community of *Anolis* in Belize.

STUDY AREA AND METHODS

Study site

The study was conducted on the Las Cuevas Research Station, which is situated at approximately 500 m elevation (16°44' N, 88°59' W) within the Cayo district of Belize. As part of the Chiquibul Forest Reserve, it lies within a much larger area of protected forest in the region totaling about half a million hectares. Typical rainfall in this deciduous semi-evergreen and deciduous seasonal tropical forest averages around 2,000 mm per year. The vegetation in the immediate vicinity has been classified as 'Broadleaf Class 2, Seasonal forest' (Penn *et al.*,

2004). It is characterised by an approximate canopy height of 20–30 m and much of the older growth trees possess buttresses and stilt roots covered with epiphytes (Stafford & Meyer, 2000). In addition, this vegetation type possesses an abundant palm layer (Penn *et al.*, 2004) and tree ferns are present where edaphic conditions permit (Stafford & Meyer, 2000). A comprehensive species list of the vegetation surrounding the station site is provided by Penn *et al.* (2004).

Norops (Beta *Anolis*)

Several species of *Norops* are known to occur sympatrically in the vicinity of Las Cuevas Research Station. In this study the name *Norops* is used to refer to the clade corresponding to the former beta section of the genus *Anolis* as suggested by Nicholson (2002). This follows the classification advocated by Guyer & Savage (1986; 1992) that also recognizes four additional genera [*Anolis (sensu stricto)*, *Ctenonotus*, *Dactyloa*, and *Xiphosurus*] in place of the former alpha section. It is customary to use the term *Anolis* to refer to either the alpha section only (and use *Norops* for the beta section), or to use *Anolis* for all included species (alpha and beta section) as in the sense of Etheridge (1960) (Nicholson 2002). However it is also important to note that opinion is still divided upon this controversial subject. For example, a recent phylogenetic study carried out by Poe (2004) suggests that this genus is in fact monophyletic and does not warrant division into several genera.

Field observations

Fieldwork was carried out from the 22nd May to the 12th June 2004, at the beginning of the summer rainy season. Random searches were carried out throughout the day and evening, but individuals were only seen during the day. Most lizards were caught by hand or net whilst basking on leaf litter scattered on the ground near trails, on the stems of vines, on the buttresses of trees or on the trunks of trees. For each species detailed notes regarding habitat and microhabitat conditions were taken and the habitat variables of mean perch height and diameter data were gathered following the guidelines outlined by Losos & Irschick (1996).

Individual lizards were observed from a distance of 5–10 m with intervening vegetation used as a blind in order to quantify aspects of inter- and intraspecific behaviour. Captured specimens were also placed in confinement together with members of their own and other species in order to further analyze the interactions of these lizards. Descriptions of these observations are documented later in this paper.

Table 1. Mean morphological and ecological values for 4 mainland anole species (values for sole *N. capito* specimen are included). Note: figures correspond to mean ± SE (first number), range (second number), and sample size (third number). Perch height and diameter are the ecological variables and are in millimeters. The remaining variables are morphological and are in millimeters with the exception of body mass and lamellae number.

Species	SVL (mm)	Body Mass (g)	Tail Length (mm)	Forelimb (mm)	Hind-limb (mm)	Lamellae number	Perch height (mm)	Perch diameter (mm)
N. tropidonotus	50.2 – 0.4 (46-56) N = 34	2.1 – 0.04 (2-3) N = 34	95.2 – 1.1 (81-104) N = 32	25.1 – 0.16 (23-27) N = 34	47.4 – 0.4 (42-50) N = 34	24.4 – 0.2 (23-28) N = 34	76.2 – 18.8 (10-440) N = 34	75.3 – 16.9 (18-410) N = 34
N. uniformis	33.5 – 0.5 (30-39) N = 17	1 – 0 (1-1) N = 17	43 – 0.7 (40-51) N = 15	15.3 – 0.5 (11-17) N = 17	28.6 – 0.5 (25-32) N = 17	26 – 0.5 (23-30) N = 17	295.9 – 50.9 (30-720) N = 17	275.6 – 23.6 (20-425) N = 17
N. Lemurinus	63.1 – 0.9 (56-73) N = 18	3.5 – 0.2 (2-6) N = 18	135.9 – 3.0 (103-150) N = 17	28.1 – 0.36 (26-32) N = 18	53.2 – 0.7 (49-60) N = 18	37 – 0.2 (34-38) N = 18	631.9 – 94.4 (40-1270) N = 18	232 – 30.3 (30-370) N = 18
N. rodriguezii	34 – 0.9 (30-37) N = 11	1 – 0 (1-1) N = 11	38.4 – 0.9 (31-41) N = 11	15.7 – 0.3 (15-17) N = 11	26 – 0.4 (25-28) N = 11	34.1 – 0.6 (31-37) N = 11	885.5 – 156.9 (170-1380) N = 11	98.5 – 18.9 (15-230) N = 11
N. capito	87 (na, na, 1)	19 (na, na, 1)	160 (na, na, 1)	38 (na, na, 1)	74 (na, na, 1)	40 (na, na, 1)	3100 (na, na, 1)	300 (na, na, 1)

Norops rodriguezii. All photographs © N. D'Cruze.

Norops tropidonotus; mating pair.

Norops capito; adult male.

Norops tropidonotus; adult female.

Norops lemurinus; adult male.

Norops tropidonotus; the darker colour is a probable response to handling stress.

Morphological data were also gathered for the Belizean mainland anole species for comparison with previous studies. Table 1 provides a list of the species names and sample sizes for individuals collected in this study. For each of the species the following six morphological traits were measured: snout-vent length (SVL), body mass, number of lamellae underlying the fourth toe of the hind-foot,

and lengths of the forelimb, hind-limb and tail. Length of the forelimb and hind-limb were measured as the distance from the insertion point of the limb to the longest toe of each foot. All morphological traits were measured on living individuals that were subsequently released at the point of capture. All measurements were taken by a single investigator (N. D'Cruze), precluding the need to correct for individual measurement error.

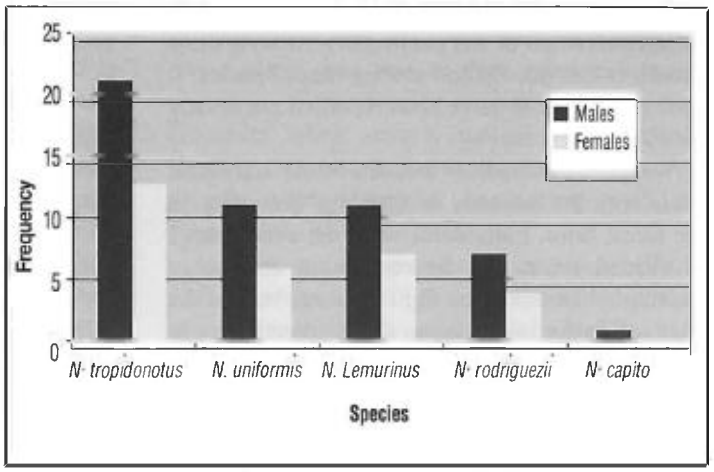

Figure 1. Frequency of captured lizards.

RESULTS AND DISCUSSION

Five species of *Norops* (*N. uniformis*, *N. lemurinus*, *N. rodriguezii*, *N. tropidonotus* and *N. capito*) were observed to occur sympatrically in this community. It is important to note that populations of *N. lemurinus* found in Belize are recognized by some authorities (e.g. Campbell, 1998) as distinct from those in lower Central America and are referred to as *N. bourgaei*. Similarly, *N. uniformis* has been previously recognized as a subspecific race of *N. humilis*.

All species were most active during late morning and early afternoon with few observations before 10:00 and after 18:00 hrs. Table 1 presents a summary of the morphological and habitat data gathered for the total number of lizards sampled (83). Figure 1 shows the frequency of each species encountered. It clearly demonstrates that *N. tropidonotus* was the most abundant and commonly encountered species of anole (or lizard for that matter) and that *N. uniformis* and *N. lemurinus* were also relatively abundant in this community. Despite efforts to increase the sample size of *N. rodriguezii* and *N. capito* these species were least abundant. *N. capito* was particularly rare and only one lone individual was observed. Figure 1 also highlights that males were more commonly observed than females with regards to all five species.

Natural history observations

Natural history observations and descriptions of the five species encountered at Las Cuevas are listed below. More detailed descriptions of these species are provided by Stuart (1955), Taylor (1956), Fitch (1975), Stafford & Meyer (2000), Lee (2000) and Savage (2002).

Norops tropidonotus (Peters)

Diagnosis and habitat: This is a medium-sized lizard readily identified by the presence of deep axillary pockets and enlarged medial dorsal scales that are of almost equal size to those of the venter (Stafford & Meyer, 2000). In addition males possess a relatively large dewlap that is bright yellow in colour with a burnt orange lower edge. The lizards encountered during this study were much smaller than previously described with an average snout vent length of 50 mm; the largest captured specimen possessed a snout-vent length of just 56 mm. Although the average unbroken tail length was around 95 mm, some unbroken tail lengths were recorded to up to 19 mm shorter than previously described. Examination of the fourth toe of the hind foot indicates that these lizards typically possess 24 to 28 sub-digital lamellae. Small pink larvae of trombiculid mites, typically ranging from 5 to 20 in number, were observed in the axillary pockets of all individuals. There is significant evidence of sexual dimorphism in this species as males were typically larger in size and mass than females, which were observed to possess rudimentary dewlaps. Although colour and pattern are known to be highly variable in this species (Lee, 2000) an additional scalloped or

'diamond' dorsal pattern was observed in several females captured in this community. Although this pattern is not uncommon among anole species, it does not appear to have been recorded previously for *N. tropidonotus*.

Norops tropidonotus was the most terrestrial anole with the majority of sightings occurring on the forest floor. Individuals were not encountered in shaded areas, but instead found commonly basking in the sun or on light coloured bark at the edge of paths away from dense vegetation. In accordance with Stafford & Meyer (2000), this species appears to be ecologically replaced by the smaller *N. uniformis* in wetter conditions of the forest surrounding the Las Cuevas Research Station, as only one individual was collected from what could be considered a moist microhabitat. However, both species were caught on trees less than 1 m away from each other, which suggests that the two species do come into contact with each other at least on an occasional basis.

Intraspecific interactions and escape behaviour: Occasionally males were found at higher positions on the lower parts of tree trunks. Here they were observed to engage in territorial and courtship displays, extending their brightly coloured dewlap, bobbing up and down and ferociously chasing any competitors away for distances up to a metre. When placed together with several other males in a container, further vigorous displays towards each other were observed to occur. Whilst in confinement, members of this species were observed in amplexus when left for several minutes. In males the dorsal pattern markings are known to disappear under conditions of stress (Stafford & Meyer, 2000). This behaviour was witnessed several times with threatened individuals on several occasions turning from the typical tan brown to pitch black in colouration.

When pursued, individuals of this species ran for distances less than 3 m and then paused motionless in leaf litter in a superficial situation, relying on cryptic behavior to avoid capture. This behaviour is in contrast to that of certain other terrestrial lizards (e.g. *Ameiva festiva*), which when disturbed continued to move into deeper foliage until safely out of sight. No lizards were seen to 'dive under leaf litter to escape' as described by Lee (2000).

Norops uniformis (Peters)

Diagnosis and habitat: This is a small, stubby bodied species that can also be identified by the presence of deep axillary pockets (Stafford & Meyer, 2000). However, it can be distinguished from *N. tropidonotus* by the scales found on the venter, which are smaller than the enlarged medial dorsal rows (Stafford & Meyer, 2000). Males have a dewlap that is relatively large, bright red in colour with dark scales and a yellow outer edge (Fitch, 1975).

The lizards encountered during this study were slightly smaller than previously described, with an average snout vent length of 33.5 mm. The maximum unbroken tail length was 51 mm, which is around 30 mm shorter than previously described. Sexual size dimorphism is not apparent in this species as males and females were similar in size and mass. Lizards possessed the typical number of 23 to 30 sub-digital lamellae under the fourth toe of the hind foot, as described by Savage (2002), and the larvae of trombiculid mites were found in the axillary pockets of all individuals.

This species has been described as the most terrestrial of all the Central American anoles (Fitch, 1975). However, for the lizards observed at Las Cuevas this was not the case. Although it was always found close to the forest floor, individuals were typically found perched on the buttresses or lower trunks of trees rather than the ground. The average perch height of 295.9 mm observed for this species was higher than that of the more terrestrial *N. tropidonotus* (76.2 mm). All but one individual observed in this study was found perched in wet conditions, with a high majority perched in the shade or on dark coloured bark, supporting claims that it is a thermoconfromer that prefers a warm wet climate (Fitch, 1975; Savage, 2000).

Intraspecific interactions and escape behaviour: Males of this species appeared secretive in comparison to the bolder *N. tropidonotus* and were not observed to engage in any territorial or courtship displays. In addition, when individuals collected in this study were placed together in a

container, previously recorded threat displays (Fitch, 1975) were not observed.

When disturbed these anoles were observed to run to the base of a tree and crouch on the opposite side to that of the investigator, or run over root buttresses, pausing under screening vegetation as described by Fitch (1975). Individuals did not move again threatened at close range, relying on cryptic behaviour to avoid detection. When escaping, this species tended to seek refuge on or very close to the ground, rather than ascending to higher elevation in accordance with the observations of Taylor (1956).

Norops lemurinus (Cope)

Diagnosis and habitat: This is a medium-sized lizard that can be readily identified by the absence of axillary pockets and presence of imbricate and strongly keeled midventral scales (Stafford & Meyer, 2000). Males have low nuchal and caudal crests (Savage, 2002) and a large dewlap which ranges in colour from dark maroon with black scales (Fitch, 1975) to reddish to light orange with a deep orange border, typically contrasted with scales of pure white (Stafford & Meyer, 2000).

The lizards encountered during this study were very similar in size to previous descriptions with an average snout vent length of 63 mm. However, one exceptionally large individual had a snout- vent length of 73 mm, a tail length of 150 mm, and weighed a massive 6 grams. The average unbroken tail length was around 136 mm, a good 16 mm longer then previously described. Lizards possessed the typical 31 to 38 lamellae under the fourth toe of the hind foot (Savage, 2002). Sexual size dimorphism was evident in this species with females typically larger than males in size and mass.

In this study this relatively abundant species appeared to be highly arboreal and was most commonly perched openly on tree trunks with an average perch height of 632 mm. However, individuals were observed to make occasional forays to the ground and several individuals were encountered on the forest floor.

Intraspecific interactions and escape behaviour: No intraspecific interactions involving this species were witnessed during this study. This is not surprising because *N. lemurinus* is commonly found alone, and due to their relative scarcity, observed intraspecific encounters are rare. However when several males were confined together they also failed to display and no actual attacks were observed, concurring with the observations of Fitch (1975).

In contrast to previous observations (Fitch, 1975; Savage, 2000) the numerous individuals observed in this study appeared to be highly active. When disturbed they were seen to dash around the tree and stop motionless on the opposite side to that of the investigator. Only then did they rely on their cryptic coloration, remaining motionless until threatened at close range. If disturbed again, this species escaped by fleeing upward along the trunk, often to considerable heights of around 5 m as described by Savage (2002).

Norops rodriguezii (Bocourt)

Diagnosis and habitat: This is a small lizard that also lacks axillary pockets. It can be distinguished from *N. lemurinus* by the presence of subconical to smooth or weakly keeled midventral scales (Stafford & Meyer, 2000). Males have a relatively large dewlap that is pastel yellowish orange in colour with a burnt orange central spot (Stafford & Meyer, 2000).

The lizards encountered during this study were much smaller than previously described. The average snout vent length of all of the lizards sampled was only 34 mm; the largest specimen caught possessed a snout vent length of just 37 mm. The average unbroken tail length was only around 38 mm which is also a great deal shorter than previously described. Lizards sampled in this study possessed 34 to 37 lamellae under the fourth toe of the hind foot.

This was one of the most arboreal of all the anole species encountered in this habitat with an average perch height of 885.5 mm and was commonly observed perched high on the thinner branches of trees. Some individuals were also encountered in small bushes and the lower parts of trees. The findings of this study conflict with Lee (2000) as it was most abundant in dense

vegetation, away from forest edges near paths. It was commonly seen basking in sunlight which indicates that it is not a thermoconformer.

Intraspecific interactions and escape behaviour: This species was commonly found alone and because of their scarcity, no intra-specific encounters were witnessed during this study. In addition no territorial or courtship displays were observed in confinement.

When disturbed these anoles were observed to attempt escape by fleeing upward along the trunks of trees, often to considerable heights in a very similar manner to the other arboreal species *N. lemurinus*. Only when safely out of reach did they pause motionless and rely on their cryptic colouration.

Norops capito (Peters)

Diagnosis and habitat: This is a large anole that is unlikely to be confused with any other allied form because of its extremely short head (Savage, 2002). It was both the largest and the rarest anole observed in this habitat as only one specimen was sighted and caught. This individual had a snout-vent length of 87 mm, a tail length of 160 mm and possessed 40 sub-digital lamellae. The dorsum of this species is typically tan to olive-brown in Belize (Stafford & Meyer, 2000). However the individual caught in this study was very green in colouration, noticeably more so than previous descriptions.

Intraspecific interactions and escape behaviour: As a result of its scarcity, no intraspecific encounters were witnessed. Previous studies indicate that this species tends to segregate on different tree trunks, maintaining exclusive territories with surface areas of about 145 m^2 (Fitch, 1975). This territorial behaviour goes some way in explaining the scarcity of this species. When released the individual attempted to escape by fleeing up the trunk of a large tree to a height of around 10 metres.

Interspecific interactions

A previous study carried out by Fitch (1975) is very informative regarding the interspecific interactions of the lizards described in this study. In this study a community composed of 17 anole species in Costa Rica at Finca Le Selva was observed and revealed that *Norops uniformis* alone was associated with 11 other species. Interspecific interactions of the five anole species found in this community from Belize are discussed below and are compared to the findings of Fitch (1975).

N. uniformis* and *N. rodriguezii

Fitch (1975) speculated that interactions must be most frequent between the small abundant species. He claimed that since *Norops uniformis* and *N. rodriguezii* were abundant in the same habitat, interactions between them must have been frequent and important to both. However, observations made in this study indicate that although the two species are very similar in size they probably do not come into direct contact with each other very often, and therefore interactions between the two are limited. Firstly, the two species differ greatly in habitat. *Norops uniformis* is a predominantly terrestrial anole that was not seen to venture above 720 mm, whereas *N. rodriguezii* is a predominantly arboreal species with an average perch height of 885.5 mm. Secondly, the two species differ greatly in climactic preferences. *Norops uniformis* was typically found in wet and shaded vegetation, whereas *N. rodriguezii* was found in drier, more open vegetation.

N. uniformis* and *N. tropidonotus

Fitch (1975) suggested that when *Norops* of similar size occur together the competition of the more abundant terrestrial species might exert selective pressure for arboreality on the other. This observation is of particular relevance because in this complex system it seems that the larger and more abundant terrestrial *N. tropidonotus* has – and possibly still is – exerting dominance over the rarer *N. uniformis*, forcing it into a more arboreal niche. *Norops uniformis* has been described as 'the most terrestrial of all the Central American anoles' (Fitch, 1975) and was typically found on the buttresses of trees with an average perch height of 296 mm. However, it was *N. tropidonotus* that was found to dominate the forest floor with an average perch height of just 76 mm. Interactions between

the two species are limited by the fact that the two species differ in microhabitat and climactic preferences. *Norops uniformis* was sighted in much wetter and denser vegetation than *N. tropidonotus*, which was typically perched in drier and more open vegetation.

N. uniformis and *N. lemurinus*

Interspecific interactions involving *Norops uniformis* and *N. lemurinus* were speculated by Fitch (1975) as individuals from both species were found in the same habitat, sometimes on the same tree trunks. However, in this Belizean community interactions between the two species are limited by the fact that *N. lemurinus* is a predominantly aboreal lizard whereas *N. uniformis* is a predominantly terrestrial anole. It is important to note that *N. uniformis* is typically only about / of the mass of *N. lemurinus*. Therefore as Fitch (1975) suggested *N. lemurinus* is large enough to be a potential predator of young *N. uniformis*.

N. lemurinus and *N. rodriguezii*

In this study these two species were observed to be highly arboreal and are likely to come into contact with each other frequently. As Fitch (1975) commented the two species differ greatly in size which is reflected in the results of this study and means that *Norops lemurinus* is a potential predator of the smaller *N. rodriguezii*. However interactions between the two species are limited by their differences in microhabitat preferences. *Norops lemurinus* was sighted on tree trunks where as *N. rodriguezii* was typically perched on branches and twigs.

N. capito

Fitch (1975) claimed that *Norops lemurinus* was more similar to *N. capito* in habitat than any other species. In this study both species were observed on the trunks of large trees in the forest. Fitch (1975) also pointed out that in addition to the similarity in habitat preference, *N. capito* can reach up to three times the bulk of *N. lemurinus* and is a known predator on other smaller lizards. It is not difficult to speculate that, as well as feeding on *N. lemurinus*, this large arboreal species may also prey upon all of the other anole species found in this mainland forest community.

Other Interspecific interactions

Interspecific interactions between *Norops tropidonotus* and *N. lemurinus* and *N. tropidonotus* and *N. rodriguezii* were not discussed by Fitch (1975). They are not likely to occur in this community because *N. tropidonotus* is a predominantly terrestrial species where as the other two are predominantly arboreal in nature.

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REFERENCES

Campbell, J. A. (1998). *The Amphibians and Reptiles of Northern Guatemala, Yucatán, and Belize*. Norman, Oklahoma: University of Oklahoma Press.

Etheridge, R. E. (1960). *The relationships of the anoles (Reptilia: Sauria: Iguanidae): an interpretation based on skeletal morphology.* Unpublished PhD Dissertation. Ann Arbor: University of Michigan.

Fitch, H. S. (1975). Sympatry and interrelationships in Costa Rican anoles. *Occ. Papers. Mus. Nat. Hist. Univ. Kansas*. **40**, 1–60.

Glossip, D. & Losos, J.B. (1997). Ecological correlates of number of subdigital lamellae in

anoles. *Herpetologica* **53**, 192–199.
Guyer, C. & Savage, J. M. (1986). Cladistic relationships among anoles (Sauria: Iguanidae). *Syst. Zool.* **35**, 509–531.
Guyer, C. & Savage, J. M. (1992). Anole systematics revisited. *Syst. Biol.* **41**, 89–110.
Irschick, D. J., Vitt, L. J., Zani, P. A. & Losos, J.B. (1997). A comparison of evolutionary radiations in mainland and Caribbean *Anolis* lizards. *Ecology* **78**, 2191–2203.
Leal, M., Rodriguez-Robles J. A. & Losos J.B. (1998). An experimental study of interspecific interactions between two Puerto Rican *Anolis* lizards. *Oecologia* **117**, 273–278.
Lee, J. C. (1980). An ecogeographical analysis of the herpetofauna of the Yucatán Peninsula, Guatemala, Belize and Mexico. *Publ. Mus. Nat. Hist., Misc., Univ. Kans* **67**, 1–75.
Lee, J. C. 1996. *The Amphibians and Reptiles of the Yucatán Peninsula*. Ithaca, NY: Comstock Publishing Associates.
Losos, J. B. (1994). Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. *A. Rev. Ecol. Syst.* **25**, 467–493.
Losos, J. B. & Irschick, D. J. (1996). Escape behaviour in Caribbean *Anolis* lizards: laboratory-based predictions and field tests. *Anim. Behav.* **51**, 593–602.
Losos, J. B., Jackman, T. R., Larson, A., De Quieroz, K. & Rodrigues-Schettino, L. (1998). Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**, 2115–2118.
Losos, J. B. (1999). Uncertainty in the reconstruction of ancestral character states and limitations on the use of phylogenetic comparative methods. *Anim. Behav.* **58**, 1319–1324.
Macrini, T. E. & D. J. Irschick. (1998). An intraspecific analysis of trade-offs in sprinting performance in a West Indian lizard (*Anolis lineatopus*). *Biol. J. Linn. Soc.* **63**, 579–591.
Macrini, T. E., Irschick, D. J. & Losos, J. B. (2003). Ecomorphological differences in toe-pad characteristics between mainland and islands anoles. *J. Herpetol.* 37, 52–58.
Nicholson, K. E. (2002). Phylogenetic analysis and a test of the current infrageneric classification of *Norops* (beta *Anolis*). *Herpetol. Monogr.* **16**, 93–120.
Penn, M.G., Sutton, D.A. & Monro, A. (2004). Vegetation of the Greater Maya Mountains, Belize. *Systematics and Biodiversity* **2**, 21–44.
Poe, S. (2004). Phylogeny of Anoles. *Herpetological Monograph* **18**, 37–89,
Pounds, J. A. (1988). Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland community. *Ecol. Monogr.* **58**, 299–320.
Savage, J. M. (2002). *Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents, between Two Seas.* University of Chicago Press, Chicago, IL.
Schoener, T. W. & Gorman G. E. (1968). Some niche differences in three Lesser-Antillean lizards of the genus *Anolis*. *Ecology* **49**, 819–830.
Schoener, T. W. (1968). The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**, 704–726.
Schoener, T. W. (1969). Size patterns in West Indian *Anolis* lizards. I. Size and species diversity. *Syst. Zool.* **18**, 386–401.
Schoener, T. W. (1975). Presence and absence of habitat shift in some widespread lizard species. *Ecol. Monogr.* **45**, 233–258.
Stafford, P. J., & Meyer, J. R. (2000). *A Guide to the Reptiles of Belize*. San Diego, CA: Academic Press.
Stuart, L. C. (1955). A brief review of the Guatemalan lizards of the genus *Anolis*. *Misc. Publ. Mus. Zool., Univ. Mich.* **91**, 1–31.
Taylor, E. H. (1956). A review of the lizards of Costa Rica. *Univ. Kans. Sci. Bull.* **38**, 3–322.
Williams, E. E. (1969). The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Q. Rev. Biol.* **44**, 345–389.
Williams, E. E. (1983). Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. In *Lizard Ecology: Studies of a Model Organism*, pp. 326–370. Huey, R. B. & Pianka, E. R. (Eds). Cambridge, Harvard University Press.

EDITORIAL

Erratum

Two of the illustrations on the front cover of the previous issue of *Herpetological Bulletin* were unfortunately printed in the wrong sequence. Viewing in a clockwise direction from top left, the third photograph (i.e., lower right) is of *Norops rodriguezii*, and the final picture is *N. humilis*. *ED*