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TORQUATUS AT BELÉM, PARÁ

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INTRODUCTION

Tropidurus torquatus Wied is one of a small number of lizard species in South America that range from the open temperate savannalike cerrados of southern Brazil into the semidesert caatingas in northeastern Brazil and through the Amazonian rain forest to reach the Caribbean coast in the Guianas and Venezuela. The widely distributed populations usually are considered to belong to a single species (Burt and Burt, 1933; Cunha, 1961) with great geographical variation that is currently under study by Dr. P. E. Vanzolini.

Because of the wide range of climatic conditions and plant formations from which this species is recorded, its ecological relationships are of great interest.

The authors spent 4 weeks in Belém, Pará, near the mouth of the Amazon, during July and August 1963 (the first part of the dry season), collecting information on the ecology of this species, particularly its distribution in different habitats, its use of the structure of the environment, and its temperature relationships.

Our observations were made primarily on the grounds of the Museu Goeldi where we conducted repeated censuses of the *Tropidurus torquatus* present and on a number of days watched those in one small area. Though we marked no lizards, some in this area were recognizable as individuals. We also made a number of short excursions in the vicinity of Belém, particularly to Utinga and the grounds of the Instituto Agronomico do Norte, where we examined a number of different habitats and collected temperature data.

We want to thank Dr. Dalcly Albuquerque, director of the Museu Goeldi, Dr. Fernando C. Novaes, chief of the vertebrate division, and

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Dr. Oswaldo da Cunha, herpetologist, for their kind assistance in providing facilities and in many other ways, in Belém. We must also thank Dr. P. E. Vanzolini of the Departamento de Zoologia, São Paulo, for suggesting this project and for reading and discussing the manuscript.

HABITAT

Tropidurus torquatus is a common lizard at Belém near the mouth of the Amazon, but not an inhabitant of the Amazonian rain forest or even of the various types of second-growth forest. All of the several hundred individuals of this species that we saw were in or on the edge of clearings.

T. torquatus was common in a variety of situations: on rocks in a bulldozed bare quarry, but not in the second growth bordering it; on piles of scrap metal at the edge of a grassy pasture and on fenceposts and telephone poles through pastures, but again not in the nearby second growth; on trees surrounded by waist-high grass at the edges of a plantation of rubber trees, but not on the rubber trees within the plantation; on fallen logs in a sparsely vegetated flat that had been cleared near a lake, but neither in the second growth nor in the primary forest which surrounded this clearing; on the wall surrounding the Bosque Municipal (a patch of tall forest within the city), on the open playground in this park, and on a large fallen tree that had opened a clearing about 10 by 30 meters when it crashed down, but not in the forest even along the narrow trails; in the open part of the park of the Museu Goeldi, but only very rarely in the parts of the park where the trees grew more closely and formed a complete canopy.

There seem to be two major factors in determining where *torquatus* occurred—one associated with microclimate, probably temperature, and the other associated with the structure of the environment, particularly the presence of suitable perches.

Structural niche.—Most of the *torquatus* observed were sitting up on some sort of perch a few centimeters to several meters above the ground, and no *torquatus* were found in places where perches were not available to them. These lizards require a perch which allows them to climb a few centimeters to a couple of meters above the ground, and one which is not of small diameter. Trees are used as perches, but the fact that the tree extends its trunk above 2 or 3 meters for an additional 10 to 30 meters seems to be irrelevant to the lizard except with respect to its escape behavior (see below).

A wide variety of things were used as perches. Rocks, bricks, cement blocks, curbs, walls, logs, and the trunks of trees were most commonly used. With two exceptions, both in a dense hedge, no lizard was seen on a slender perch (i.e., less than 3 cm. in diameter).

The usual height at which lizards were seen during a series of censuses around the grounds of the Museu Goeldi is shown in table 1. In each of seven, approximately 50-minute censuses two of us followed the same course, walking slowly and recording for each lizard the height above the ground at which it was first seen. (Heights were measured with a steel tape.) The number of lizards seen during a census varied from 26 to 47. Since perch height did not vary at different times of day, all the censuses are combined.

TABLE 1.—Perch height. The number of individual *Tropidurus torquatus* observed at various heights above the ground during censuses.

Height above ground (cm)	Number of individuals		
	On trees	On other perches	Total
400-449	2		2
350-399			
300-349	4		4
250-299	6		6
200-249	6	1	7
150-199	14	3	17
100-149	15	11	26
50-99	36	23	59
1-49	28	43	71
On ground			38
Total	111	81	230

On these censuses no lizard was seen above $4\frac{1}{2}$ meters and most were below $1\frac{1}{2}$ meters. Relatively few—only 38 out of 230—were seen on the ground, and most of these were small individuals.

Many individuals were seen on perches other than trees, such as rocks, walls, etc., where the height to which they could climb was limited. A lower proportion of the available trees than of these other sorts of perches were used. The *torquatus* on trees which would allow them to climb higher than 5 meters still are usually seen within 2 meters of the ground (table 1).

Temperature.—The association of *torquatus* with open areas and its avoidance of forests may be associated with its temperature requirements.

Tropidurus torquatus is a heliotherm that, when weather conditions

permit, uses variation in environmental temperatures to raise its body temperature considerably above that of the air and maintain it within a relatively narrow range.

The temperatures of 51 individuals were taken with a Schultheis quick-reading thermometer immediately after they had been shot with .22 caliber dust shot. These temperatures were taken on sunny days

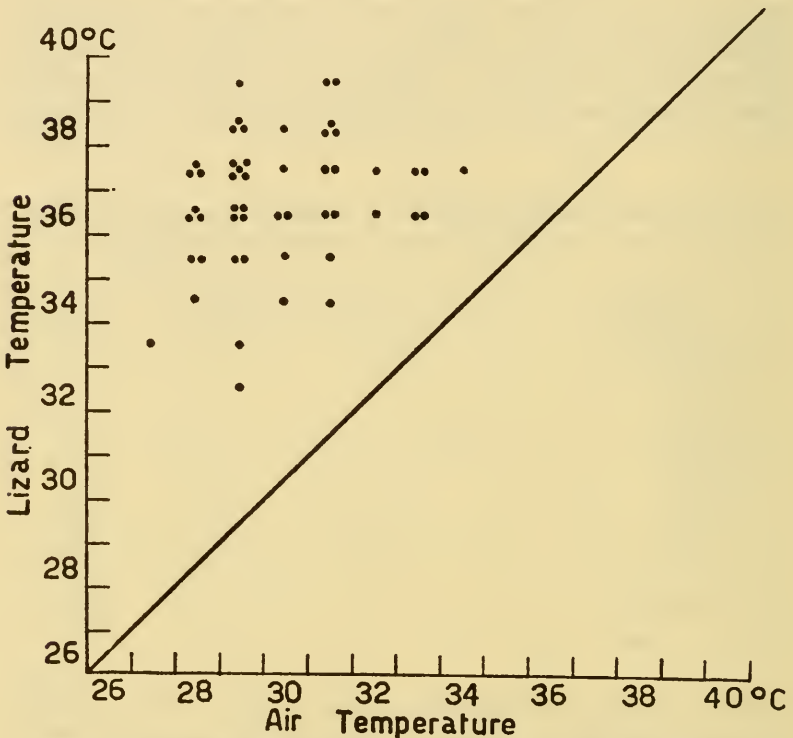


FIG. 1.—*Tropidurus torquatus* temperatures: lizard body temperatures plotted against ambient air temperatures.

when the lizards had the opportunity to thermoregulate. The air temperature in the vicinity was taken immediately after capture.

The temperatures were recorded over an air temperature range of 8°C, from 26.6° to 34.4°. The lizard temperatures also ranged over 8°, from 31.6° to 39.4°. However, 80 percent of the records fall within a 4° range from 34.6° to 38.4° and 58 percent in a 2° range from 35.6° to 37.4°. The body temperatures are plotted against air temperatures in figure 1.

An even more striking way of demonstrating the behavioral thermoregulation in these animals is to plot the air and body temperatures simultaneously against time of day (figure 2). This shows a regular rise in air temperature as the day progresses but no corresponding trend in the lizard temperatures.

DAILY ACTIVITY

This species is strictly diurnal. None was active at night, and activity began after sunrise and ceased about sunset.

Early morning.—One morning was devoted to watching three

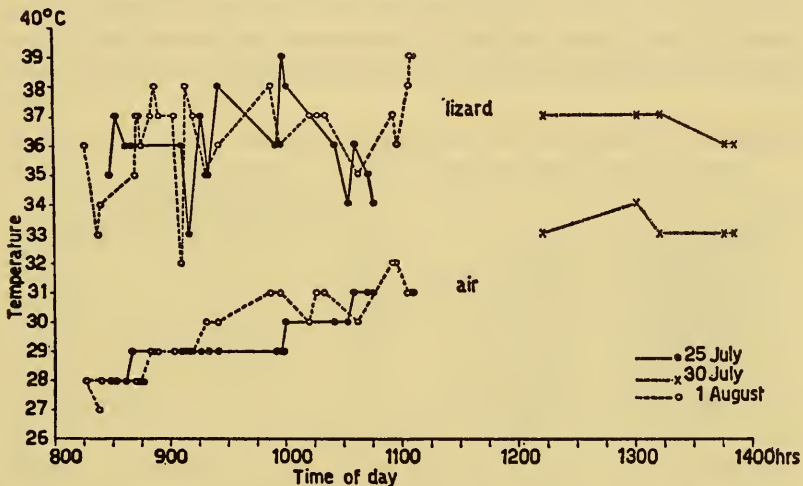


FIG. 2.—*Tropidurus torquatus* temperatures: lizard body temperatures and ambient air temperatures plotted against time of day.

torquatus, a large male and two females, as they began their daily routine. These three lizards had been located asleep the night before, flattened close together against the side of the trunk of a small tree about $3\frac{1}{4}$ meters above the ground.

Observations were started at 0550 hours, after dawn but before sunrise (0620 hrs.) They remained asleep until about 0640 when their eyes were noticed to be open. Five minutes later one of the females lifted her head from the trunk slightly. The first patch of sun reached the tree about 0715. The first female moved around the trunk at 0722 and at 0743 up into a patch of sun. The large male lifted his head at 0736 and moved into the sun at 0752. The second female moved into the sun at 0759. At 0820 the first female ran down the

tree and across the ground to her usual perch. The male and the other female remained sunning for some minutes longer before leaving the tree where they had slept.

Other observations supported the general picture that the lizards remained in their sleeping sites after sunrise. They were usually sunning by 0800 but seldom much before this.

Sunning and thermoregulation.—Once a *torquatus* has left its sleeping site it may move into the sun directly or it may move to a perch where there is no sun. Usually it does not remain long on a shaded perch but moves again into the sun. During the morning the lizard's activities may take it into the shade but usually it moves back into the sun. Later, during the heat of the day, the *torquatus* are more frequently seen perching in the shade. In the late afternoon as the air cools the lizards again are seen basking and also sitting on sub-

TABLE 2.—*The relation between time of day and number of Tropicurus torquatus seen in the sun during censuses.*

Time of census	Date	Number of lizards		
		Sun	Shade	Part sun
0900-0952	19 VII	30	4	2
0908-0957	2 VIII	30	9	3
1100-1150	17 VII	6	19	3
1100-1150	29 VII	11	12	7
1300-1352	23 VII	8	21	1
1527-1635	15 VII	4	19	0

strates which have been warmed by the sun, though these may no longer be receiving direct sunlight. This reaction to warm substrates is particularly noticeable when clouds hide the sun in the afternoon (a common occurrence during our stay in Belém).

The relationship between time of day and sunning is shown in table 2.

Even more striking than whether the animals are in the sun or not are the changes in posture at different times of the day and under different conditions.

In the morning when the animals begin to sun and also in the afternoon when they seek sun, if available, or warm substrates (e.g., cement walks that have been in the sun all day), they flatten themselves against the substrate so that all of their ventral surfaces are in contact with it—belly and chest, throat, tail, arms, and legs. When they are on warm substrates this probably raises their temperature, though it cannot do so in the early morning. As the day progresses and both

lizard and environment heat up, the lizard seldom assumes this flattened posture, but usually sits with at least its head and chest raised.

In the middle of the day when a lizard is sitting on a very warm substrate, it assumes a posture which is almost the exact opposite of the flattened one. The animal raises itself so that it is in contact with the substrate as little as possible. Not only are the head and body raised but also the tail (though the tip may sometimes touch). Even the toes and fingers are raised so that the only parts of the animal to touch are the palms of the hands and the soles of the feet. This presumably reduces the amount of heat which is transferred from the hot substrate to the body of the animal.

We have the impression that when the animals are sunning in the morning they orient themselves to expose the maximum surface to the sun.

This species shows little color change and none which we could see associated with temperature or sunning.

Reaction to rain.—These *T. torquatus* remained active during cloudy periods during the day, but on one occasion when it began to rain they behaved differently. They ignored the first sprinkle except to wiggle when struck by a raindrop as if they had been crawled on by an ant. When it began to rain somewhat more heavily, most, but not all, of the lizards moved into concealed hiding places. In one case the hiding place was that used for sleeping, in two other cases it was not. These hiding places concealed them and also protected them from the rain.

Late afternoon.—*T. torquatus* seem to have definite places to sleep. We watched three *torquatus* go to their sleeping sites: one, a female, climbed up to her sleeping site on a tree at 1805 hours; one, a larger female, climbed to hers in a brick pile at 1804; and one, a large male, climbed up a tree to sleep at 1820. These lizards sought their sleeping places as it began to get dark but while we could still see them clearly. On cloudy afternoons they remained active until about sunset, but probably went to sleep earlier than on bright afternoons. In all of the cases observed the lizard slept in a place it did not visit when active except as a hiding place. Going to the sleeping site was simple and direct with few pauses.

Sleeping sites.—Four sleeping sites were found: (1) Between the vertical sides of two bricks in a brick pile about one-half meter above the ground; used by a single lizard. (2) On the trunk of a tree three-fourths meter in diameter about 3 meters above the ground

under the leaves of an epiphyte which hung down along the trunk; used by a single lizard. (3) On the 12-centimeter trunk of a tree $3\frac{1}{4}$ meters above the ground behind a small branch which grew parallel to the trunk and just above where it joined the trunk; usually used by two and on one occasion by three lizards. (4) In a deep but narrow crevice in a very large tree, about 1 meter above the ground; used by three lizards on occasion at least. All four of these sleeping sites were used repeatedly, almost surely by the same lizards. The crack in the large tree and the brick pile were used by lizards as hiding places from us. The two more exposed spots on the tree trunks were not so used.

These places have in common that they were above the ground and that they more or less hide the lizards (in two cases quite well, and in two cases only moderately so) and that they were on the west side of the structure.

MAINTENANCE ACTIVITIES

Posture.—*T. torquatus* on tree trunks or other vertical surfaces frequently rests head downward with its neck bent so that the head is almost parallel to the ground. On lower perches such as rocks it usually climbs to the top of the perch and rests in a horizontal position. It also is frequently seen on the side of a rock with its body vertical and its neck bent forward so that the head is over the top of the perch and parallel to the ground.

Feeding and foraging.—*T. torquatus*, like most other iguanids, does not search actively for its food, which is primarily insects.

Some prey was captured when it lit on the lizard's perch or passed near the lizard; in other cases the lizard left its perch and traveled some distance to the insect. The longest excursion seen was by a large male that ran 4 meters across the ground to seize a large fluttering dragonfly. We have the impression that *torquatus* traveled farther for large than for small prey. In the case of the dragonfly, the lizard ran directly to it and seized it. Another lizard approached a large butterfly more slowly in a series of short runs, keeping his head and body close to the ground as if he were stalking it. Several times we saw a *torquatus* jump into the air to snap at a flying insect and one lizard on two successive days stationed himself in an area where many small flies were hovering and repeatedly leaped up at them. Most of these attempts were unsuccessful but we saw him make several captures. In these leaps the front feet certainly and perhaps the hind feet left the ground.

One *torquatus* was seen to pick an insect off a green leaf and an-

other to reach under a leaf and seize one. This latter insect was probably seen by the lizard as it crawled under the leaf.

Many times a *torquatus* on the ground picked up a number of insects, six or seven within a half minute, from the same place. These probably were ants, since ants were the only insects present in concentrations and lizard feces contained large numbers of ants. However, a lizard sitting on its perch ignored a great many ants that we could see running up and down his perch and even over him.

On one occasion we saw a *torquatus* run a short distance and seize a seed with white plumes that drifted to the ground.

Small insects were picked up with the tongue and swallowed immediately. Larger insects were picked up with the jaws as well, and were chewed before being swallowed. A lizard which had come to the ground to capture one of these larger insects frequently carried it back to its perch or to another perch before eating it.

Though most of the lizard's time was spent on an elevated perch and some insects were caught on it, most of the captures we saw were made on the ground. The lizard either left its perch to capture an insect seen from its perch, or encountered an insect while on the ground.

During the periods when the lizards were active we observed frequent captures and attempted captures of prey, certainly at the rate of several an hour.

Fecal pellets collected in the park of the Museu Goeldi contained a large variety of orders of insects. The commonest item was ants which were present in all but one pellet that contained instead a number of termites. Most of the food taken was small, up to $1\frac{1}{2}$ centimeters in length, though one large male was seen to eat a dragonfly with a body of approximately 7 centimeters.

All but one of the food items were of groups that are active in the open during the day. The only exception was the fecal pellet full of soldier termites. During the day these usually are found in their nests or foraging in covered tunnels. However, when a tunnel is broken the soldiers rush out and probably the lizard had encountered a freshly broken tunnel.

A considerable amount of plant material was found in the feces. Some of this was probably taken incidentally with insects. Some may have been taken when mistaken for an insect as described for the plumed seed above. We saw no other lizard eat any plant material.

Water.—No *torquatus* were seen drinking. They may occasionally do so but certainly not as frequently as they feed. Water is available

to them during rains and as dew on some occasions, but since they seem to hide during rains and do not become active in the early morning much of their necessary water must come from the food which they eat.

Defecating.—Waste material is defecated in the form of a pellet, roughly cylindrical with bluntly tapered ends about four to five times as long as wide and with a white cap more or less loosely attached to one end. Fecal pellets vary from about 1 to about 3 centimeters in length; some of this variation related to the size of the animal defecating. A fresh pellet is dark, almost black in color, damp, and soft to touch, and contains much moisture. The white cap is nearly dry when extruded and represents the material excreted by the kidneys.

Defecation seems to occur in the morning, within an hour or two after the *torquatus* become active but we did see one individual defecate at midday. How frequently an individual defecates is unknown.

Defecation seems to occur wherever the lizard is at the time and fecal pellets accumulate on and around the most frequented perches until the pellets are broken up by ants or disintegrated by rain.

A lizard may defecate when on either a vertical or a horizontal surface. In the three cases noted closely, the lizard flattened against the substrate and raised its tail base and vent and the fecal pellet was extruded white cap first. In one case the tail was jerked upward slightly during this, as if the lizard were straining. Once the pellet has been extruded, it may fall to the ground if the lizard is on a vertical surface, or may hang attached if the lizard is on a horizontal surface; in the latter case the lizard moved a few steps away, lowering the vent to the ground so that the fecal pellet was brushed off.

The *torquatus* took no interest in their freshly defecated pellets or in those of others.

Escape reactions.—The escape reactions of *torquatus* seemed to depend largely on the position of the animal when disturbed.

The initial reaction seemed to be to run, frequently out of sight, sometimes toward but seldom into a hiding place. A *torquatus* on a rock or a tree usually ran around to the other side; one on the ground might run to a tree and a short ways up it, it might run to a rock pile, or it might just run away a few meters. If followed or approached again the *torquatus* on trees usually ran up out of reach; most of the others hid in a crack or crevice or behind or under something.

In its initial run a *torquatus* sometimes ran toward some particular

hiding place even if it stopped before reaching it. On one occasion a lizard ran toward and past us to disappear through a broken window into a basement. In their reactions the lizards seem to make use of a knowledge of their surroundings and a lizard on a tree might leave the tree at our approach to run across the ground to another tree or to something under which it could hide. Though the lizards tolerated our presence at 10 meters or more, and sometimes at 3 or 4 meters, closer approach usually sent them running and at even 10 or 15 meters they seemed aware of our presence.

Predators.—We have no information at all on the predators of this species but it is probably taken, at least occasionally, by most diurnal predators that hunt in open areas and also probably is found by nocturnal predators occasionally.

Shedding and comfort movements.—A number of individuals were seen in the process of shedding. In this species the skin is not shed all at once. Instead pieces of old skin a few square centimeters in area come off separately. Many individuals have part of their body brightly patterned where the old skin has sloughed off while other parts are very dull and dark where the old skin still adheres. We have no data on how long the whole shedding process takes or the interval between sheddings.

Individuals were seen occasionally making what seem to be comfort movements. One scratched briefly at its right shoulder with its right hindleg in what looked to be a rather ineffective manner. Several times a lizard wiped or scraped its jaws or lips on the ground or perch; once the lizard had a bit of loose skin on its jaws, once it had a plume of a seed caught in its mouth and another had just seized a small insect which may have had an unpleasant taste or have stung him.

Another sort of comfort movement was a twitch or shake of leg or head. This seemed to be in response to an ant crawling on the lizard, though frequently ants crawling on them were completely ignored, and sometimes when a lizard twitched or shook a leg no ant could be seen.

One female was seen sitting in the shade with one hindleg extended almost straight up in the air, the body twisted to allow this. This was seen only once and its significance is completely unknown.

HOME RANGE

Each *torquatus* seemed to restrict its activities to a small area centering on a few perches and their vicinity.

One male whom we recognized as an individual was observed over our 4-week stay in Belém in the same small area. We recorded his

movements during several periods in different days. These observations for 6 different days are presented in figure 3, a total of 1023 minutes with the lizard under observation 91 percent of the time. One can join the most distant points at which the lizard was seen to

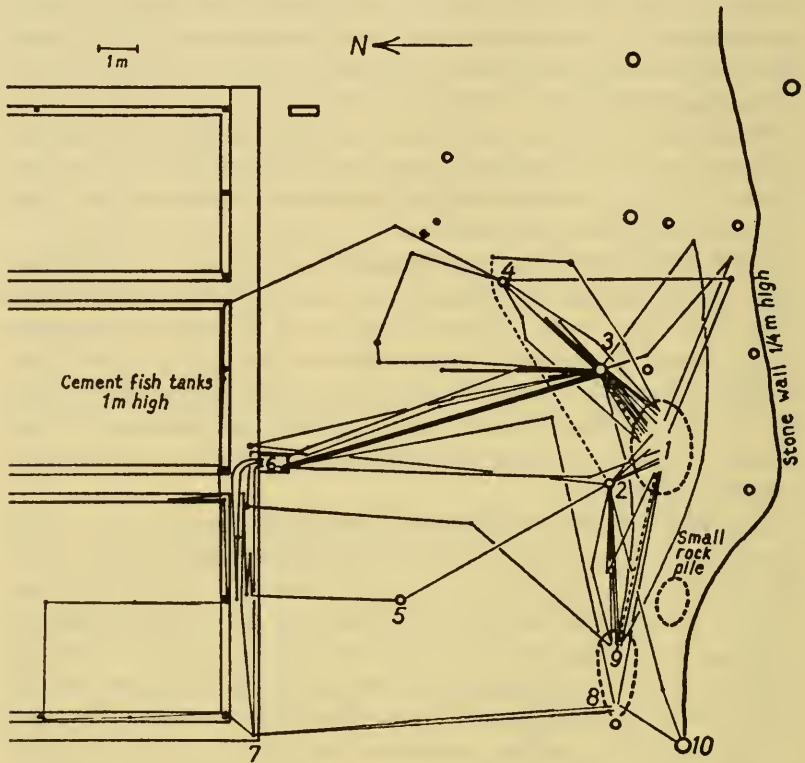


FIG. 3.—Habitat utilization in *Tropidurus torquatus*. The movements of one adult male during 936 minutes in nine observation periods over 6 days. Heavy lines indicate structural features, and circles represent trees. Fine solid lines show observed movements; fine dashed lines show movements not observed, but deduced. Small dots indicate stops of less than 5 minutes; large dots stops of longer than 5 minutes. The time spent on the numbered perches is shown in table 3. Movements of less than 1 meter have been omitted.

form a convex polygon with an area of 195 square meters, but from figure 3 it is evident that his activity is concentrated in only a small part of this. The lizard spent most of his time (63 percent) on three perches, a rock pile, a stump, and a palm tree (perches labeled 1, 2, and 3 in figure 3), and moved frequently from one of these to another.

He also made numerous excursions from these perches to other places in the vicinity, repeatedly visiting certain perches and not visiting others which seemed similar. He spent an additional 18 percent of his time on these perches. The remaining 19 percent of the time was spent on the ground or on perches which he visited only once during these observations. This data is presented in table 3. The region of greatest concentration is not in the center of the home range but to one side of it and consists not of a central point but of three different perches. We think the lizard ranged to the north rather than to the south because the area to the south was more heavily shaded.

The route the lizard took during one observation period is shown in

TABLE 3.—*Habitat utilization: Time spent on certain perches by a large male Tropicurus torquatus during nine observation periods on 6 days, July 11-19 (see figures 3 and 4).*

Perch	Number of minutes on perch	Number of days on which perch was visited	Number of visits to perch
1. Rock pile	274	5	14
2. Stump	168	6	10
3. Palm	150	6	15
4. Tree	58	3	5
5. Tree	35	2	2
6. Small pile of scrap sheet iron	28	3	5
7. Southwest corner of cement walk	23	2	3
8. West end of sandpile	25	2	3
9. East end of sandpile	20	4	4
10. Large tree away from major perches	6	1	1
	149		
Total	936		

figure 4. In this period he moved from one to another of his three principal perches four times for no apparent reason. He made several longer excursions, chasing another male three times and approaching a female once. He also made shorter excursions (not indicated) in the immediate vicinity of his major perches to catch insects. It is striking how much of the total area visited in 6 days (fig. 3) he visited in this one 3-hour period.

After the observations described were made, a tree was felled so that the trunk lay near the base of the palm which the lizard used frequently. By the next day he was using this trunk as one of his favored perches.

This male shared his home range with at least three adult females and we occasionally saw another adult male invade it from the east.

forest but because of the behavior of *torquatus* most of it is not available to this species.

Because these lizards seldom climb more than 3 or 4 meters above the ground they are excluded from the well-lighted canopy. The sunlight which reaches the lower levels of the forest does so as isolated patches, the positions of which are continuously changing as the sun moves and as branches and leaves in the canopy are blown by the wind. Consequently, the surfaces of the sunlight patches are not heated to anywhere the extent that the sun heats surfaces in the open, and thus opportunities to use heated substrates for thermoregulation are strongly restricted in the forest. Inger (1959) has shown that a skink living in the rain forest in Borneo is able to maintain a body temperature above the surroundings by basking in the patches of sunlight (though the temperature it maintains is still 4° or 5°C below that measured for Belém *torquatus*).

T. torquatus restricts its activities to a small area, probably usually less than 200 square meters, and spends most of its time on a few perches within this area. This behavior would certainly interfere with following the movements of the sun on the forest floor necessary to using them for thermoregulation.

Certainly the insect food which *torquatus* takes is available in the forest, particularly since it includes a large number of ants and these seem always to be abundant. Water is more available in the forest than in the open. The influence of predators on this species is completely unknown, but it seems unlikely that the predator pressure in the forest is sufficiently great to exclude them from it completely. The availability of suitable egg-laying sites in the forest is impossible to evaluate without much more information, and this may be an important factor in preventing populations establishing themselves there. But the absence of any individuals more than a very short distance inside the forest suggests that the factors operating do so throughout the life of the individual.

From these arguments it seems likely that *torquatus* is absent from the forest basically because its thermoregulatory behavior is such that it cannot maintain a sufficiently high body temperature under forest conditions. It probably is absent not because the necessary radiant energy does not exist in the forest, but because the animals' behavior is not adapted to taking advantage of it.

Even in open areas *torquatus* is not uniformly distributed. The lizards only occur where suitable perches are available. Thus the animals are absent in absolutely bare fields, clearings, and in grassy pastures and meadows that lack trees or fenceposts.

The lizards are arboreal in Collette's (1961) sense in that they spend

much of their time above the level of the ground. They are not arboreal in the sense that they are more closely associated with trees as such than with any other surface irregularity. Lizards are frequently seen on top of low perches as well as the vertical sides of taller ones.

These two requirements—suitable perches and suitable conditions for thermoregulation—seem basic to the ecology of the *Tropidurus torquatus* at Belém. This species does not occur where either of these is absent. Together they seem to provide a suitable habitat for the species. Other factors are undoubtedly important (e.g., food supply, egg-laying site, etc.), but these latter seem less critical in determining the distribution of *Tropidurus torquatus* at Belém.

At the present, suitable habitats for *Tropidurus torquatus* at Belém have almost entirely been created and maintained by man. The only exception that we saw was a small clearing created by the fall of a large forest tree which was close to the edge of the forest.

Tropidurus torquatus is definitely a component of the fauna of the Belém area but not of the forest. Presumably it is a species that evolved in more open environments and subsequently penetrated the forest in clearings and along the edges. It may have invaded the Belém area only after there were manmade clearings. It is also possible that it has a longer history in the region, and before man began to modify the environment may have lived in natural clearings, perhaps those caused by fallen trees, those along the banks of the rivers, or others. Whichever is true, it is certain that man has provided a much greater extent of suitable habitats than ever have occurred in the area before.

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