

## RESOURCE PARTITIONING OF SYMPATRIC *NOROPS* (*BETA ANOLIS*) IN A SUBTROPICAL MAINLAND COMMUNITY

NEIL C. D'CRUZE<sup>1</sup> AND PETER J. STAFFORD<sup>2</sup>

<sup>1</sup>*Department of Biological Sciences, Imperial College of Science, Technology and Medicine, London, UK*

<sup>2</sup>*The Natural History Museum, Cromwell Road, London, UK*

During an approximately four-week period the ecology and interrelationships of sympatric anoles (*Norops* spp., *Beta Anolis*) was studied at a lowland forest site in Belize. The primary aim was to investigate aspects of niche overlap and resource partitioning among species in a typical mainland forest community by quantifying the dimensions of morphology, structural habitat and microclimate. Through characterization of each ecological niche we aimed to determine how these lizards partition the complex resource base and habitat in which they co-exist. Anole species at the study site clearly appear to partition environmental resources along the three major resource axes of microclimate, habitat structure, and probably also prey size, as originally defined by Pianka (1974). Two of the species also show evidence of sexual size dimorphism, indicating that the 'total' niche of these species is further divided into two 'sub-niches' corresponding to each sex. Further experimental manipulations are required, however to demonstrate conclusively whether interspecific competition alone is responsible for structural patterns within anole communities such as this, and also to define the function of differential susceptibility among species to parasites. In the case of three species, a positive correlation between the number of lamellae on the fourth toe of the hind foot and perch height was observed, supporting the notion that lamella number is highly adaptive for an arboreal lifestyle and related to habitat use.

*Key words:* ecological niche, lizard, sexual dimorphism, toe-pad morphology

### INTRODUCTION

*Anolis* is a speciose and ecologically diverse clade of Neotropical lizards that has been described as "a model system for addressing biological questions" (Nicholson, 2002). Several aspects of their biology are responsible for this unique distinction. They are often relatively common, and are also of sufficient size to allow direct observation both in the field and in more contrived environmental conditions where they respond relatively well (e.g. Leal *et al.*, 1998). In addition, *Anolis* communities are typically composed of several, often closely related species that successfully coexist in the same ecosystem, presenting numerous opportunities for geographical comparisons, experimental manipulation, and detailed studies of interspecific behaviour. Such is the potential of anoles in helping to improve our understanding of ecological relationships and community structure in lizards that they have been the subject of numerous field studies (e.g. Fitch, 1973, 1975; Talbot, 1976, 1979; Corn, 1981; Guyer, 1986; Pounds, 1988; Vitt *et al.*, 2003; D'Cruze, 2005).

Communities of lizards that are composed of several species can often be observed to partition environmental resources along the three major axes of prey size, microclimate, and habitat structure (Pianka, 1974). These have indeed proven to be important measures that segregate

sympatric taxa and have been used in many other studies relating to anoles (e.g. Rand, 1964; Schoener, 1968; Irschick *et al.*, 1997). Understanding the basis of resource partitioning within a complex fauna, however, is complicated by the fact that the 'total' niche of each species can often be further divided into two 'sub niches' corresponding to each sex (Butler *et al.*, 2000). Anoles vary considerably in the extent of sexual dimorphism (Stamps *et al.*, 1997), differences in size between males and females ranging from striking to practically absent. Intraspecific differences in resource use must therefore also be considered in order for resource partitioning at a higher community level to be fully comprehended.

A distinctive feature of anole morphology is the expanded subdigital toe-pad, which exhibits variation among species in both the degree of expansion and number of lamellae (Savage, 2002). Earlier studies have repeatedly demonstrated positive correlations between toe-pad size or the number of toe-pad lamellae with increasing perch height (Collette, 1961; Moermond, 1979; Glossip & Losos, 1997), suggesting that variation in these characters is highly adaptive for an arboreal lifestyle and related to habitat use.

The major aims of this study were to (1) define the extent of inter- and intraspecific resource partitioning among anoles in a subtropical mainland community along the main resource axes outlined by Pianka (1974), and (2) to determine whether the particular anole species found therein demonstrate a positive correlation between the degree of arboreality and the

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*Correspondence:* N. C. D'Cruze, Department of Biological Sciences, Imperial College of Science, Technology and Medicine, London SW7 2AY, UK. *E-mail:* cruzecontrol@gmail.com

number of subdigital lamellae. In this study the name *Norops* is used to distinguish the former beta section of *Anolis* as suggested by Nicholson (2002), which follows the classification advocated by Guyer & Savage (1986; 1992). For other recent assessments of relationships in this complex group see also Glor *et al.* (2001) and Nicholson *et al.* (2005).

## MATERIALS AND METHODS

Fieldwork was conducted at the Las Cuevas Research Station, a lowland (ca. 500 m) sub-humid forest site in the provincial district of Cayo, Belize (16°44' N, 88°59' W). Six species of *Norops* are known from the general area of this locality (Stafford & Meyer, 2000), of which the following five were recorded: *N. capito*, *N. lemurinus* (= *N. bourgaei*), *N. rodriguezii*, *N. tropidonotus* and *N. uniformis*. Observations were made between 22 May and 12 June 2004, at the beginning of the summer rainy season. Searches were conducted throughout the day and evening, but lizards were seen only during the day. Most were caught by hand or net in leaf litter near trails, on the surface of broad leaves of creeping vines, stems of vines, buttresses of trees, or on the trunks of trees. Observations were recorded from a distance of 5–10 m, with intervening vegetation used as a screen in order to minimize any possible detrimental effect on natural behaviour caused by human presence. Habitat variables were measured at the point where lizards were sighted, and mean perch height and diameter were gathered following the guidelines outlined by Losos & Irschick (1996). In addition, the following other data were recorded for each individual: habitat type, time of day, whether the perch site was located in a generally wet or dry position, and whether the perch site was located in dense, shaded vegetation or in more brightly lit peripheral situations on the perimeter. Habitats were categorized into three principal groups as described for the area by Penn *et al.* (2004); broadleaf seasonal forest ("Class 2"), broadleaf semi-evergreen forest ("Class 3"), and broadleaf semi-evergreen forest (lowland) ("Class 4a"). Microhabitats included (1) ground, (2) tree buttresses or roots, (3) tree trunks and (4) twigs and branches.

For each species the following morphological variables were recorded: sex (determined by appearance of dewlap, colouration, and extent of swelling at base of the tail), 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. Tail lengths from lizards with broken or damaged tails were not included. These same morphological traits have been used in other, similar studies of anole ecology and shown to be highly informative (Irschick *et al.*, 1997). Descriptive statistics and statistical analyses were computed using SPSS 11.5 for Windows (SPSS Inc., 2002). Means  $\pm$  SE are given with  $\alpha \leq 0.05$  accepted as significant, and to examine whether

variables remained statistically correlated once the effect of size was removed, residuals were also used from regressions of each variable against SVL (Macrini *et al.*, 2003).

In order to determine if any pattern was apparent in the ordination of results, and thus illustrate the general extent of niche separation among species, the data collected from captured individuals was assessed using non-metric multidimensional scaling. Sample sizes were restricted to 10 specimens (5 males and 5 females) of each species in order to aid visual interpretation and to ensure that sample numbers remained equal. Assessment focused specifically on the adult population with analysis restricted to the largest 10 individuals of each species. The characters used were SVL, number of lamellae, perch height, perch width, and proportional ratios of tail length (e.g. tail length divided by SVL), forelimb length, and hind-limb length. Values for each character were standardized before analysis to *z*-scores with a mean of 0 and standard deviation of 1, and the ordination of specimens along two NMMDS dimensions was plotted. A two-dimensional NMMDS solution was sought because the alternative hypothesis suspected the existence of three similarity-based groupings.

Correlations and non-parametric tests were carried out using standard statistical procedures rather than phylogenetic comparative methods (Purvis & Rambaut, 1995; Freckleton, 2000). These were chosen for several particular reasons. Firstly, Irschick *et al.* (1997) demonstrated for a very similar set of anole species (several of the same species) that no phylogenetic effect exists for the ecological and morphological variables used in this study. Macrini *et al.* (2003) did not use phylogenetic comparative methods when investigating similar anole species based on these findings. In addition, Losos (1999) stated that phylogenetic comparisons may not always be necessary as closely related species are not necessarily similar ecologically or morphologically. Most importantly, the use of phylogenetic comparative methods is rendered difficult by the fact that our understanding of anole relationships, especially mainland species, is still incomplete (Nicholson, 2002).

## RESULTS

Data were collected for a total of 83 lizards representing all five species. However, only *Norops lemurinus*, *N. rodriguezii*, *N. tropidonotus* and *N. uniformis* occurred in sufficient numbers to allow the collection of meaningful data. Fig. 1 shows that male lizards were more abundant (or alternatively more conspicuous) than females with regard to these four species. Due to the limited sample size, data gathered for *N. capito* was not used in any analysis, and not all data gathered for the other species were included. Despite efforts to increase the sample size of *N. rodriguezii* and *N. capito* these species were least abundant. All species were most active during late morning and early afternoon with few observations before 10.00 hr and after 18.00 hr.

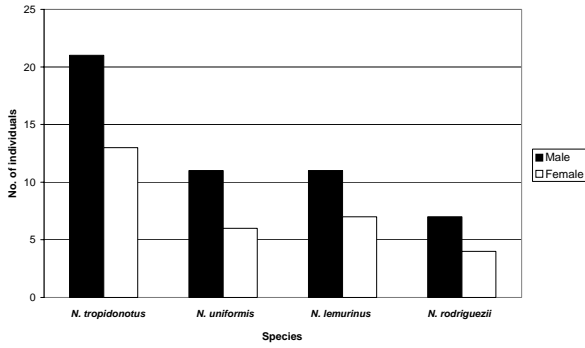


FIG 1. Sex ratios (adult) of captured lizards.

DIFFERENCES IN HABITAT OCCUPATION

One method of examining interspecific spatial differences among species is to list them according to the various habitat categories (as defined by vegetation types) in which they are observed, in the hope that “at least partial two-dimensional allopatry can be demonstrated” (Schoener, 1968). If this concept is applied to the three principal vegetation classes recognized for the area by Penn *et al.* (2004), a clear pattern emerges (Table 1). *Norops lemurinus* was the most widespread and abundant of the four species, and was found in all four vegetation types. It was the only species observed in broadleaf semi-evergreen forest (lowland) vegetation (“Class 4a” of Penn *et al.*, 2004). *Norops tropidonotus* was abundantly present in two of the three vegetation types. *Norops uniformis* and *N. rodriguezii* were also found in two of the three vegetation types, but only rarely sighted in Class 3 vegetation. All four species were classed as abundant in Class 2 type vegetation. Thus the question of how these anole species coexist at Las Cuevas, despite the number of different vegetation types present, can be simplified by addressing the wider issue of coexistence in a broadleaf seasonal forest. If a detailed study is made of microhabitat preferences within this general vegetation type, then the degree of restriction for each species within the range of vegetation available will be possible to determine.

Table 2 presents observations regarding the perch location of individual lizards, and shows that *N. tropidonotus* and *N. uniformis* are predominantly terrestrial forms, the former being most commonly encountered on the ground and the latter on tree buttresses or roots. However, these two species appear to show separation along the microclimate axis as 95% of *N. tropidonotus* were sighted in dry conditions, whereas 94% of *Norops uniformis* were sighted in generally

mesic situations. This evidence supports previous claims that *N. uniformis* appears to ecologically replace *N. tropidonotus* in wetter conditions (Stafford & Meyer, 2000). In addition, the two terrestrial species appear to have different preferences with regard to vegetation density, with 82% of *N. tropidonotus* having been found basking in relatively open situations (e.g., at the edges of trails), and 71% of *N. uniformis* in dense vegetation. Table 2 also indicates that *N. lemurinus* and *N. rodriguezii* are predominantly arboreal species, as the former was most commonly encountered on tree trunks and the latter on twigs and branches. Unlike the terrestrial species these arboreal forms do not appear to show the same degree of separation along the microclimate axis, as 67% of *N. lemurinus* and 91% of *N. uniformis* were encountered in dry conditions. However, the two arboreal forms appear to have different preferences regarding vegetation density, as 72% of *N. lemurinus* were first sighted in relatively open situations whereas 91% of *N. rodriguezii* were encountered in dense vegetation.

INTERSPECIFIC AND SEX-BASED VARIATION

All four species differed significantly in snout vent length (two-way ANOVA with species and sex as factors:  $F_{7,32}=222.4, P<0.005$ ), tail length (two-way ANCOVA with species and sex as factors and SVL as covariate:  $F_{8,31}=342.7, P<0.005$ ), forelimb length ( $F_{8,31}=130.0, P<0.005$ , hind limb length ( $F_{8,31}=175.8, P<0.005$ ) and mass ( $F_{8,31}=48.5, P<0.005$ ). There was also a significant difference in perch height between the four species ( $F_{8,31}=8.1, P<0.005$ ) and perch width ( $F_{8,31}=5.0, P<0.005$ ).

Inspection of the mean ranks revealed that *N. uniformis* and *N. rodriguezii* obtained the same values for both mass and forelimb length. This suggests that differences between them may not be significant for some of the variables and therefore require further investigation. Statistical analyses revealed that *N. uniformis* and *N. rodriguezii* differed significantly in hind-limb length (two-way ANCOVA:  $F_{4,15}=7.1, P=0.002$ ) and tail length ( $F_{4,15}=8.2, P=0.001$ ), but not in forelimb length ( $F_{4,15}=0.4, P=0.812$ ) or overall snout-vent length (two-way ANOVA:  $F_{3,16}=0.5, P=0.709$ ). Variation among the four species in morphological and habitat parameters are summarized in Table 3.

Differences in certain variables were apparent also between the sexes of two species, *N. tropidonotus* and *N. lemurinus*. Based on the largest five individuals of

TABLE 1. Distribution of species at Las Cuevas according to principal vegetation type (as defined by Penn *et al.*, 2004). A=abundant relative to other areas where the species was seen. R=present but rarely seen. O=not observed.

	<i>N. tropidonotus</i>	<i>N. uniformis</i>	<i>N. lemurinus</i>	<i>N. rodriguezii</i>
Broad leaf: Class 2, Seasonal forest	A	A	A	A
Broad leaf: Class 3, Semi-evergreen forest	A	R	A	R
Broad leaf: Class 4a, Semi-evergreen forest (lowland)	O	O	A	O
Total habitats where seen	2	2	3	2

TABLE 2. Numbers of adult lizards observed at Las Cuevas within specific microhabitat categories.

	<i>N. tropidonotus</i>		<i>N. uniformis</i>		<i>N. lemurinus</i>		<i>N. rodriguezii</i>	
	males	females	males	females	males	female	male	female
Number on ground	13	10	1	1	1	1	0	1
Number on tree buttresses or roots	6	3	8	4	0	2	2	0
Number on tree trunks	2	0	2	1	10	4	1	1
Number on twigs and branches	0	0	0	0	0	0	4	2
Number on perimeter	17	11	3	2	8	5	1	0
Number in dense foliage	4	2	8	4	3	2	6	4
Number in wet conditions	1	0	11	5	4	2	0	1
Number in dry conditions	20	13	0	1	7	5	7	3
Overall sample size	21	13	11	6	11	7	7	4

each sex, male *N. tropidonotus* snout vent lengths were significantly greater than those of females (males  $54.8 \pm 0.49$ , range 53-54 mm; females  $50.2 \pm 0.37$ , range 49-51 mm; ANOVA:  $F_{1,8} = 55.684$ ,  $P < 0.005$ ), whereas in *N. lemurinus*, female snout-vent lengths were significantly greater than those of males (males  $63.2 \pm 0.20$ , range 63-64 mm; females  $67.2 \pm 1.50$ , range 65-73 mm;  $F_{1,8} = 7.018$ ,  $P = 0.029$ ). However, males and females of these species did not differ significantly in forelimb length, hind limb length, tail length, or mass, and there was also no apparent difference between the sexes in either of the tested perch variables.

#### TOE-PAD MORPHOLOGY AND DEGREE OF ARBOREALITY

The number of lamellae were significantly correlated with perch height for *N. tropidonotus* ( $r_s = 0.67$ ,  $P < 0.05$ ), *N. uniformis* ( $r_s = 0.66$ ,  $P < 0.05$ ) and *N. lemurinus* ( $r_s = 0.66$ ,  $P < 0.05$ ), but not for *N. rodriguezii* ( $r_s = 0.22$ ,  $P = 0.52$ ). The number of lamellae across all of the species studied in this community were signifi-

cantly correlated with perch height ( $r_s = 0.77$ ,  $P < 0.05$ ), and when the effect of body size was removed, all correlations remained significant: *Norops tropidonotus* ( $r_s = 0.41$ ,  $P < 0.05$ ), *Norops uniformis* ( $r_s = 0.67$ ,  $P < 0.05$ ), *N. lemurinus* ( $r_s = 0.64$ ,  $P < 0.05$ ), all species ( $r_s = 0.78$ ,  $P < 0.05$ ).

#### MORPHOMETRIC ANALYSIS

An ordination plot of seven variables (see Material and Methods) based on non-metric multidimensional scaling reveals the existence of four distinct clusters (Fig. 2). These correspond to each of the four species at Las Cuevas for which sufficient data was obtained (i.e. *N. lemurinus*, *N. rodriguezii*, *N. tropidonotus*, and *N. uniformis*). Separation along the first dimensional axis relates mostly to differences between the species in perch height and number of lamellae. Separation along the second dimension primarily separates the species from each other with regards to size, as this axis is related to differences in SVL and the other morphological variables. Three data points corresponding to speci-

TABLE 3. Morphological and ecological data collected for anole species at Las Cuevas, Belize. Data are mean  $\pm$  SE, range (in parentheses), and sample size.

Species	SVL (mm)	Body Mass (g)	Tail Length (mm)	Forelimb (mm)	Hind-limb (mm)	Lamellae number	Perch height (mm)	Perch diameter (mm)
<i>N. tropidonotus</i>	$50.2 \pm 0.4$ (46-56) $n=34$	$2.1 \pm 0.04$ (2-3) $n=34$	$95.2 \pm 1.1$ (81-104) $n=32$	$25.1 \pm 0.16$ (23-27) $n=34$	$47.4 \pm 0.4$ (42-50) $n=34$	$24.4 \pm 0.2$ (23-28) $n=34$	$76.2 \pm 18.8$ (10-440) $n=34$	$75.3 \pm 16.9$ (18-410) $n=34$
<i>N. uniformis</i>	$33.5 \pm 0.5$ (30-39) $n=17$	$1 \pm 0$ (1-1) $n=17$	$43 \pm 0.7$ (40-51) $n=15$	$15.3 \pm 0.5$ (11-17) $n=17$	$28.6 \pm 0.5$ (25-32) $n=17$	$26 \pm 0.5$ (23-30) $n=17$	$295.9 \pm 50.9$ (30-720) $n=17$	$275.6 \pm 23.6$ (20-425) $n=17$
<i>N. lemurinus</i>	$63.1 \pm 0.9$ (56-73) $n=18$	$3.5 \pm 0.2$ (2-6) $n=18$	$135.9 \pm 3.0$ (103-150) $n=17$	$28.1 \pm 0.36$ (26-32) $n=18$	$53.2 \pm 0.7$ (49-60) $n=8$	$37 \pm 0.2$ (34-38) $n=18$	$631.9 \pm 94.4$ (40-1270) $n=18$	$232 \pm 30.3$ (30-370) $n=18$
<i>N. rodriguezii</i>	$34 \pm 0.9$ (30-37) $n=11$	$1 \pm 0$ (1-1) $n=11$	$38.4 \pm 0.9$ (31-41) $n=11$	$15.7 \pm 0.3$ (15-17) $n=11$	$26 \pm 0.4$ (25-28) $n=11$	$34.1 \pm 0.6$ (31-37) $n=11$	$885.5 \pm 156.9$ (170-1380) $n=11$	$98.5 \pm 18.9$ (15-230) $n=11$
<i>N. capito</i>	87 ( $n=1$ )	19 ( $n=1$ )	160 ( $n=1$ )	38 ( $n=1$ )	74 ( $n=1$ )	40 ( $n=1$ )	3100 ( $n=1$ )	300 ( $n=1$ )



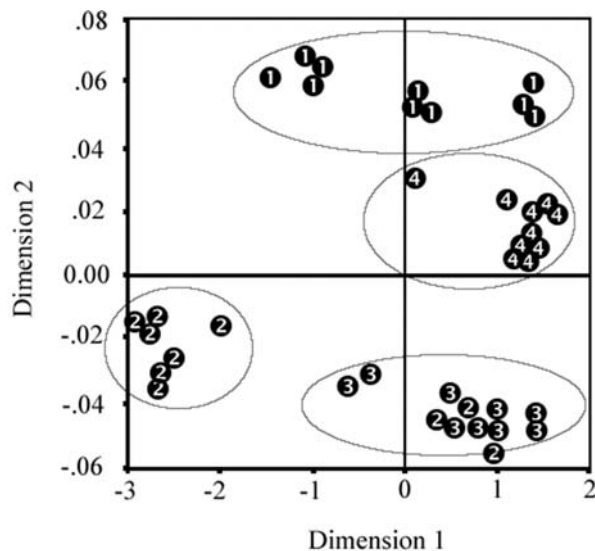


FIG 2. Ordination of specimens of *N. lemurinus* (1), *N. rodriguezii* (2), *N. uniformis* (3), and *N. tropidonotus* (4) based on results of multi-dimensional scaling analysis (Euclidean distance model). For details of characters used see text.

mens of *N. rodriguezii* occur within or very close to the *N. uniformis* cluster; this is because the two species are similar in size and the particular individuals concerned were observed close to the ground. Despite this apparent overlap the ordination pattern nonetheless indicates a significant difference in the extent of niche separation between these two species.

DISCUSSION

The four main species of *Anolis* studied at Las Cuevas clearly appear to partition environmental resources along the major resource axes of habitat structure, microclimate, and probably also prey size. Although a specific analysis of diet was not undertaken (several unsuccessful field trials were attempted), studies of other communities have indicated that prey size in anoles tends to be strongly correlated with body size (e.g. Roughgarden, 1974). These niche dimensions are not independent (Pianka, 1974), but together they separate pairs of ecologically similar sympatric species. Habitat structure appears to be the resource axis along which the greatest degree of partitioning occurs. Each of the five species may be broadly categorized as either predominantly terrestrial or arboreal, but varied significantly in respect of preferred perch height and width.

Both the terrestrial and arboreal microhabitats are occupied by two ecologically similar species that differ greatly in size. It is thus likely that species coexisting in the same microhabitat are able to do so by targeting and consuming prey of different size and possibly type. However, specific dietary analyses are clearly required in order to determine if this is indeed the case. The arboreal species appear to show greater partitioning of resources along this axis than their terrestrial counterparts, conforming to trends observed in Caribbean communities (e.g. Losos, 1994).

The two terrestrial species show clear segregation along the microclimate axis. These species were rarely observed together, suggesting that partitioning along this axis has developed to such an extent that they have become almost allotropic, with overlap at ecotones explaining sightings of the two species together (e.g. Rand, 1964). In contrast to Caribbean communities (Losos, 1994), these closely related forms differ significantly in body size. Resource partitioning in this mainland community conforms to another trend observed in the Caribbean (Losos, 1994) in that the more arboreal species do not show the same distinct level of partitioning along the microclimate axis.

SEX-BASED VARIATION

The anole species studied at Las Cuevas do not show pronounced sex-based separation along either the microclimate or structural habitat resource axes. However, the males and females of two species, *N. lemurinus* and *N. tropidonotus*, may differ significantly along the third prey size axis (ND'C pers. data based on anecdotal observations). Males of the terrestrial *N. tropidonotus* were found to be significantly larger than females; in highly territorial species such as this sexual selection may favour larger males because they typically acquire larger territories containing more females, resulting in greater mating success (Rand, 1964; Trivers, 1976; Butler *et al.*, 2000). The more arboreal *N. lemurinus* also displays evidence of sexual size dimorphism, although in contrast to *N. tropidonotus*, females were found to be significantly larger than males. In non-territorial systems, small male size may be favoured (Zamudio, 1998). However, field observations suggest this scenario is doubtful and other selective pressures relating to prey size are more likely to be responsible.

A possible explanation for the observed sexual size dimorphism in *N. lemurinus* and *N. tropidonotus* is that different habitats can vary greatly in their degree of visibility. As demonstrated by Butler *et al.* (2000) for Greater Antillean species, habitat structures favoured by the two species displaying prominent sexual size dimorphism are both relatively open with a high degree of visibility, *N. lemurinus* being typically found on the trunks of trees and the terrestrial *N. tropidonotus* restricted mostly to open vegetation near paths and clearings (Table 2). Conversely, habitat structures favoured by the two non-dimorphic species are relatively dense, *N. rodriguezii* being typically found amongst interconnecting matrices of branches and twigs, and the terrestrial *N. uniformis* in dense understory vegetation (Table 2). Degree of visibility may therefore be implicated as a contributing factor towards the development of sexual size dimorphism, and this would benefit from further investigation

TOE-PAD MORPHOLOGY AND HABITAT USE

Variation is evident in both the degree of expansion and number of lamellae among the anoline lizards at Las

Cuevas. A positive correlation between the number of lamellae on the fourth toe of the hind-foot and perch height was observed for three species, and in agreement with Glossip & Losos (1997), statistically robust relationships were observed even when the effect of size was removed. As demonstrated in previous studies this suggests that variation in toe pad morphology is highly adaptive for an arboreal lifestyle and related to habitat use (e.g. Collette, 1961; Moermond, 1979; Glossip & Losos 1997; Macrini *et al.*, 2003). Species with more lamellae are potentially able to utilise higher perch sites because toe-pads with more lamellae have more setae and thus greater adhesive ability (Peterson, 1983). Species that select higher perch sites may also need this greater adhesive ability either because they encounter smooth surfaces more frequently, or because the consequences of falling are much greater (Macrini *et al.*, 2003).

#### DRIVING FORCES BEHIND RESOURCE PARTITIONING

Interspecific interactions, specifically in the form of competition, have been invoked as the causal basis for resource partitioning in communities of organisms since the studies of Gause (1934) and Park (1948). Losos (1994) stated that "ecologically syntopic species compete strongly, creating strong selective pressure for species to diverge in resource use, thereby allowing co-existence". Rapid micro-evolutionary adaptation in response to these shifts in resource utility is typically believed to ensue (Taper & Case, 1992), and these "adaptive shifts" are known to occur along all three of the major axes highlighted in this study (Losos, 1994).

Despite the wealth of evidence supporting interspecific interactions as the major force behind resource partitioning and structuring within *Anolis* communities, are there any other processes that could be responsible for these patterns? Both predation and "intra-guild predation" (Polis *et al.*, 1989) have been largely dismissed as major factors in resource partitioning (Losos 1994), leaving differential susceptibility to parasites as a possible influential determinant of community structure (e.g. Grosholz, 1992; Schall, 1992). The larvae of trombiculid mites in particular are commonly found on a wide range of reptile species in Belize (Stafford, pers. obs.). Among the species of *Norops* studied, however, these small parasites (typically ranging from 5 to 20 in number) were observed only in the deep axillary pockets of *N. tropidonotus* and *N. uniformis*. The presence of mites on only two of the species may thus be altering competitive relationships and facilitating their existence in sympatry. Another potentially influential and unknown factor that may affect ecological relationships among the anoles studied at Las Cuevas is the occurrence of other species that were not directly observed. At least one additional anole, *N. biporcatus*, is known from the general vicinity of this locality (Stafford, pers. obs.). *Norops biporcatus* is a large (90 mm SVL), bright green, arboreal species that is more of a canopy inhabitant, and as well as feeding on

invertebrates is known to include other anoles in its diet (Taylor, 1956).

Results of this study are consistent with natural history observations reported elsewhere for the particular species concerned (Lee, 1996; Campbell, 1998; Lee, 2000; Stafford & Meyer, 2000), and mainland communities of these lizards in general (Fitch, 1973, 1975; Talbot, 1976, 1979; Corn, 1981; Guyer, 1986; Pounds, 1988). In order to draw inferences about the processes responsible for community structure and ecological divergence among anoles in this area, however, further studies are clearly required in combination with investigations of other mainland communities. Our principal results can be summarized as follows: (1) five species of anole were observed at the study site and found to be broadly sympatric; (2) male lizards were more abundant (or otherwise more conspicuous) than females with regard to the four species for which sufficient data were obtained – *Norops lemurinus*, *N. rodriguezii*, *N. tropidonotus*, and *N. uniformis*; (3) these species clearly appear to partition environmental resources along the three major axes outlined by Pianka (1974); (4) the species differed significantly in perch height and perch width; (5) two were predominantly terrestrial (*N. tropidonotus* and *N. uniformis*) and two were predominantly arboreal (*N. lemurinus* and *N. rodriguezii*); (6) the two most terrestrial species differ in microclimate preferences and density of vegetation surrounding the perch site; (7) the two arboreal lizards show the greatest partitioning along the body size axis; (8) *N. uniformis* and *N. rodriguezii* are similar in body size but differed significantly in terms of resource use; (9) male *N. tropidonotus* were significantly larger than females in SVL; (10) female *N. lemurinus* were significantly larger than males in SVL; (11) both species were commonly found in habitats that possessed a high degree of visibility, which may be a driving factor behind the evolution of sexual size dimorphism; (12) the number of lamellae on the toe-pad of the fourth toe (hind foot) was significantly correlated with perch height for *N. tropidonotus*, *N. uniformis* and *N. lemurinus*; (13) none of the correlations listed above were affected when the effects of body size were removed.

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