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NOTES ON HISPANIOLAN HERPETOLOGY 5. THE NATURAL HISTORY OF THREE SYMPATRIC SPECIES OF *ANOLIS*

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The lizard genus *Anolis* is abundant in species and individuals in the Greater Antilles. Quite a number of the common species occur together over wide areas. There is thus a special opportunity to study the ecological relations of sympatric species of a single genus under conditions genuinely favorable for field observation.

Several papers have now been published which have begun to exploit this fortunate opportunity: Ruibal (1961) and Collette (1961) working on the anoles of Cuba; Oliver (1948) on those of Bimini in the Bahamas; Williams and Rand (1961) on the *semilineatus* group in Hispaniola. These and earlier workers — Grant (1940) for Jamaica; Stejneger (1904) and Schmidt (1928) for Puerto Rico and especially Mertens (1939) for Hispaniola — have established that in each well studied case there are small but definite differences in microhabitat among the sympatric *Anolis*.

In this paper I document the same point for the three commonest species of *Anolis* in Hispaniola. I describe also a number of behavioral differences which seem to be associated with the ecological differences and attempt to assess the adaptive significance of these behavior patterns. This study was made during a two-month field trip to the Dominican Republic and supplemented with observations on captive lizards kept in the laboratory in Cambridge.

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MATERIAL AND METHODS

The field observations during the summer of 1958 were made incidentally to the main project, a survey of Dominican caves for vertebrate fossils. Consequently, they include no lengthy observations in any one locality but are a synthesis of data collected from widely separated places. Though I noticed no geographical variation in behavior, obviously this is a possible source of error that runs throughout the present study. This is particularly true as observations are lumped for different subspecies in two cases: *Anolis chlorocyanus chlorocyanus* and *A. chlorocyanus cyanostictus;* and *Anolis distichus ignigularis* and *A. distichus dominicensis.*

The main areas, where observations were made, were: Santo Domingo and vicinity, Santiago and the nearby Sierra Septentrional, Padre Las Casas, Sabana de la Mar and the mountains south of there, and the Sierra de Neiba. These field observations are least complete on *A. chlorocyanus* and uneven on the other two species. For example, I found eggs only of *cybotes,* while I observed copulation only in *distichus.*

The laboratory observations made at the Harvard Biological Laboratories involved only two species, *A. cybotes* and *A. chlorocyanus chlorocyanus.* These animals, ten of each species, all adults and about half of them males, were sent to me by Professor Eugenio de Jesus Marcano. The lizards were released in a room 12 x 20 ft. and 9 ft. high. The room was a constant 80° F. and lighted by a south window. Eight small tree trunks 7 feet tall, mounted on bases so that they stood upright, an 8 foot rubber tree, a potted pine bush, and some other potted plants were arranged around the room.

The lizards were fed meal worms on the floor and in dishes taped at various heights above the floor, on the tree trunks. Fruit flies were also released in the room. The whole room was watered daily.

For a period of about three weeks, daily observations of varying lengths were made. The lizards quickly came to ignore me as I sat quietly in one corner of the room and watched them with low power binoculars.

This was obviously not a natural situation but the observations that could be checked against the field notes show a gratifyingly close agreement. This method seems to be a useful adjunct to field observations though obviously no substitute for it.

All three of these species are small to medium sized lizards possessing the characteristic specializations of the genus: enlarged subdigital lamellae and a throat fan or dewlap that is best developed in the male. In each species the males grow to a larger size than do the females.

Anolis distichus varies in dorsal coloration from green to gray to brown, frequently with mottling on the back. The dewlap is yellow in *A. d. dominicensis*, and red with a yellow border in *A. d. ignigularis*. The males measure 51 mm in snout-vent length (Cochran 1941).

Anolis cybotes is dorsally gray or brown, sometimes reddish, frequently with two indistinct greenish lateral stripes. The dewlap is whitish or yellowish in color. The males measure 67 mm in snout-vent length (Cochran 1941).

Anolis chlorocyanus is usually bright green with the ability to change to brown. *A. c. cyanostictus* also has a rust-red spot in front of the shoulder and one on the head. *A. c. chlorocyanus* has a dewlap that is light blue anteriorly and dark, almost black posteriorly. *A. c. cyanostictus* has the dewlap proximally cadmium yellow, distally sky-blue. The males measure 71 mm. in snout-vent length (Cochran 1941).

OBSERVATIONS

The observations from both field and laboratory have been combined and arranged according to topics. Under each topic heading all three species are compared.

Geographical Distribution. All three species are widespread in the Dominican Republic. Apparently they avoid only the high, wet pine forests of the Cordillera Central and are less common in the dry regions on the south coast near Asua and in the northwest near Puerto Plata. However, *A. chlorocyanus* is replaced by *A. coelestinus* in the Barahona Peninsula. Geographical variation in each of these species has been described by Mertens (1939).

Habitat. I found these three species at almost every locality I visited in the Dominican Republic. Mertens called *distichus* and *cybotes* eurytopic forms and *chlorocyanus* only slightly less so. He records both *distichus* and *cybotes* from the mangrove areas along the coast to the lower pine forests around Constanza at some 1200 meters altitude.

The most significant environmental factor for all three species seems to be some sort of vertical perch, a tree trunk, fence post or cliff face, but *A. chlorocyanus* seems to avoid the most open areas.

Anolis distichus lives primarily on isolated trees and fence posts and along the edges of woods and trails and in open woods. *A. cybotes* lives in these situations but also occurs in the deeply shaded interiors of densely wooded areas that *distichus* avoids. *A. chlorocyanus* certainly occurs in the edge situations that *distichus* prefers and probably in the heavier woods as well.

Though there are differences such as these in the extremes tolerated, these animals live in the same habitats over most of the Dominican Republic and part, at least, of Haiti. Mertens notes that in separated localities he observed individuals of all three species living in the same tree. My observations agree with this.

Microhabitat. These three species, though living in the same habitat, have differences in their microhabitat preferences.

A. distichus lives almost exclusively on exposed (i.e. not closely surrounded by vegetation) tree trunks, fence posts and similar structures, within 10 to 15 feet of the ground. It is seldom seen on the ground or in the smaller branches of bushes or trees. Though it must descend to the ground to reach isolated trees, it does not spend much time on the ground. *A. distichus* is often very common on the palisade fences in small villages.

A. cybotes is also primarily an animal of exposed tree trunks and fence posts within 10 feet of the ground. However, it also frequents rocks and fallen logs and smaller individuals are frequently seen on the ground. It also avoids, during the day at least (see *Sleeping*), small twigs and foliage. These field observations are confirmed by the laboratory data which show *cybotes* spending most of its waking time on perches less than five feet from the floor.

A. chlorocyanus lives also on tree trunks and fences but unlike the other two, frequently ranges high in the trees and out among the smaller branches. I saw a female fall from the crown of a 30 foot palm tree. I suspect that this species is one that lives primarily up among the branches and ranges down the trunk

rather than the reverse. However, individuals were seen also on fences and once I saw a dozen individuals on a pole framework nine feet high that with a few bits of palm thatch was all that was left of a shed in the middle of a treeless pasture. Like *distichus, chlorocyanus* must occasionally descend to the ground to reach isolated trees.

In the laboratory, *chlorocyanus* spent most of its time high on the perches and ventured out among the leaves of the rubber plant much more than did the *cybotes.*

Territoriality. As Mertens noted, all three species appear to be territorial. He says that for *A. cybotes* and *chlorocyanus* he found only a single adult male and one or more females of each species on any one tree. When he placed an additional male on one of the occupied trees it was immediately attacked. *A. distichus,* he says, defends a smaller territory and the large trees may have several males, each with its own territory, as well as a number of females.

These observations agree with mine, although it was only in areas where *distichus* were extremely common that I found more than one adult male *distichus* on the same tree, and then only on large trees.

Certainly in the laboratory no male of either *cybotes* or *chlorocyanus* would tolerate another male of the same species in his immediate vicinity for long, and even females were chased away if they approached too closely. Occasionally a male of one species would display to an individual of the other species.

In addition to this horizontal effect a vertical stratification on individual trees or posts is evident in at least two of the species, *distichus* and *cybotes.*

On the smaller trees that were occupied by two individuals of *distichus,* the lizards were usually of opposite sex and the male was usually closer to the ground than was the female. On one tree there were four lizards of this species: a large male near the base, a female above him, a slightly smaller female above her and, highest of all, a juvenile who was about 7 feet above the ground. During the hour that I watched this tree all of the lizards moved a number of times but this stratification remained the same for it was actively enforced. When one of the higher individuals moved in sight of and within 2 or 3 feet of a lower one, the lower animal immediately reacted to it. The male did this by bobbing his head and pumping his dewlap, the female by a short charge in the direction of the intruder. In every case the intruder retreated immediately, around the tree and up.

In *cybotes* almost all of the individuals on the trees were large and most of them were males. The individuals that were seen on the ground were almost always juveniles or females; the females are much smaller than the males in this species. This spatial distribution seems to be a real phenomenon but I have no field evidence to support the hypothesis that it is the result of territorial defense. However, there are certain laboratory observations that support this contention. In the laboratory I saw no vertical stratification but I also saw no evidence that the females tended to spend more time on the ground than did the males. This may be because the perches were small and numerous enough so that each lizard could occupy its own, as they usually did. However, there was a definite stratification horizontally with the large males on the perches near the window and the smaller males and females on those farther away. When a smaller individual invaded a perch near the window, and this happened quite frequently, the resident male would display to it and the intruder would retreat. Thus, though there is no direct evidence that the distribution seen in the field is due to territorial defense, there is evidence that defense could be at least a contributing factor: the males taking the most desirable positions, the elevated perches, and chasing away any smaller individual that attempted to move in, with the result that the juveniles and females would spend most of their time on the ground.

It is of interest to note that this vertical stratification in *cybotes* and *distichus* results in greater difference in size between the individuals that occur together. Adult *cybotes* are larger, and the adult males much larger, than adult *distichus*. This size difference could be reflected in the size of the prey items taken and so reduce the competition for food between the two species. The young of *cybotes* are of course no bigger than adult *distichus* but these are the individuals that live primarily on the ground and so do not occur on the tree trunks with the *distichus*. The importance of this in reducing competition for food, if it acts in this way at all, is of course unknown. It would be interesting to have an analysis of the stomach contents of various sized individuals of each species.

In *chlorocyanus*, I have no clear evidence for vertical stratification either in the field or in the laboratory. However, the fact that most of the individuals caught on fences and tree trunks were adult males suggests that the females and the juveniles may

stay higher in the trees. This phenomenon may also give maximal emphasis to the size difference between this species and the *distichus* with which it comes in contact for it is the large individuals of *chlorocyanus* that descend the tree trunks and they meet first and presumably would compete most for food with the smallest *distichus*.

Posture. Seen in silhouette these three species are usually immediately recognizable. This is partly because of their different proportions but even more because of their very different postures.

A. distichus rests facing either up or down or angling across the tree with its head and at least the anterior part of its body well off the substrate and with its neck bent so that its head is parallel to the substrate but further away from it than are its shoulders (Cf. figure 4, plate 2, Mertens).

A. cybotes typically rests facing down the tree with the fore part of the body off the substrate and the neck bent dorsally so that the head is nearly parallel to the ground. In one individual seen resting on the underside of a log which slanted at about 45°, the neck was bent back well over 90°. This posture is true in the laboratory as well as in the field. On the ground the posture is much like that of *distichus* with the neck bent so that the head is parallel to the ground and raised above it.

A. chlorocyanus usually rests with both its head and body quite close to the substrate and its neck bent only a little if at all, both in the field and in the laboratory.

While these postures are typical of the normal resting position, both *cybotes* and *distichus* when mildly alarmed flatten against the substrate, and *chlorocyanus*, when about to display, raises itself up on its legs.

I believe these differences in posture can be correlated with feeding behavior as discussed below.

Mertens says that most *Anolis* rest with their heads pointing toward the ground. I noticed this most commonly in *cybotes* and less so in the other species.

Activity. *A. distichus* appears to be a much more restless lizard than either of the other two species. Like them it spends most of its time resting quietly but an individual seldom remains in one place for more than a few minutes. It then moves quickly a few inches away on its tree trunk and rests quietly again for another few minutes.

A. cybotes, on the other hand, seems to spend much longer periods of time resting in one spot. Again, when a change is

made, it is made quickly. In the laboratory when a *cybotes* moved from one tree to another, the lizard frequently ran down to the base of the tree, stopped for a few moments, left the tree with a jump and ran part way across the floor, paused, ran the rest of the way and with a jump started up the new tree, usually pausing again before settling down.

A. chlorocyanus, though also spending periods of time immobile, moved quite frequently, going slowly and deliberately about in the trees, in the laboratory as well as in the field. In the laboratory, moving from one tree to another was a single process. The lizard moved slowly down to the base of the tree, jumped off, dashed across the floor and with a jump started up the new tree. As little time as possible was spent on the floor.

Climbing. I have no observations on the climbing ability of *distichus*.

In the laboratory *A. cybotes* did not appear to be as sure a climber as *A. chlorocyanus*. I saw several of the former fall to the ground from the smooth leaves of the rubber plant while I noted that only one of the latter did so even though *chlorocyanus* spent much more time on these leaves than did *cybotes*. While both these species started their climbs in the lab with a jump up on to the vertical surface, and I saw a large male *cybotes* make a 6 or 7 inch vertical jump to reach a hanging branch, *chlorocyanus* made a great many more horizontal jumps. Particularly common was one used to cross the 10 inches that separated the two closest perches.

A. cybotes is apparently a quickly moving lizard, quite at home on the ground but not so much so in the more treacherous footing of smooth green leaves and small twigs. *A. chlorocyanus*, on the other hand, is shy of the ground, moving across it only occasionally and then with as much speed as it can manage, while in the less secure footing of more arboreal situations, its deliberate movements help keep it from falling.

Feeding. On several occasions a *distichus* was seen to move from its resting position on a tree trunk or fence post and snap up something small from the bark. Twice I saw a male interrupt his displaying to do this. Once I saw a male move up to an ant about an inch away, follow it up the tree a couple of inches and then apparently lose interest and turn away. Thus there seems to be some selection of food and not everything small that moves within range is eaten.

A. cybotes was never seen to catch anything in the field, though on two occasions I saw an individual struggling with a large dragonfly; each time the lizard had the head and thorax in his mouth and the wings and abdomen still protruding. In the laboratory, *cybotes* came willingly to the floor to take meal worms. Sometimes a lizard would return to a tree to eat the meal worm but usually it remained for several additional minutes before returning either to its old tree or a new one. I never saw a *cybotes* moving around on the floor looking for food. On one occasion a male left his perch and ran about 10 feet across the floor to make an unsuccessful attempt to capture a 2-inch cockroach.

I have no data on *chlorocyanus* feeding in the field. In the laboratory several individuals were seen snapping at small objects on the leaves and twigs. This species only rarely came down to the floor to capture meal worms and each time that one did so it moved slowly to the base of the tree, then rushed out, seized the meal worm, ran back and climbed up the tree before stopping to eat its captured prey.

On the basis of this limited evidence, some tentative generalizations about the relations of feeding, posture and movement can be made.

A. distichus seems to feed primarily on smaller insects that it catches on the tree trunk. The posture with the head held high above the substrate would enable it to see more of the tree trunk than it could if the head was held low. The frequent movements are necessary if the lizard is to take advantage of the insects that happen to be on the opposite side of the tree trunk. The head is held parallel to the surface in which the lizard is most interested.

A. cybotes males get at least part of their food from the ground after sighting it from their elevated perch. The posture of this species keeps the head roughly parallel to the surface in which the lizard is most interested, in this case the ground. Since the lizard can see a large sector of the ground around him at all times, he need not change his position frequently to maintain a careful scrutiny of a considerable area.

A. chlorocyanus almost certainly gets most of its food from the trees in which it usually lives and its slow movements suggest that at least part of the time, unlike the other two species, it goes looking for it instead of lying in wait. The head is held parallel to the surface in which it is most interested.

We need more observations on all of these points and particularly on the feeding of *A. chlorocyanus*. But it is interesting that the two species, *distichus* and *cybotes*, that occur in the same microhabitat, on the tree trunks, seem to differ so markedly in feeding behavior.

Mertens remarks, in passing, that most *Anolis* get their food on the ground and among the roots of the trees and that their usual posture, as he records it, oriented toward the ground, may be related to this. I believe that this is true of *cybotes* but not of the other species.

Escape. Each of the arboreal species has a noticeably different method for evading herpetologists and presumably other predators.

A. distichus, when approached, quickly moves around to the other side of its tree trunk, usually moving up or down at the same time. If followed, the lizard may continue this maneuvering to keep the tree trunk between itself and the pursuer for some minutes. Soon, however, the lizard will either run up the tree out of reach or run down it to the base where it is concealed by the surrounding vegetation. Only when very hard pressed will one leave his tree or post and run out into the grass. Occasionally, and this was noted especially early in the morning, *distichus* would hide under a bit of bark or in a hole in the tree. Mertens says that *distichus*, when approached, runs around to the other side of its tree or post and then down to its base to hide. He does not mention any of the other behavior described here.

A. cybotes showed the same tactics in the field and in the laboratory. When approached, an individual would remain still until I came very close, then suddenly it would dart around to the other side of the tree; it might stop there but only until I moved into view again, then, instead of employing evasive action on the tree, it would usually run down and, unlike *distichus*, frequently leave the tree completely. In the laboratory the lizard usually ran a few feet away, where it might remain on the floor for some moments or might immediately climb a new tree. Mertens records these same flight reactions for this species. An *A. cybotes*, discovered on the ground or on a fallen log, frequently hid under whatever cover was available. Sometimes a large male, when first approached, would display his dewlap to me before fleeing. This was observed occasionally in the wild and became very common with one male in the laboratory after he became accustomed to me.

Usually in the field, *chlorocyanus*, when approached, immediately began to climb up the tree. This action was slower and more deliberate than that of the other two lizards but, since it was started sooner, the lizard was usually carried safely out of my reach. In the laboratory and in the field, when on a fence, where the lizard could not climb out of reach, it usually climbed as high as it could get and then dodged about there. Only very occasionally did one run down to the ground, though frequently one jumped to a nearby perch, if available, or ran out among the foliage and twigs at the ends of the branches. Mertens also notes that *chlorocyanus* usually climbs up its tree and conceals itself in the crown.

The escape behavior of the three species closely parallels the feeding behavior. *A. distichus* conducts its evasive behavior on the tree trunk. *A. cybotes* willingly leaves its perch to escape on the ground, and *A. chlorocyanus* retreats whenever possible up into the top of the tree.

Daily Activity. Since I did not spend long periods of time watching any one lizard or groups of lizards, I have no detailed information on the variations in activity during the day.

All three species seem to be strictly diurnal. They were seen sitting in the sun more frequently in the early morning than at other times of the day, presumably to raise the body temperature to the preferred level. *A. distichus,* at least, seems to feed more actively in the morning than at any other time. On several occasions I captured one with food in its mouth and three times I had one snap at the knot of the thread noose with which I was trying to snare it.

Sleeping. I do not know where *A. distichus* spends the night but, since individuals sometimes use holes in trees as hiding places in the early mornings, they may possibly use these during the night.

Two individuals of *A. cybotes* were found asleep at night, in the field. Both of them were males and were asleep on top of the foliage of the outermost twigs of small bushes. They were plainly visible from my vantage point, though perhaps not to a predator, such as a snake, climbing the bush. In the laboratory one evening during an examination of the room, I located seven *cybotes* asleep. Five of them were in the needles at the tips of the branches of the pine bush, one on a small vine where it stretched away from the tree trunk, and the last on top of the topmost leaf of a large-leaved potted plant. Shaking a branch on

which a *cybotes* was sleeping woke the lizard but it did not move until the branch was shaken vigorously or the lizard touched. Then it jumped immediately to the floor and remained there unmoving.

A. chlorocyanus was seen asleep only in the laboratory where during the period mentioned above I located six animals. Three of them were sleeping between large leaves of the rubber plant and the wall, one was between a board and the wall, one inside a cold radiator, and only one exposed, on top of its perch. When disturbed, the *chlorocyanus* immediately sought new hiding places.

As Mertens notes, *A. distichus* and *A. cybotes* sleep with their hind legs partly flexed, while *chlorocyanus* usually sleeps with them extended along the tail.

I do not know enough about the real and potential nocturnal predators of *Anolis* to speculate on the adaptive significance of these sleeping places. But it is striking that they are so different from the situations in which the animals spend the day. Male *cybotes*, which in the daytime live on substantial vertical surfaces, during the night sleep on the small flexible foliage and twigs of bushes and vines. *A. chlorocyanus* during the day is usually exposed to view and during the night sleeps under or behind some sort of cover.

Reproduction. Since copulation was observed only in *distichus* and eggs found only of *cybotes*, it is not possible to compare these species with respect to reproductive behavior. I am including these data in the hope that eventually comparative data will be available.

Three times pairs of *distichus* were seen in copulation in early to mid-afternoon on tree trunks from four to six feet above the ground. In no case was the preceding courtship observed. In one case the lizards were oriented diagonally up a large tree six feet from the ground. The larger male was on the higher side and on top of the smaller female. One of his front legs was across her shoulders and holding on to the tree in front of her front leg; one of his hind legs was across the base of her tail, the toes resting on her thigh and the trunk in front of it. His other legs were spread out holding the tree. His tail was bent under hers and his head was resting on but not biting her neck. Her position was that of any resting lizard except that her tail was strongly arched. The position observed in the other cases was virtually identical.

SUMMARY AND CONCLUSIONS

These observations on the behavior and ecology of these three species of lizards, *Anolis distichus*, *A. cybotes* and *A. chlorocyanus* in the Dominican Republic are obviously incomplete. However, certain tentative conclusions can be advanced.

These species are sympatric and occupy the same macrohabitats over much of their ranges. The species differ somewhat in their microhabitats but they are not clearly separated spatially in this way; members of each species occur on the same tree within feet and sometimes within inches of each other. They all have the same basic body form, though differing somewhat in size, in proportions and in morphological adaptations such as development of the enlarged subdigital pads. They are all insectivorous in diet. However, in the details of their behavior they are very different. These details can be fitted together to form a picture of three morphologically similar species of the same genus living together in the same habitat but living three very different lives.

Reviewing these very briefly, *Anolis distichus* is strictly an animal of the lower tree trunks. Its territorial pattern results in spacing out the individuals living on the same tree with the largest at the bottom and the smallest higher up. This species feeds on small insects on the trunk, utilizing a posture and pattern of activity that enables it to forage effectively in this sort of place. When frightened it takes evasive action on the tree trunk, and copulation takes place there.

A. cybotes, though partially an animal of the tree trunks, is also closely associated with the ground below. Its territorial behavior results in a spatial distribution with the large individuals on the trees and the smaller ones on the ground. Even for the individuals on the trees the perches there seem to be primarily lookouts from which to survey the ground. The postures and patterns of activity seem fitted best for this and much less so for watching the tree on which the lizards sit. Certainly they do go to the ground to capture food spotted from these perches. They run to the ground when frightened and they bury their eggs in the ground.

A. chlorocyanus in its behavior seems as closely related to the tree tops as *cybotes* is to the ground. It seems to be mainly the large males that descend the tree trunks. Some feeding undoubtedly occurs high in the trees even in these large males and

chlorocyanus retreats upwards when frightened. Its slow deliberate movements seem adapted to the more precarious arboreal footing among the leaves and twigs.

These are not just three similar animals doing the same things in the same way in slightly different places but three similar animals, each with a unique set of complex behavior patterns which interlock functionally so that each species has its own way of life within the same habitat.

This situation can be an example of the operation of the Gause-Volterra hypothesis that closely related species can live together only if they differ in ecology.

Since many of these differences can be correlated with feeding behavior they can be interpreted further as serving to reduce interspecific competition for food.

However, the demonstration that these conclusions are valid must await the collection of further data, particularly data on just what environmental factors act to limit the population densities of each species.

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