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## FIELD STUDY OF THE SOCIAL BEHAVIOR OF THE BLACK LIZARD, *CTENOSAURA* *PECTINATA*

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### INTRODUCTION

When a colony of the big black iguana, *Ctenosaura pectinata*, was located on the outskirts of the village of Acapancingo, just southeast of Cuernavaca, Morelos, Mexico, an excellent opportunity was presented to make a field study of the group behavior of a lizard species.

Colony formation and the interactions of individuals within the group have not been studied in lizards while in their natural habitat so far as known except for the brief report by Schmidt (1935) to which reference will be made later. Most of the field work on lizard behavior emphasizes the tendency on the part of individuals to disperse. Newman and Patterson (1909), Fitch (1940), and Evans (1946) describe such dispersal, especially on the part of males, in the genus *Sceloporus*, while Strecker (1928), Evans (1938a), and Ellis (1940) confirm the same tendency in the genus *Anolis*. Rollinat (1900) and Wiedemann (1909) describe the phenomenon in the European genus *Lacerta*. A few years later Prashad (1916) and Mahendra (1936) mention it as being well shown in the East Indian gecko, *Hemidactylus flaviviridis*, while Asana (1931) makes indirect reference to the same habit in *Calotes versicolor*.

Each male of the types mentioned selects an area, designated as a territory, which is usually large enough to supply the food and water needed by the occupant. Each territory also provides shelter and an elevated lookout point from which the occupant can observe the approach of other lizards. The female seems to

select both the territory and the male. She moves from one area to another early in the mating season until her choice is made. Occasionally more than one female selects the same territory, and in such instances a primitive form of polygamy appears. This was particularly emphasized by Lamborn (1913) in the African species *Agama colonorum*, but it has been noted also by Evans (1938a, 1946), and especially in the marine iguana by Schmidt (1935).

With the exception of the nocturnal gecko, *Hemidactylus flaviviridis*, the male of each of the genera or species mentioned above makes known his presence and sex by very noticeable head or body movements or by displaying a patch of color on his throat, trunk, or flank. Such posturings most frequently take place from the top of an elevation such as a fallen tree, fence post, or even a rock within the boundaries of his territory.

An intruding male of the same species, upon observing the resident's display, may turn and run away but usually will respond by repeating the same movements or display himself. The resident then proceeds with what might be called the challenging or bluffing strut. This varies with the species, of course, but usually the resident begins a very slow, deliberate advance towards the rival.

In this preliminary phase of lizard combat the resident assumes a threatening posture which, in the Iguanidae, creates a transformation in his appearance. His mouth is partly open, his throat is distended, his sides are flattened, usually vertically, while the dorsal spines or dorsal crest along neck and back are raised. The strange male assumes the same posture, and both move back and forth across the space between them, exposing first one side then the other to the rival. If neither male moves away during this phase, one (usually the resident) will attack with open jaws and try to bite the other. This often ends the battle, with the victor chasing the defeated off the territory. Upon returning to the lookout post the successful combatant proceeds to strut or bob his head for several seconds in the same display pattern that was performed when the fight began.

If the visitor is a female the response to the resident's initial display will frequently be a simple repetitive nod of the head, whereupon the male shifts to his typical courting display. This is likewise specific for each species. It differs from the challenging advance in several particulars, but in many, if not in all,

iguanid species the resident comes towards her with a curious jerky or jiggling gait which is accompanied by rapid head nods and full display of throat, flattened sides, and erected crest.

*Hemidactylus flaviviridis* and certain other nocturnal geckos utilize vocal sounds as a means of establishing social contact. Such displays as characterize the Lacertidae and Iguanidae, for example, which are notably diurnal, are lacking as are bright colors or the capacity to extend the gular pouch or to flatten the sides of the body. Direct bodily contact and vicious fighting, often to death, typifies the territorial defense technique of such nocturnal lizards (Fischer, 1887; Evans, 1936a).

In the case of *C. pectinata*, dispersal seems to occur in regions that are removed from villages and cultivated soil, whereas aggregations exist in the vicinity of villages and gardens. Here ecological conditions favor the formation of lizard communities.

Being herbivorous, the species gravitates to the tilled land where young bean and corn shoots and the blossoms and leaves of fruit trees are perhaps more attractive than the wild plants of the semidesert it inhabits. The loose-rock walls that enclose almost every garden patch serve admirably as dwelling places. The niches between the stones hide the iguanas from dogs and humans, while the high points along the walls are used as lookout and sunning posts. Adequate water for drinking is present in the irrigation ditches.

#### DESCRIPTION OF *CTENOSAURA PECTINATA*

Large specimens of *C. pectinata* are considerably more than 1 meter in total length. The largest male I collected weighed 1000 grams and measured 32 cm. from snout to vent. Its head length was 7.7 cm., while each of the five pairs of femoral pores averaged 2.5 mm. in diameter. The length of its nuchal and dorsal spines measured 1.5 cm. The largest female in the collection weighed 950 grams and was 32.5 cm. from snout to vent, with a head length of 6.6 cm. The femoral pores were only 1 mm. in diameter, while the height of the dorsal spines was not over 2 mm.

To what extent the endocrine system controls head size, height of dorsal spines, and diameter of femoral pores is not known for this species. So far as femoral pores are concerned, however, it has been shown by Padoa (1933) that castration brings about atrophy. Forbes (1941) has shown that injections of female sex hormone into the male also results in atrophy of these pores.

In life, *C. pectinata* differs in color from preserved specimens as described by Bailey (1928). In almost every instance where he uses the word brown, I would use the term black or gray. The general body color of individuals that have recently shed their outer epidermal coats is black or dark gray. Those that have not shed recently are a lighter gray. Alternate bands of dull yellow and dark gray decorate the tail, while an irregular chalky yellowish patch usually occurs on the throat and sides of the neck. Spots of yellowish gray are sometimes scattered over the body.

The landscape to which the black iguana has become adapted is, in general, characterized by black volcanic rocks, black soil, and rather sparse vegetation. In this environment, the animal matches the rocks so closely that, when motionless, it is almost invisible.

#### PROCEDURE

Figure 1 shows diagrammatically the cemetery wall and the relative positions of the 18 adults and four juveniles that are the subject of this report. The symbols adjacent to the letters on the diagram indicate the sex of the individual concerned, the position of each being represented by a capital letter. Two sex symbols by the same letter indicate that a male and female dwelt together on that particular portion of the wall. The small letters "a" and "a'" indicate the position of two small mango trees. Trees were present within the cemetery but were omitted in figure 1. A field of about 2 acres, newly planted with beans, was located off the north corner of the cemetery. A stream, used to irrigate the field, was located about 125 meters northeast of the wall. The road to Acapancingo from the south passed the southwest wall and the entrance to the burial ground. Just beyond the east corner of the wall was a precipice, below which the valley spread out in a patchwork of rice paddies and irrigation canals.

Reconnaissance indicated that most reptile activity took place along the northwest wall and at the north corner. Hence, for observation purposes, I took up a position daily beneath a spreading mango tree just at the far edge of the bean field, about 52 meters from the north corner. The position was well screened from view as far as the lizards on the wall were concerned. When activities of the animals believed to be significant were observed

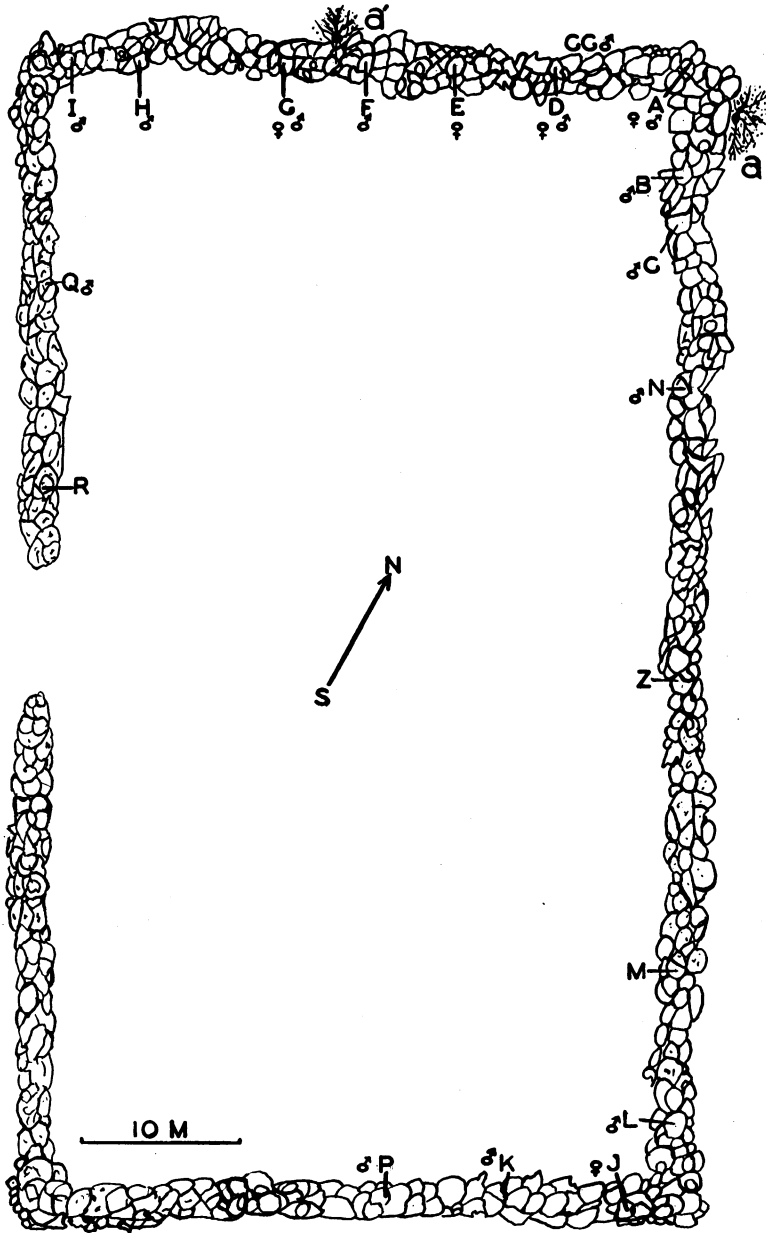


FIG. 1. Diagram of cemetery southeast of Acapancingo. Bean field and stream referred to in text are north of north corner of wall. Capital letters designate each lizard and its lookout rock on wall. Sex of individuals marked where known; two symbols indicate that a female shares the home site with a male. Small letters "a" and "a'" represent trees.

with 6× binoculars, a line was pulled and a photograph was secured. After the film for the next exposure was changed, as much as an hour was often necessary before the lizards reappeared and resumed their activity. Sometimes only one exposure could be secured per day because of the extreme wariness of these giant lizards. The mere presence of the camera and tripod near the wall caused some of the iguanas to avoid their favorite lookout rocks. Instead, these individuals would emerge from the wall at points 10 feet to the right or left of the accustomed site, a maneuver that placed them outside the photographic field. The use of a blind was discarded because the creatures were even more wary of it than of the cameras. It was frustrating to see the courtship pattern cut short as a pair disappeared below the wall when a peon happened to pass by, even when behind me at least 100 meters from the wall.

However, this very wariness is probably a factor in the survival of the lizards. Here was a colony permanently established within a quarter of a mile of the village square. Owing to the inroads inflicted by dogs and perhaps humans, the colony was probably in a state of flux. Individuals of all ages, from very small juveniles to old adults, were present, and replacements from outside the colony were known to take place occasionally.

It is pointless to give here all the data collected daily on the behavior of each of these iguanas. However, the following selected notes give the changing social pattern that occurred with the removal by death of male C, of his replacement with male CC, and the relation of the latter to male A. Details given concern the mating, the capture of two females at the time of oviposition, and the characteristic traits of other males in the hierarchy.

#### SAMPLE PROTOCOLS

March 30, 11:20 A.M. Male A is first seen on D's lookout rock; he moves westward to male G's rock, passing male F. In five minutes male A returns. As he approaches male F, the latter flattens his sides vertically but does not distend his gular fold. Male A struts with his sides flattened, crest up, and with the gular fold distended or erected passes male F, taking short, stiff-legged steps and circling around the latter, thus exposing a side view of himself to F. Soon after passing F, male A resumes his ordinary gait and moves along the top of the wall to his own rock at the

corner. When he reaches it he challenges, with the head bobbing, mouth open, and the abdomen flattened, exactly as when facing male F.

April 2, 10:40 A.M. Males A, B, C, F, and G are on their respective posts. Male C soon leaves his post and descends to the bean field to feed. At 11:00 A.M. a village dog suddenly leaps out from the underbrush and catches male C. Amid the dust thrown up in the struggle, the dog finally rises up with the big lizard in his jaws and runs with it from the field in the direction of the village to the west.

April 3, 10:00 A.M. Males A, D, F, and G are on their regular lookout rocks. Soon male A moves towards the rock formerly occupied by male C. Female A climbs up to male A's rock on the corner. A huge black male (CC) appears for the first time today on the point marked M in figure 1. Another new male, designated as I, appears at the southeast corner of the cemetery.

April 4, 10:30 A.M. Males F, G, H, and I are on their respective rocks, with male A between the positions G and H in figure 1.

April 6, 10:00 A.M. Males F, G, H, I, and the two newly recognized males designated as L and N on figure 1 are observed today. Male A is located between the positions ordinarily occupied by males F and G. Male A soon passes to the right to rest for about five minutes between the rocks favored by males G and H. Then male A returns to his corner rock, meeting no opposition from males G and F (male D emerges from the rocks later).

April 7, 11:40 A.M. Female E is on the corner belonging to male A; he is on a high round rock, with the female approximately 18 inches away. A struts with the body flattened vertically, the gular fold distended, and the mouth open; he moves his head up and down. She holds her head and body high with the legs straight, but makes no move. He turns around, showing both his sides to her; she remains quiet. He then relaxes, sinking down upon his rock. Soon female E turns towards male A and nods her head five times, then crawls up beside him on the round rock. She nudges his head and neck, even bites him on the head. She does not flatten her sides nor distend her gular fold as a female does when angered (fig. 8). Male A immediately flattens his body, distends his throat and bobs his head with the mouth open; the male and female push each other's heads. Then he moves alongside, and she immediately moves rapidly

off his rock, and male A settles back to rest and watch. Soon he climbs a tree within the cemetery.

In male A's absence from his corner, male B passes around it at 11:55 A.M. and descends to the bean field, crosses it quickly, passing me on my left not 10 meters away. He passes on into the mango tree grove, takes a drink from the irrigation ditch, and slowly returns, breaking into a run as he passes me, this time on my right. He climbs the cemetery wall at a point very close to male H's lookout rock. Male B rests there for about three minutes. Both males H and G watch his return from the field and make no antagonistic gesture towards him as he passes them along the wall on his return to his own post just around the corner from male A. However, male F, who has not seen male B reach the wall, turns suddenly and challenges as the latter is about to pass him on the wall, but male F allows B to pass by him without further display. B returned the challenge, head high, gular fold distended, and stopped close to F before proceeding to his own post.

April 8, 11:30 A.M. A huge black male (CC) is standing on the red rock usually occupied by male D, 15 feet to the right from male A's post. There are four females at points on the wall where males F, G, and H usually stand; the heads of the females are high, and one of them nods in response to CC's extremely fast, vigorous nodding with the mouth wide open. Occasionally male CC gapes with the mouth wide open and directed upward. He runs rapidly along the top of the wall towards female A on her rock; she nods but runs down into the rocks as he reaches her. During the big male's presence, male A is down at the base of his corner out of sight of the intruder. (Male CC was first observed April 3 on point M in fig. 1, on the northeast wall just beyond the former lookout rock of male C. When the latter was killed, CC moved in to occupy C's territory. This was shown when a group of boys passed close by; he disappeared among the rocks only to reappear on the wall on C's rock a few minutes later.)

About 1:00 P.M. male CC is again on male D's rock, strutting and head-bobbing. One of the four females mentioned before comes towards him. At this moment a peon passes and male CC disappears, only to reappear at male C's former post ten minutes later.

April 10, 10:00 A.M. A peon is hoeing the bean field. Females A and H are the only ones visible on the wall. At 11:30 A.M.



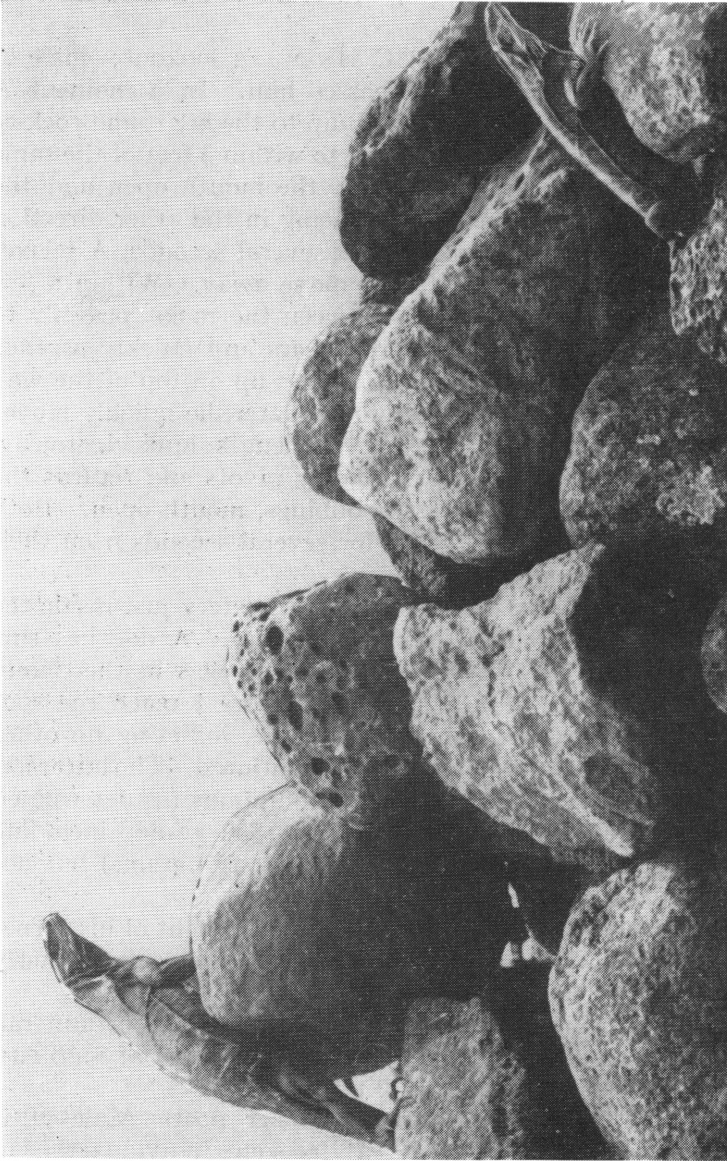


FIG. 2. Male A on his favorite rock at the north corner, challenging male CC, who is departing towards male D's rock to the right. Picture taken April 11, 2:00 P.M.

male CC appears on A's round rock, stays there while a horse grazes only 10 feet away, opposite male B's post; a crow is perched 4 feet above CC and chatters at him. Male K is on his favorite<sup>1</sup> rock.

April 11, 12:30 P.M. Male CC is on D's lookout; male A challenges CC and then boldly passes him. In a moment A turns to look back and sees CC climb up to the big round rock at the corner. Male A then comes back to within 5 feet of the same rock and challenges vigorously, with the mouth open and the throat distended. However, CC is facing in the other direction and does not appear to see A. After several seconds, A relaxes and settles down to wait for CC to move away. Within a few minutes both lizards crawl down between the rocks, possibly to escape the sun. At 2:00 P.M. A reappears and quickly ascends to the round rock. When male CC comes up on top of the wall quite close to the round rock 10 minutes later, he quickly moves over towards D's red rock, as A challenges him vigorously. Upon reaching the red rock, CC quickly pivots and returns the challenge with high and low head-bobbings, mouth open. Both males continue to bob their heads for several seconds from their respective posts (see fig. 2).

Later, two females are captured in the cemetery just inside the north corner about 10 feet from A's lookout. A dog has surprised them while they are depositing their eggs in the damp, loose, sandy soil of a very old grave. Before I reach the spot the dog has bitten off the tail of one female, inflicting no other injuries upon her. The second female is uninjured. The latter has already deposited her eggs and weighs 540 grams (as determined later). The injured female weighs about 850 grams, including 49 eggs still in the oviducts (weight of eggs, 250 grams) but not including the weight of the severed tail.

April 13, 10:00 A.M. Male A is 5 feet to the right of his corner round rock and is challenging male CC on the red rock (formerly D's rock).

April 14. Morning activity suspended because of funeral. Male CC on D's post and female G on male G's post at 5:10 P.M. No other lizards are visible at 5:10 P.M.

April 15, 10:45 A.M. Female A on her post. Male H is challenging from his post by tree "a" at some individual within the cemetery. Male A is on his corner rock at 12:15 P.M.

<sup>1</sup> The term "favorite" is used here and henceforth to mean habitual.

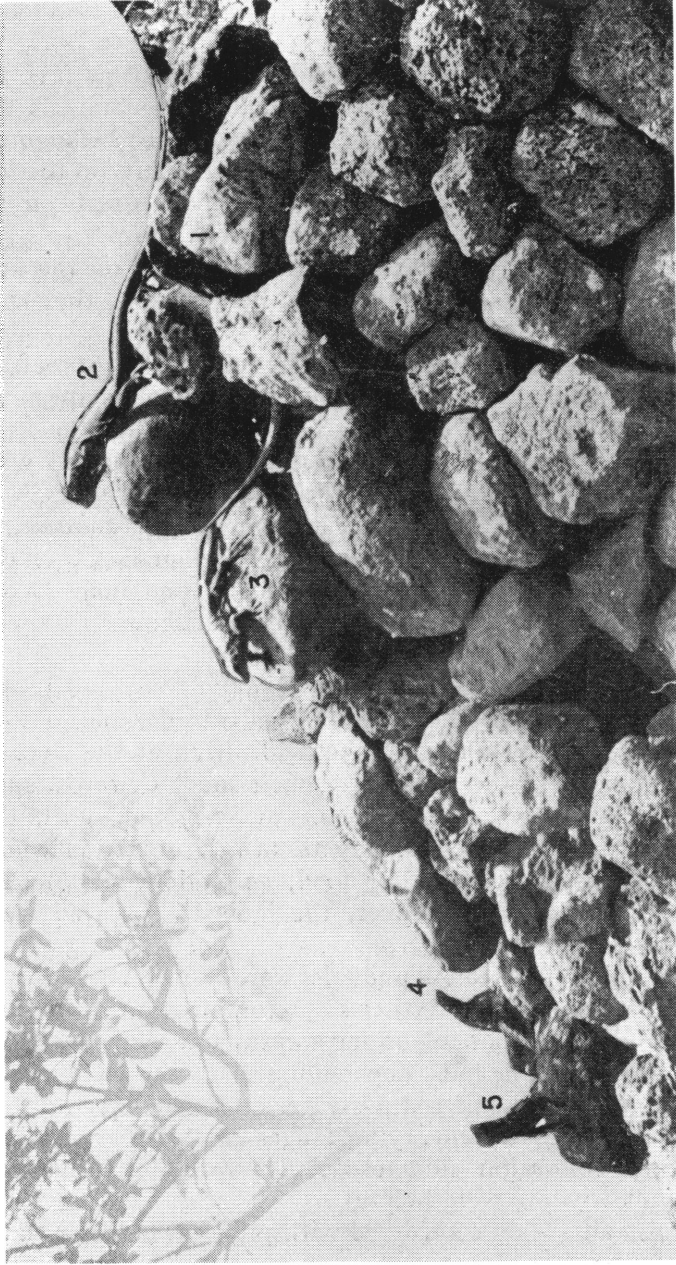


FIG. 3. April 17, 1:10 P.M. Male A withdraws from his favorite round rock; his head is shown by the end of male CC's tail, as the latter ascends to A's rock. Male D is just below and to the left of male CC. Male B is farther down to the left, on the left side of the small mango tree; female A rests on the right side of the latter. Numbers 1 to 5 refer to A, CC, D, female A, B, respectively.

April 17, 11:15 A.M. Male A and female A are on A's rock, the male holding his head high and courting her with his mouth open.

April 17, 1:10 P.M. Male A is withdrawing from his favorite round rock; his head is by the end of male CC's tail, as the latter ascends to A's round rock. Male D stands just below male CC and to the left. Male B stands farther to the left, on the left side of the small mango tree ("a" in fig. 1); female A rests on the right side of the latter. This episode is shown in figure 3.

April 18, 12:35 P.M. Male A is bobbing his head on the first rock below his favorite round one, while male B is in the small fruit tree to the left.

April 18, 1:10 P.M. Male CC is on the round rock of male A with his head bobbing very high and very low, challenging male A, who stands below.

April 19, 12:00 noon. Female A clutches tail of male A with her claws, while both are on the favorite round rock of male A at the corner. Male CC is in tree "a" above, eating a blossom.

April 20, 10:00 A.M. Male A on his corner rock, male CC on the red rock to the right of A's lookout; male B and male D are present. The latter is very close to female E's lookout.

#### ROUTINE ACTIVITIES OF THE LIZARDS

Almost daily, although the distance was considerable, one or another black iguana would cross the field, drink at the stream, and then race back to the wall. Although smaller lizards, such as *Sceloporus*, also occupied niches in the cemetery wall, the iguanas were never observed to pay them any attention whatsoever, much less pursue them for food, as Gadow (1905) suggests. As far as I could discover, the iguanas observed were strictly herbivorous.

Identification of individual animals was difficult because of their natural wariness. Nevertheless, a combination of devices made absolute identity possible in most cases and a fair degree of certainty in others. The most dependable character was the tail. Twelve individuals had suffered a greater or lesser degree of tail mutilation, thus exhibiting varying stages of tail regeneration. General body coloration and especially variability in neck patches of yellow-white were helpful.

Behavioral traits when considered with physical marks usually clinched the identity of any specimen. The commonest trait

was that of territoriality. Except for male A, and to a lesser degree males B, CC, and D, each male of the colony restricted his movements to his own limited footage of cemetery wall and to the bean field and irrigation ditch.

Male A began his daily routine by walking along the top of the wall northwest, usually to the corner occupied by male I. Upon returning to his north corner he rested a short time and then walked down to eat in the field. He rarely returned directly to his corner. Rather, he preferred to reach the wall, passing close to male F or G and then going to his favorite post along the top. After another rest he would leap approximately 2 feet up from the rock to the trunk or branches of the tree "a," bite off a few leaves or blossoms, and then climb down to his favorite rock. Apparently reluctant to leave his post at noon, he would crawl into a crevice just beneath the topmost rock at the corner and, thus shaded from the sun, would gaze out upon his domain. In the afternoon he frequently "inspected" the northeast wall as far as the east corner. When thirsty, he set out for the ditch directly, drank for as long as a minute, then returned to the wall full speed, never feeding en route. He rarely drank oftener than once a week. It should be added that the lizards rarely left the wall except to feed or drink.

On his excursion along the wall his pace seldom slackened, even when passing a strutting rival. He could shift into his challenging strut, flattening the body vertically, with the mouth open and the gular pouch distended, and still not alter the rhythm of his walk. He would sweep by each male in turn, in full array if the latter challenged his right of passage. If no challenge was forthcoming, male A would pass his opponent with just the suggestion of a challenge, such as merely opening his mouth, partly distending his gular sack, or partially flattening his sides.

Male A was never stopped nor was his supremacy seriously challenged during the period of observation, except by male CC on those eventful days of April 17 and 18 (see protocols for these dates, and fig. 3). Exactly how male A regained his corner site after the 18th is not known. He may have succeeded by a show of force or by simply refusing to give up the corner, always being there when CC appeared. By retaining title to his corner site, male A also clung to the "right of trespass," enjoyed in its fullest expression by the top ranking male in the hierarchy.

The next male in order of rank was undoubtedly CC. But

despite his great size and vigor, he was most circumspect in his approach to another's territory. He was careful to enter it only when the rightful occupant was out of sight or some distance away. He was never seen on the northwest wall beyond male D's position. The episode of April 11, at 12:30 P.M. (see protocol), is indicative of the more or less symbolic fighting of males A and CC.

From April 3 male CC occupied successively: C's lookout on the northeast wall, D's red rock, A's corner temporarily (April 11,



FIG. 4. Female A approaching male A from the left and clutching his tail with her fore feet (a common gesture in the preliminary phase of courtship of this species).

17, and 18), and finally D's position permanently. This forced D to share the next footage to the northwest with female E and female D.

Male C appeared to be third in the hierarchy. Although he died April 2, the notes that concern his dominance over male B are sufficient to place him above the latter animal. Although male B, like male F, was smaller than other high-ranking males, B was placed fourth on account of his ability to hold his lookout

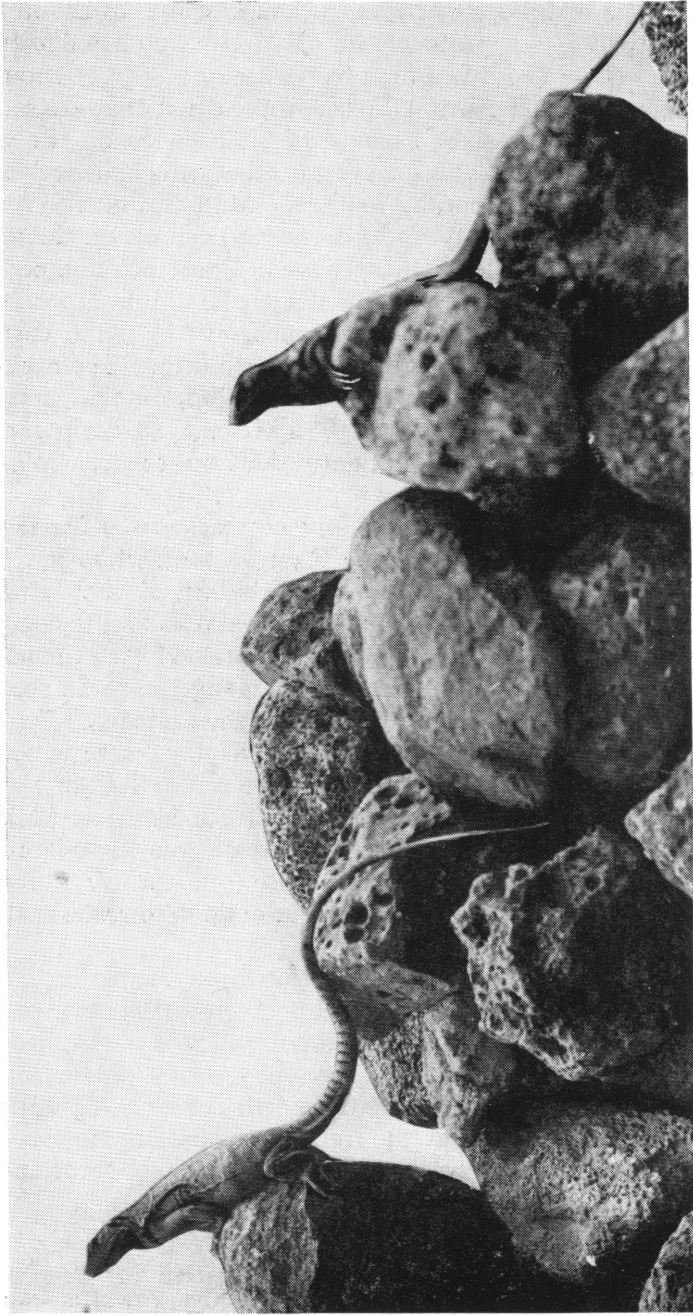


FIG. 5. Male F, to the right, has just emerged from a crevice below his lookout rock after male A, to the left, has passed by en route to his corner post.

position on the wall next to A, and because of his success in the episode of April 7 (see protocols for that date and for April 17, also fig. 3). Male D ranked fifth by virtue of his slight show of bravado against A on April 17 (see protocol for that date and fig. 3). Male F came sixth because of his position on the wall next to that of D and E, and for his propensity to challenge those lizards that trespassed upon his footage. Male G ranked seventh on account of his pugnacity and his chosen position on the wall, next to that of F. Male H, being next in linear position on the northeast wall, should probably rank eighth. Male I occupied the farthest point on the northeast wall from the north corner. For this reason, if for no other, he is ranked ninth. The ranking of the other males in the colony is obscure, and, for that matter, that of any of the individuals might have shifted temporarily. Doubtless changes occur with fluctuations in the size of the colony.

The only female that exhibited any pugnacity was female E. On March 18 she approached male F on his lookout rock. She stopped when within 4 feet of him as he challenged her. In five minutes she continued on her way, passing him boldly, to come to rest close to the very large male G. She remained with the latter for some time, and when G went below among the rocks she returned to her post. Male F moved aside as she came by. Female E was as large as males G or D, but her displays were never so dramatic. This was because her dorsal spines and gular pouch were definitely smaller than those of males of her size. Moreover, her behavior in the presence of a male was less vigorous, whether her display was of a sexual nature (see April 7, protocol) or of a dominating type as shown by her actions towards male F on March 18, as mentioned above.

Proof that the north corner was, for this colony, superior to any other site on the entire cemetery wall is given in the struggles of B, D, and CC to dislodge A. Additional evidence is supplied by the fact that lesser males in this hierarchy rarely crossed other wall sites between their own and the north corner. This is important also as evidence that the right of trespass in this species rests almost entirely with the "tyrant," although occasionally other high-ranking males indulge in this privilege.

#### DISCUSSION

It seems evident that the hierarchical system in *Ctenosaura pectinata* evolved from the individual territorialism that is typical





FIG. 6. Male G challenging male A (not shown) while standing on his rock, to the right of tree "a" (see fig. 1). This posture, with the mouth open and the head high, is characteristic of the species. It is assumed during courtship and is also used to intimidate other males.

of the species in undisturbed areas. There may be a clue in this evolution that explains the behavior of male A in daily patrolling the northwest and northeast sections of the cemetery wall. In a previous study (Evans, 1936b, p. 107) it was mentioned that in the case of caged lizards (*Anolis carolinensis*), "The defeated males cannot leave the area so the victorious male is kept continually in an aggressive mood because he constantly sees others in his domain. Their proximity serves as an ever present stimulus to fight to hold his territory. Each day, therefore, the dominant male may be expected to express his territorial urge by the customary challenge. . ."

The "tyrant" of a colony of black iguanas likewise observes and challenges other males that are located at regular intervals along the wall, the entire extent of which would be less than the territory held by a single lizard in a non-agricultural region. Male A, then, responded in the ancestral way to any rivals present on the cemetery wall within the domain that he patrols. Of course, the presence of these same males on the same lookout rocks along the wall called forth the same familiar "excursion of bluff" or daily patrol; this latter originally served the function of keeping intruders from the territory, but has now become more or less symbolic, because the males he passes do not leave the area but merely move a few inches beneath a rock.

It has sometimes been assumed that when the dominant male of any group of animals has been defeated by a rival, he never again takes command. In the case of male A, however, his greater familiarity with the topography of the corner site, his dominance over the rest of the colony, and his experience in fighting (largely bluff in this species), gave him just the psychological edge over male CC to "conquer" him, even though male A did suffer a temporary setback on April 17. This was shown by the fact that on April 18 and 19 male A challenged CC's right to the corner territory. By April 20 male A had "clinched" his title to the north corner. At no time thereafter was he again threatened by male CC, at least for the next two months. A similar situation in which a dominant male lizard (*Anolis carolinensis*) lost a battle but came back finally to win has already been recorded (Evans, 1936b, p. 105).

Fitch (1940, p. 163) removed the largest *Sceloporus* male from a large pile of logs and three weeks later replaced it. Immediately, fights ensued between the intruder (which had probably domi-

nated the others previously) and other males, particularly with a large one that had apparently dominated the group in the absence of the biggest one. At the end of about an hour, when both fighters were exhausted, the big intruder withdrew, seemingly with much reluctance. Fitch implies that, had the stranger been released on its territory a few days sooner, the outcome of the encounter would have been in its favor. The amazing persistence shown by the dispossessed male *Sceloporus* is quite similar to that shown by the big iguana, male A, and by the unusually large male *Anolis* referred to above (Evans, 1936b).

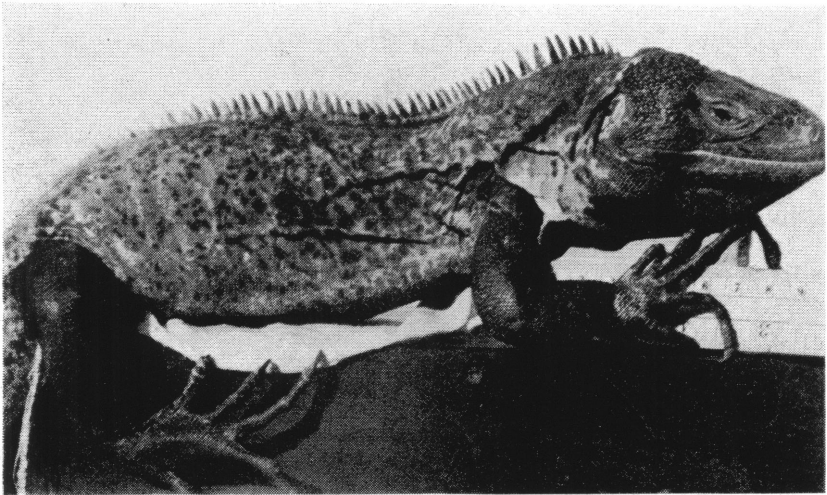


FIG. 7. Adult male *Ctenosaura pectinata*. Note the massive head, gular fold, dorsal spines, and general body coloring.

It will be recalled that two females were discovered to be laying eggs on April 11. This occurred two days after the first rains of the season had moistened the soil. It was surprising how closely courtship, mating, and oviposition coincided with the advent of the spring rains.

Very little has been given on the subject of courtship in lizards of the genus *Ctenosaura*. The posturings described in the protocols indicate, however, that the preliminary phases of courtship involve the active participation of both sexes, despite the contention of Noble and Bradley (1933) that the female lizard takes a purely passive role. It is also evident that females respond

to the head-nodding and side-flattened strutting of the male. The display of the male is very similar both in the courtship of females and in the intimidation of rival males. It was noted that females reacted positively to a male's display by approaching and nodding, not only if he is strutting before her but also if he is challenging another male. In these details *Ctenosaura pectinata*, despite its great size, differs little from *Sceloporus* (Fitch, 1940; Newman and Patterson, 1909) or *Anolis* (Evans, 1938a; Strecker, 1928).

Figure 3, depicting the episode of April 17, indicates that when the "tyrant" is seriously challenged by a powerful contender,



FIG. 8. Adult female *Ctenosaura pectinata* in typical bluffing posture, showing flattened sides, uptilted head, open mouth, and full throat. The dorsal spines are about 1.5 mm. high.

other high-ranking males also enter the fray and simultaneously trespass on the "tyrant's" footage of the wall. Not until the dispute is settled, and the old or new "tyrant" takes over, do the others respect the "tyrant." Essentially the same observation holds for *Anolis*. It often happened that if a strange male was placed in a cage containing several males, the dominant male of the group would, of course, quickly begin to strut and to challenge the newcomer. However, one or two other large males would also strut and challenge the stranger, although in the absence of the latter they were not observed to do so (Evans, 1938a, 1938b).

Newman and Patterson (1909) as well as Fitch (1940) state that lizards of the genus *Sceloporus* are usually solitary and strongly territorial, but the latter describes two examples in

which several males occupied the same pile of logs or rocks. If a strange male was dropped upon the pile, the biggest resident animal would attack and ultimately defeat the intruder. During the fighting, other smaller males would enter the fray, usually against the stranger, then depart under cover as the resident succeeded in defeating the outsider.

This would indicate an incipient condition that could lead to a social system similar to that seen in *Ctenosaura pectinata*. A slightly more pronounced degree of hierarchy in *Sceloporus grammicus microlepidotus* was described by Evans (1946), in which the "tyrant" attacked every other male that resided on the particular ruin whenever any of the latter indulged in any strutting, whether in courtship or towards any other male. The "tyrant" reserved the right to court all females in the group.

Schmidt (1935) describes what may be the peak of lizard social organization as found in the marine iguana, *Amblyrhynchus cristatus*: "The shelving plates of glassy lava which form the shores of Narborough are in any case a favorable habitat for the marine lizards, which rarely go more than forty or fifty feet inland. . . . There were about seventy-five marine iguanas within a space of thirty feet square. . . . Some sixty females and young massed together, often piled one on top of the other three deep, about thirty feet from the water's edge. The old males, much larger than the largest females, were scattered over the area between the massed lizards and the water, spaced from five to ten feet apart, each one keeping to his own sunning territory.

"Trespass on the sunning terrain of a large male by another was invariably the occasion for a fight. Fighting was carried on by butting, each contestant endeavoring to get the rough horny knobs on his forehead beneath his opponent's chin. . . . At Conway Bay (Indefatigable Island) marine iguanas were found to be assorted in family groups composed of a single large male with from two to four females, these groups separated by twenty to fifty yards of shoreline without iguanas."

Schmidt's report has an important bearing on the present study, for he describes a social system that has evolved in the presence of an unusual but plentiful food supply—seaweed. It was obtainable at all seasons of the year in sufficient amounts to feed the ever-increasing hordes of lizards. Storms, pounding surf, and the constant shifting of the tides, which of course affected the time for feeding, not only called for great exertion in

securing food but required that the resting areas be located as close as possible to the feeding grounds, which were between low- and high-tide marks. It was natural that the beach located just above high tide should serve for resting and sunning. As crowding became more acute the territories of individual males became increasingly restricted in size, until the extreme condition observed on Narborough Island was finally reached.

By comparison, the social grouping in *C. pectinata* at Acapancingo differs from that of the marine iguana only in being less extreme, but it arose as a result of a comparable set of circumstances. More favorable diet furnished by the Mexican gardens and the loose-rock walls provided an ecological niche that permitted a greater concentration of lizards than could be found in undisturbed areas. Moreover, in both species the consequent crowding close to the food supply resulted in a reduction in the size of the territories held by the big males.

It has been emphasized elsewhere (Nice, 1933) that mere occupancy of a given territory is only partial evidence of territoriality. An active defense of territory is what is commonly accepted as the true criterion of territoriality. There would seem to be little doubt that at least seven of the males comprising the black iguana colony at Acapancingo exhibited active defense of their wall footage at some time or other during the period of study, and a few of them did so repeatedly.

It was observed that when a black iguana male returned to his favorite post after an absence of several minutes, he would challenge any and all other lizards by the usual high head-nodding, with mouth open, throat distended and sides flattened. This was especially noticeable, in the case of male A, after a recent encounter with another male. Male CC was also very apt to display from his position (formerly held by male D). However, every male was noted as having strutted in like manner at least once during the period of study.

The male *Anolis* quite regularly struts and displays from a lookout point after defeating a rival, even though the latter has been driven away (Evans, 1936b). A comparable trait in the African lion might be the roar emitted at fairly regular intervals throughout the night, presumably to warn away other males from his pride or harem and his domain. It has been shown that the mocking bird has a special territorial song that serves to keep other males away (Michener and Michener, 1935).

The exaggerated head bobbing of the black iguanas and the habit of tilting the head high are not greatly unlike those of other iguanids, but are in sharp contrast to the posture that is taken by males of *Lacerta melisellensis* Braun (Kramer, 1937) and by males of *Lacerta agilis* and of *L. viridis* (Kitzler, 1941). In these species the male advances slowly, with head pointed sharply downward and arched at the neck, during preliminary display before another male.

The relationship that existed between the size of the black iguanas and their exposure to the noonday sun was notable. The largest specimens were the last to seek shelter beneath the rocks and were usually the first to reappear in the afternoon, while the smallest individuals, such as were presumed to be two or three years old, were the first to seek shade, and they remained out of sight longer than the larger lizards during the heat of the day.

#### SUMMARY

A colony of 22 lizards (*Ctenosaura pectinata*) was located on the loose-rock wall of a cemetery near the village of Acapancingo, near Cuernavaca, Morelos, Mexico. This colony was studied during the late winter and spring. Animals were identified by such distinguishing marks as broken or regenerated tails, specific markings of the neck, the degree of blackness of the skin, and by individual behavioral traits. Each tended to remain on or in the vicinity of a particular rock, usually one located slightly higher than others along the wall. These sunning or lookout stones were between 15 and 30 feet apart. Three of the females shared sunning rocks with their mates, while two females occupied separate points along the wall.

Among the adult males a hierarchy, which comprised at least eight individuals, was found to exist. The highest ranking male preëmpted the right to trespass upon the footage of any other male that dwelled upon the wall. If he encountered any sign of opposition as he crossed a territorial boundary he merely opened his jaws threateningly and passed on while his lesser rivals crawled down into the crevices until he had passed. The "tyrant's" nearest neighbors on the wall possessed the same right of trespass but to a very much more limited degree. They never passed over the "tyrant's" holding, which was located at the highest

point of the wall, at the north corner, even though it was closest to the food supply.

All members of the colony fed, unmolested by the "tyrant," upon bean seedlings in the near-by field and drank from the near-by stream. Each individual actually possessed no more "territory" than the narrow strip of wall that extended halfway between his lookout rock and that of his neighbors on either side of him. This small footage was defended against encroachment by all except the "tyrant" himself, and on rare occasions by a male who held a footage on the wall next to that of the "tyrant." All lesser males in the hierarchy respected one another's territorial rights and were never observed to trespass.

It is believed that this colony type of lizard society evolved from the simple individual territoriality, which is still prevalent in *C. pectinata* that occur far from tilled soil. The daily "tour of inspection" that the "tyrant" makes along the walls of the cemetery represents a vestige of the habit that black iguanas, like most lizards that live in non-agricultural regions, have of patrolling their individual territories, each of which would be greater in area than the entire bean field and cemetery combined.

With the advent of agriculture in Mexico many centuries ago, the concentration of succulent food in small fields surrounded by loose stone walls provided ideal ecological conditions for large herbivorous lizards such as those of the genus *Ctenosaura*. Such an environment may have resulted in adaptive behavioral changes, especially on the part of low-ranking individuals in the group. This is indicated by the fact that, although all eight males in the hierarchy exhibited varying degrees of pugnacity during the period of observation, only male A regularly threatened the others and preempted the right of at least temporary trespass on their resting areas. By yielding to male A, the lesser members of the hierarchy gained the unusual security of the rock walls as dwelling places and enjoyed the bountiful food to be found in the gardens. In untilled areas no colonies were observed; instead, individuals were widely dispersed, and no hierarchy was possible. Rivals no doubt fought for a territory, but the defeated animal simply moved on in search of another area.

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