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SHIFT IN THE STRUCTURAL HABITAT OF ANOLIS OPALINUS DUE TO CONGENERIC COMPETITION¹

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Abstract. The Jamaican Anolis opalinus has different perch height characteristics depending on locality. Toward the center of the island, around Mandeville, A. opalinus characteristically perches low, being classified as a trunk-ground species. In Kingston, however, A. opalinus perches high, classified as a trunk-crown species. Evidence indicates the Kingston A. opalinus would also perch low except that interaction with Anolis I. lineatopus forces A. opalinus into perch sites higher than appear to be the species' preference.

INTRODUCTION

Since Darwin, competition has been recognized as the driving force of natural selection, and has become the underlying principle of such evolutionary concepts as adaptive radiation, character displacement, and competitive exclusion. There is a fundamental dependence upon interspecific competition to explain species diversity. Yet very few field studies have satisfactorily established interspecific competition as the causal agent for allopatry or nonsynchronous spatial overlap of closely related species (Elton and Miller 1954, Miller 1967). Miller (1968: 43) points out that "with the relatively few examples of interspecific competition that have been documented from natural communities, we know very little about the process of competitive exclusion or the essential conditions of the interaction." The present investigation provides direct observation of competitive interference between two sympatric lizards, Anolis opalinus and Anolis I. lineatopus, and demonstrates a shift in perch characteristics as a result of this competition.

A number of studies (Collette 1961, Rand 1964, 1967a, b, Rand and Rand 1967, Rand and Williams 1969, Ruibal 1961, Schoener 1968, 1970a, Schoener and Gorman 1968, Schoener and Schoener 1971) have compared certain perch characteristics of sympatric anolines. Such comparisons of perch height and diameter (structural habitat) and cloacal temperatures (climatic habitat) have shown that the congeners tend to separate themselves out according to these niche dimensions. This partitioning of the habitat among syntopic anoles is felt to reduce direct competitive interactions. It is tempting for the reader to draw the inference, though for the most part unintended, that the reported structural and climatic habitat characteristics of the various anoline lizards are species-specific. Such extrapolations can be misleading, as will be discussed in this paper.

FORMULATION OF THE PROBLEM

The structural perch characteristics of A. opalinus and its behavioral interactions with syntopic congeners were studied in two geographical areas on Jamaica. The first locality was in Mandeville (elev. 690 m), which is situated on a plateau approximately in the island's center. On three distinctly different study areas in Mandeville, A. opalinus maintained relatively low perch heights. These perch heights did not fit those described for the species in Kingston, which were reported as being much higher. This initiated a 2-week observation period of A. opalinus perch sites in Kingston, located 60 air kilometers east of Mandeville. On the Kingston study area (elev. approx. 200 m) the nature of the interaction between A. opalinus and the Kingston A. l. lineatopus was considerably different than that observed with the Mandeville *lineatopus* subspecies, A. l. neckeri.

METHODS AND MATERIALS

From a year-long investigation of *A. opalinus* ethoecology in Mandeville, only the structural habitat data are presented here, serving strictly as a comparison for the perch characteristics of the *A. opalinus* population in Kingston. Furthermore, these perch site data were selected from only one of the three Mandeville study areas as it contained an abundance of *Anolis lineatopus neckeri*, a subspecies of the congener competing with *A. opalinus* for perch sites in Kingston.

Initially I made rough maps of the Kingston and Mandeville study areas incorporating every prominent object (e.g., trees, bushes, dead branches, large rocks). I assigned these potential perch sites individual code numbers on their corresponding maps, thus facilitating a lizard's location with respect to two dimensions. Chalk marks and tape markers were also placed at 0.6 m increments on the taller habitat objects to increase the accuracy of estimating the third dimension of a lizard's location, perch height. At the conclusion of the investigation transects were laid out and accurately detailed maps made of the

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coded perch sites for both study areas. The diameters of these perch sites were also recorded.

I captured the lizards using a fiberglass pole with a fine nylon noose. At times hand catching would have been quicker, but the noose insured that the captured lizards would not be injured. Once noosed, a lizard was placed in a small jar on which the perch height and the code number of the perch site were recorded. The lizard was taken to a mobile laboratory near the study area where it was weighed to the nearest 0.01 g (O'Haus Dial O-Gram balance), its total and snout-vent lengths measured to the nearest millimeter, its toes clipped for permanent identification, and that perch site data recorded. To be able to recognize individuals in the field, I then painted on the lizard's back a series of colored marks that corresponded to a numerical code (Jenssen 1970: 3); I used non-toxic acrylic artist's paints because anoles eat their skins after shedding. The lizard was returned to its jar, carried back to its capture site, and released.

Once the lizards were marked, I watched them from a distance with 7-power binoculars. On the Kingston study area, censuses were taken at approximately 1-hour intervals. Since the population size was known, special effort was made to locate every individual. At least 70% of the population was found during each census. The visual search was conducted at a distance of 4-15 m from the trees to minimize disruption of the lizards' normal behavior.

When mean perch heights and diameters for the various lizard classes are calculated, certain biases would be introduced if the data contained unequal observations for individual lizards. For example, the large adult male anoles usually perch higher than juveniles and adult females and are more conspicuous, possibly contributing disproportionally to the recorded data and thus giving a biased estimate of the population's mean perch height. To avoid these complications, I calculated mean perch height and diameter for each individual and used each of these values as a single observation in calculating the statistics for the perch heights and diameters. Standard errors of the means were also calculated and follow where averages are provided for the various data classifications (e.g., perch height, perch diameter, s-v length, body weight).

STUDY AREAS AND RESIDENT SPECIES

Mandeville

The Mandeville area is described as cultivated pasture and second growth scrub (Asprey and Robbins 1953) with an annual rainfall of 225 cm (10-year mean based on data collected by Mandeville resident, Robert Sutton). Observations from the Mandeville study area were made from March through May 1970 on a 32×11 m plot marked off at the base of a hillside. The study area contained a group of 10 medium to large sized trees 8–18 m high, of the following species: broadleaf (*Terminalia latifolia*), trumpet (*Cecropia peltata*), sweetwood (*Nectandra sp.*), and maiden plum (*Comocladia sp.*). The area had been recently cut over and most of the low vegetation was new secondary growth that was still recovering from the winter drought period.

The study area held 50 resident A. opalinus, 20 males (s-v 45.8 ± 0.9 mm, wt 2.29 ± 0.12 g) and 30 females (s-v 37.6 ± 0.5 mm, wt 1.15 ± 0.21 g). These animals were mostly older juveniles and adults; very few hatchlings were present because of the winter dry season. A. opalinus occupied almost all aspects of its physical environment (i.e., leaf litter, rocks, vines, bushes, saplings, and trunks of trees).

Sharing the study area with A. opalinus were approximately 60 A. l. neckeri. The A. l. neckeri showed indications that some integration had taken place with the subspecies, A. l. lineatopus, which is common below the Mandeville plateau but rarely seen in Mandeville. The integration, however, did not appear extensive, and in this paper the Mandeville population will be referred to as A. l. neckeri. Only 31 A. l. neckeri on this Mandeville study area were actually marked, as the primary purpose was to observe A. opalinus. Of the marked A. l. neckeri, 18 were males (s-v 50.6 ± 1.19 mm, wt 3.42 ± 0.37 g) and 13 females (s-v 37.8 ± 1.3 mm, wt 1.48 ± 0.16 g); these individuals, particularly the males, represented a wide range of snout-vent lengths.

Kingston

For 2 weeks in August 1970 a 50×27 m plot was studied at the base of Long Mountain near the University of the West Indies campus. This region receives approximately 130 cm of rain annually (Handbook of Jamaica, 1966), and is classified as dry limestone scrub forest (Asprey and Robbins 1953). The study plot was unique (Fig. 1); it was marked off within a small park-like area that had been recently carved from the surrounding forest. The latter was composed of old secondary growth with many large trees 10–20 m high. The sylvan area containing the study plot still retained many of the original trees, all of which were logwood (Haematoxylum campechianum). The trees were surrounded by mowed grass, which was poor habitat for the anoles and discouraged frequent movement between trees via the grass. One or two trees tended to make up a lizard's territory, and many of these territories were semi-isolated. This discontinuous habitat allowed a partial separation of the two principal species (A.



FIG. 1. Kingston Study Area

opalinus and A. l. lineatopus) and permitted clear interpretations of interspecific behavior when the species came together. In addition, the limited habitat enhanced the competition for perch sites.

With few exceptions, the lizards on the study area were adults. There were 23 resident *A. opalinus*, composed of 12 males (s-v 51.2 ± 1.3 mm, wt 2.91 ± 0.20 g) and 11 females (s-v 42.6 ± 0.8 mm, wt 1.55 ± 0.09 g). There were 20 resident *A. l. lineatopus*: 11 males (s-v 60.9 ± 2.6 mm, wt 5.93 ± 0.63 g) and 9 females (s-v 46.7 ± 0.9 mm, wt $2.35 \pm$ 0.12 g).

For more information on the morphological distinctions and distributions of these two species, a thorough taxonomic treatment of the Jamaican anoles is available elsewhere (Underwood and Williams 1959).

RESULTS

Mandeville

Paired perch height and diameter data for A. opalinus came from 889 separate observations of 50 individuals. The mean perch height and perch diameter for this population was 0.42 ± 0.03 m and 3.6 \pm 0.4 cm, respectively. Though not statistically different (P > 0.05), males tended to perch higher and on larger diameter perch sites than did females. The more dominant males secured perches from which they could easily monitor their territories and adjacent habitat. However, it was rare to find A. opalinus perching more than 2 m above the ground, even though ample perch sites were available above this height. Only during occasional intraspecific chases or toward the evening, when some members of the population searched out arboreal sleeping sites, was this species seen higher than 2 m.

From 103 paired observations of 17 individuals, A. l. neckeri took perches averaging 0.31 ± 0.07 m above the ground and 2.7 ± 0.7 cm in diameter. These mean values for structural perch dimensions do not differ statistically from those observed for A. opalinus. There was a definite overlap in the two species' structural niche, though A. *l. neckeri* tended to spend more time on the ground. This was probably in response to a lower preferred body temperature, as A. *l. neckeri* frequented the leaf litter and rock crevices during the heat of the day. However, in May, with the approach of the rainy season and the increased cloud cover, this occasional temporal separation ceased and both species were simultaneously sharing the same structural class of perch sites throughout the day.

It was rare to find individuals of both species closer than 0.6 m to one another. When A. opalinus and A. l. neckeri confronted each other, it was usually the larger of the two animals, regardless of species, that retained the perch or continued without deviation on its original course. The smaller lizard either moved and perched a short distance away or detoured around the larger lizard. Interspecific aggressive behavior was occasionally seen, but not in the form of territorial defense; instead, the agonistic behavior was associated with the intrusion of one species into what might be considered the other's individual distance. Below are anecdotes paraphrased from field notes, illustrating the nature of the interspecific encounters.

- 6/5/70 (male opalinus 187, s-v 44 mm, wt 1.94 g; male neckeri 32, s-v 58 mm, wt 5.65 g)
 - 1245 A squeak (most Jamaican anoles will vocalize when their well-being is threatened) turned my attention toward Tree 9. Male opalinus 187 had his throat lowered and body raised on all four legs while presenting laterally toward the larger male *neckeri* 32. Then Op 187 extended his throat fan and held it out. Ne 32, about 15 cm away, made several intention movements toward Op 187, but then backed off a step after 2 min.
 - 1248 *Op.* 187 slowly retreated. *Ne* 32 never appeared threatened and remained facing *Op* 187.
- 20/4/70 (female *opalinus* 41, s-v 38 mm, wt 1.23 g; female *neckeri* 3, s-v 36 mm, wt 1.37 g)
 - 1830 Female opalinus 41 scurried on the ground past fallen branch 101 and stopped at rim of bank. She went up on all four legs. A smaller female neckeri (Ne 3) was approximately 0.3 m away on a twig in the direction Op 41 was going.
 - 1831 Op 41 chased Ne 3 a short distance

and continued on her way south and out of sight into the brush.

- 7/5/70 (female *opalinus* 110, s-v 41 mm, wt 1.25 g; male *neckeri* 28, s-v 62, wt 5.35 g)
 - 1535 Female opalinus 110 ran south on fallen branch 400, jumped to tree 13, and "squirreled" 0.3 m up the trunk. There she suddenly found herself about 7 cm from a large male neckeri (Ne 28). She immediately went up on all four legs, presenting laterally, her throat lowered, and back arched. Op 110 held this position for about 10 sec while Ne 28 remained motionless. Then she turned and ran to the base of tree 13.

Compared with intraspecific interactions, such interspecific encounters were infrequent and brief. For the most part they resulted when one species inadvertently found itself in close proximity to the other or when one species tried to pass directly by the other while crossing part of the habitat. The brief chases mainly involved females and juveniles, with the larger of the participants being the aggressor. There was no

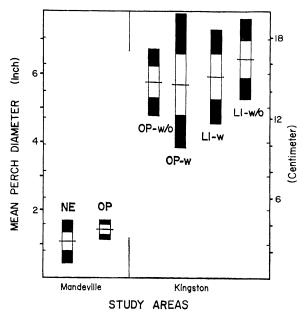


FIG. 2. Mean perch diameters of Anolis lineatopus neckeri (NE) and Anolis opalinus (OP) in Mandeville, Jamaica. Mean perch diameters of opalinus alone on tree (OP – w/o), opalinus with A. l. lineatopus on same tree (OP – w), A. l. lineatopus with opalinus on same tree (LI – w), and A. l. lineatopus alone on tree (LI – w/o) in Kingston, Jamaica. Outer edges of black boxes are the 95% confidence limits of the mean, outer edges of white boxes are the standard errors of the mean, and horizontal lines through the white boxes are the mean perch diameter values.

TABLE 1. Statistical comparison (t-tests) of mean perch heights for Anolis opalinus (Op), Anolis l. lineatopus (Li), and Anolis lineatopus neckeri on study areas in Mandeville, Jamaica (March-May 1970) and Kingston, Jamaica (August 1970)

Species and locality	Species and locality	Probability
opalinus - with Li,	opalinus - without Li,	
Kingston	Kingston	<0.01
opalinus – with Li,	lineatopus - with Op,	
Kingston	Kingston	<0.01
opalinus – without Li,	lineatopus – without Op,	0.06 N.S.
Kingston	Kingston	
lineatopus – with Op,	lineatopus – without Op,	
Kingston	Kingston	0.95 N.S.
opalinus, Mandeville	neckeri, Mandeville	0.10 N.S.
opalinus, Mandeville	opalinus – without Li,	
	Kingston	0.01

N.S. - not statistically significant

evidence, however, that one species was displacing the other from the immediate habitat.

Kingston

From censuses of the Kingston study area, perch height and diameter data were separated into three categories: (1) only *opalinus* on a tree trunk (Op without), (2) only *lineatopus* on a tree trunk (Li without), and (3) *opalinus* and *lineatopus* sharing a tree trunk (Op with and Li with). The resulting mean perch diameters were not statistically different between A. *opalinus* and A. *l. lineatopus* for any of the three categories (Fig. 2). These data were calculated from 677 observed perch diameters of the 17 most frequently seen individuals of both species.

In contrast to perch diameter, perch height was the more revealing of the structural niche dimensions showing the interspecific competition for perch sites. A. opalinus perched low when A. l. lineatopus was not present on the tree. From 497 observations of 17 individuals, the mean perch height was 0.70 ± 0.09 m. Characteristically, A. l. lineatopus perched low whether A. opalinus was present on the tree or not. When sharing a tree with A. opalinus, the mean perch height of A. l. lineatopus was 0.98 ± 0.12 m, calculated for 17 individuals from 144 observations. On those occasions when A. opalinus was also present on the same tree, the mean perch height for A. *l. lineatopus* remained almost unchanged at $1.02 \pm$ 0.11 m. However, when A. l. lineatopus appeared on the same tree with A. opalinus, the latter species perched significantly higher than when A. l. lineatopus was absent (Table 1, Fig. 3). In 36 instances when A. opalinus and A. l. lineatopus shared the same tree trunk, A. opalinus always perched above A. l. lineatopus, averaging 2.40 ± 0.20 m above the ground.

This upward shift of *A. opalinus* perch sites due to the presence of *A. l. lineatopus* is very likely a con-

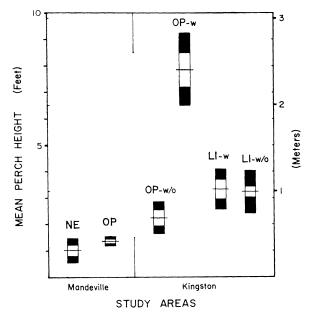


FIG. 3. Mean perch heights of Anolis lineatopus neckeri (NE) and Anolis opalinus (OP) in Mandeville, Jamaica. Mean perch heights of opalinus alone on tree (OP -w/o), opalinus with A, l. lineatopus on same tree (OP -w), A. l. lineatopus with opalinus on same tree (LI -w), and A. l. lineatopus alone on tree (LI -w/o) in Kingston, Jamaica. Outer edges of black boxes are the 95% confidence limits of the mean, outer edges of white boxes are the standard errors of the mean, and horizontal lines through the white boxes are the mean perch height values.

servative estimate. On 12 different occasions various *A. l. lineatopus* crossed to trees consistently occupied by *A. opalinus;* the latter individuals, however, could not be immediately located. It was presumed the *A. opalinus* were hidden in their trees' canopies. Usually on the next census after the *A. l. lineatopus* had left the "opalinus trees," the same *A. opalinus* were again observed low on the trunks of their trees. Since the *A. opalinus* were not seen in the canopies, their actual locations could only be suspected and not entered in the perch height data.

The following paraphrased field notes are typical of the *opalinus-lineatopus* interactions observed on the Kingston study area, and indicate how closely the lizards monitor each other's movements.

- 2/9/70 (male *opalinus* 6, s-v 52 mm, wt 3.04 g: male *lineatopus* 4, s-v 66 mm, wt 6.87 g)
 - 0920 Male *lineatopus* 4 arrived at Tree 7 from Tree 6, climbed to 2 m. Male *opalinus* 6 was at 1.3 m, but moved to 2.7 m and displayed (laterally presented and throat fan pulsing) at Li 4.
 - 0924 Both Op 6 and Li 4 are 2.3 m up, but on different trunks. Op 6 is displaying

at Li 4, and keeping the trunk between himself and Li 4.

- 0936 Li 4 moved down to 1.3 m level. Op 6 still at 2.7 m.
- 0955 Li 4 is displaying at a male *lineatopus* on an adjacent tree. Op. 6 has not moved.
- 1004 Li 4 moved up to 1.6 m, again displaying at neighboring *lineatopus* male, while Op 6 displays at Li 4 from 2.7 m up.
- 1012 Op 6 moved up into canopy and out of sight. Li 4 still 1.6 m up.
- 1215 Op 6 has moved out of canopy and is
 2.3 m up. Li 4 is 1.3 m up. Now Li 4 advances up to 1.7 m level and Op 6 goes back up into canopy.
- 1340 Li 4 has moved off of Tree 7 to a fence post 4.3 m NE of Tree 7.
- 1350 Op 6 has come out of the canopy and is now at the 1.6 m level on trunk of Tree 7.

A factor which can make the *opalinus-lineatopus* interactions less obvious is the relative complexity of the habitat. At the edge of the study area was a dense stand of six small logwood trees no more than 0.6 m apart. *A. opalinus* commonly perched under 2 m even though there was occasionally an adult male *A. l. lineatopus* a leap away on an adjacent trunk. Apparently with an increase in possible avoidance routes, the tendency of *A. opalinus* to ascend in the near presence of the larger *A. l. lineatopus* is more subtly expressed. Nevertheless, in the continuous habitat of the adjacent woods, a cursory census and the observations of Rand (1967b) indicate that *A. opalinus* tend to perch higher than *A. l. lineatopus*.

The influence of female A. l. lineatopus upon A. opalinus perch sites was far less evident than that of adult male A. l. lineatopus. Presence of an adult female A. l. lineatopus on an A. opalinusoccupied trunk did not initiate the dramatic upward shift of A. opalinus as was observed to happen when an adult male A. l. lineatopus reached the tree. Whether this is a size-related factor since adult female A. l. lineatopus are smaller than adult male A. opalinus or because female A. l. lineatopus may be less aggressive than male A. l. lineatopus was not determined. Adult female A. l. lineatopus, however, were seen on several occasions chasing the smaller adult female A. opalinus.

There is the possibility that Kingston A. opalinus perch higher than Mandeville A. opalinus because of climatic differences between the two localities. Kingston receives less rainfall and remains $2-5^{\circ}$ C warmer than the more elevated Mandeville locality. If A. opalinus prefer lower body temperatures than A. l. lineatopus and ambient temperatures are less in the tree canopies than at tree trunk heights, this might explain the Mandeville-Kingston perch height difference. However, the Kingston A. opalinus perch sites of the present study were not consistent with the above hypothesis. A. opalinus perched low on the sun-exposed tree trunks unless approached by a larger A. l. lineatopus; observations for this generalization were made during August, one of the warmest months of the year.

Comparisons of perch height and especially perch diameter between the Mandeville and Kingston study areas for all combinations of species categories were statistically significant (Fig. 2 and 3). This is not surprising since the physical characteristics of the habitat have a decided influence on perch site dimensions. For example, even though Mandeville and Kingston A. opalinus (w/o Li) populations perched low (Fig. 3), the difference was still statistically significant (Table 1). No A. opalinus was ever seen on the ground in the Kingston study area as it was open grass lawn. On the Mandeville study area, there was much ground cover and the A. opalinus frequently moved between elevated perch sites over fallen herbacious debris. When perch diameter is compared between study areas, the contrast is even greater. Only tree trunks were available for perch sites below the canopy on the Kingston plot; this is reflected in large values for the mean perch diameter of A. opalinus (14.7 cm) and A. l. lineatopus (16.4 cm). On the Mandeville plot, where most of the area was covered by young secondary growth of small diameter and where the residents made greater use of the ground, the mean perch diameters for A. opalinus and A. l. neckeri were only 1.4 and 1.1 cm, respectively.

DISCUSSION

An objective of this paper is to point out how a behavioral characteristic (e.g., particular range of perch heights) can be shared by a population and still not reflect a stable species trait, much less imply an inherited factor. A. opalinus tends to take low perch sites in the Mandeville area. This species maintains a preference for low perches even when it shares its structural habitat with the larger A. lineatopus neckeri. The Mandeville A. opalinus would be described as a trunk-ground species. In the Kingston area, however, A. opalinus perches high and would be considered a trunk-crown species. Here, interactions with A. l. lineatopus shift A. opalinus to perches above those of A. l. lineatopus, which also has a propensity for low perch sites.

In Kingston, Rand (1967b) and Schoener and Schoener (1971) conducted censuses of unmarked

anoline populations in the same area as the present study. In fact, Rand's "Mona bush" census area was the woods surrounding my Kingston study area. These investigators compared intra- and interspecific perch heights by the following categories: percentage of individuals seen < 1, 1–2.5, 2.5–3.3, and > 3.3 m above the ground. If their data are combined for both adult male-sized and adult female-sized lizards, approximately 69% of the *A. opalinus* were observed perching 1–3.3 m and approximately 70% of the *A. l. lineatopus* perch sites were 0–1.6 m high.

Similar-perch height trends were also found for A. opalinus and A. l. lineatopus on the Kingston study area of the present investigation. By adding a standard deviation to both sides of the mean perch height, an estimate is derived for the range of 68% of the observed A. opalinus and A. l. lineatopus. Thus, a range of 1.2-3.6 m is calculated for A. opalinus sharing the immediate habitat with A. l. lineatopus ("Op with" category) and a 0.3-1.7 m perch height range for A. l. lineatopus ("Li with"). These ranges of perch heights for mixed groups of A. opalinus and A. l. lineatopus inside the present study area reflect the same trends found by Rand (1967b) and Schoener and Schoener (1971) outside the immediate study area. In contrast, however, is the range estimated for 68% of the perch height observations for A. opalinus not simultaneously sharing trees with A. l. lineatopus ("Op without"); this was 0.3-1.1 m.

A second objective is to emphasize this reported instance of competition between two congeners under field conditions. The occurrence of competitive exclusion and character displacement are strong theoretical agents used to explain the distribution and possible evolution of Anolis in the West Indies (Rand 1969, Schoener 1969, 1970b, Williams 1969). The Kingston opalinus-lineatopus interaction for perch sites is an exaggerated instance of competitive interference, and a form of competition not yet stabilized at the genome level. The opalinus-lineatopus perch relationship is not fixed, as Kingston A. opalinus still show a penchant for low perches when the occasion permits. This low perch pattern is consistent with that of the Mandeville A. opalinus, which does not demonstrate a perch height shift in the presence of the larger conspecific, A. l. neckeri.

The fact that A. opalinus is able to utilize a different portion of the immediate habitat during interactions with A. l. lineatopus rather than be excluded entirely from the region of sympatry is noteworthy. A. opalinus is the smallest and most wide-spread of the Jamaican anoles. It is found in many different habitat types and associates with almost all of the other six Jamaican anoles (Anolis reconditus a possible exception). It is important that A. opalinus have the behavioral flexibility to adjust to various environmental conditions, a feature most likely common to many other anoline species. Differing species composition and almost certainly differing habitat characteristics may have a significant effect on certain ethoecological patterns of a species. This presents a much more complex problem for the biologist, but is an obvious advantage to a species co-existing with a number of congeners.

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