SOCIAL BEHAVIOR OF THE WESTERN BANDED GECKO, COLEONYX VARIEGATUS BAIRD[1,2]

(Ten figures)

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Although scattered observations on the habits of various species of Gekkonidae are to be found in the literature, surprisingly little is known of their social behavior. Nocturnal lizards are especially elusive under field conditions, but in the laboratory they can be induced to display apparently characteristic behavior patterns. During the summer of 1939 a large number of the western banded gecko were made available. At the time we were engaged in an extensive analysis of breeding behavior in the American chameleon (manuscript in preparation). It therefore was of great interest to undertake a comparative study of the nocturnal desert-dwelling gecko.

The social behavior of lower vertebrates includes four general activities: (1) aggregation, (2) dominance and territory, (3) sexual behavior, and (4) parental care. Many species are solitary; others show no aggressiveness. Parental service may be entirely absent or limited to the burial of eggs. Nevertheless, these four elements of social organization may be traced through the vertebrate series. The broad, phylogenetic implications of such natural-history data have recently been reviewed by Noble (1939). A somewhat related problem is the determination of the functions of morphological differences between the sexes. The present study was performed in order to provide data on the behavior patterns of *Coleonyx variegatus* and to discover the functions of a remarkable complex of secondary sex characters found in these and many other geckos.

MATERIALS AND METHODS

The animals were maintained within four large adjoining cages, each with floor space of 24×31 inches. Movable glass partitions enabled the observer to combine the areas and inhabitants of adjacent cages. A layer of fine sand several inches deep, strips of green moss, pieces of hollow bark, and water dishes completed the experimental environment.

For convenience of observation, the lizards were kept in dim red light from 9:00 A.M. to 5:00 P.M. and in bright artificial light during the remaining 16 hours. During the period of observation (June 2–August 25, 1939), ordinary room temperature and humidity were adequate. The geckos readily ate mealworms (*Tenebrio*), blowflies (*Calliphora*), and any other insect larva or soft-bodied adult.[3]

[1] This study was completed under the direction of the late Dr. G. K. Noble, curator of the Departments of Herpetology and Experimental Biology of the American Museum of Natural History, whose unfailing interest, inspiration, and guidance in the work are here gratefully remembered. Thanks are due to Professor Emil Witschi, Professor P. L. Risley, Dr. F. A. Beach, and Mr. C. M. Bogert for their kind criticism of the manuscript and to Mr. C. B. Perkins for supplying the geckos.

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Altogether, almost 100 geckos were studied, but the cages usually contained the following numbers of animals: Cage I, 4–6 females; Cages II, III, IV, 4 males each. Individuals were identified by enamel-paint spots and cutting of toes. An additional large cage with floor space of 32×67 inches served for a study of aggregation tendency, from October 28 to December 12, 1939.

EXTERNAL FEATURES

Detailed descriptions of the external characters of this species have been given by Cope (1900) and Van Denburgh (1922). The following summary is supplemented by our own observations and those of Noble (1921), Noble and Bradley (1933), Wellborn (1933), and Klauber (1939).

Van Denburgh (1922) describes the color pattern of a living specimen of *C. variegatus* as follows: "Across the back, five wide bands of dark walnut brown, palest centrally and separated from one another by dull Naples yellow bands of half their width. The tail is similarly cross-banded. . . . ." The pattern is variable; many specimens are spotted rather than banded, but the differences are not related to sex or age.

Cope found the body lengths of the adults to be 57–68 mm., with a thick tail almost as long (Fig. 1). Males are somewhat smaller than females and may be distinguished by a pair of short spines on each side of the base of the tail, curved a little upward and forward like spurs. A second pair of ventral bones lie free under the subcloacal epidermis in close association with the transverse openings of two peculiar pouches, one over each hemipenis—the subcaudal sacs (Fig. 2). The latter are lined with thin, loose, mechanically eversible squamous epithelium and not filled with erectile tissue as Cope supposed. Males also exhibit (Cope) "a series of well-defined preanal pores in the centers of six or seven large circular scales." These are the openings of glands which secrete small wax cones. The females possess all the above structures in various degrees of development. Largest are the subcaudal sacs which are quite similar to those of males (Fig. 3). Although the special preanal scales are present, they have no pores and do not secrete the wax cones. The spurs are reduced to small epidermal elevations.

Various interpretations of the functions of these structures have been offered on the basis of their appearance in preserved specimens. Wellborn (1933) assumed that the bones lying at the openings to the sacs are protective and called them the *ossa apoclistica*. She ruled out a copulatory use of the spurs, since they are directed sharply upward and outward. Noble and Bradley (1933) suggested that the subcaudal sacs of the male might function to quiet the female during copulation. They observed in *Tarentola* that the curved bones at the openings to the sacs apparently aid them to gape widely. However, Wellborn considers that the sacs "vielleicht dienen zur Aufspeicherung des Samens oder irgendwelcher Sekrete." The present study of the copulatory pattern of *C. variegatus* has resulted in an entirely new conception of the functions of these specializations.

COURTSHIP AND MATING

Under our laboratory conditions the banded gecko was sexually very reactive during the summer period of observation. Thirty copulations were recorded; the ratio of these to the total of observed courtships was approximately 1 to 12. The complete initial performances leading to 15 of the matings were fully ob-

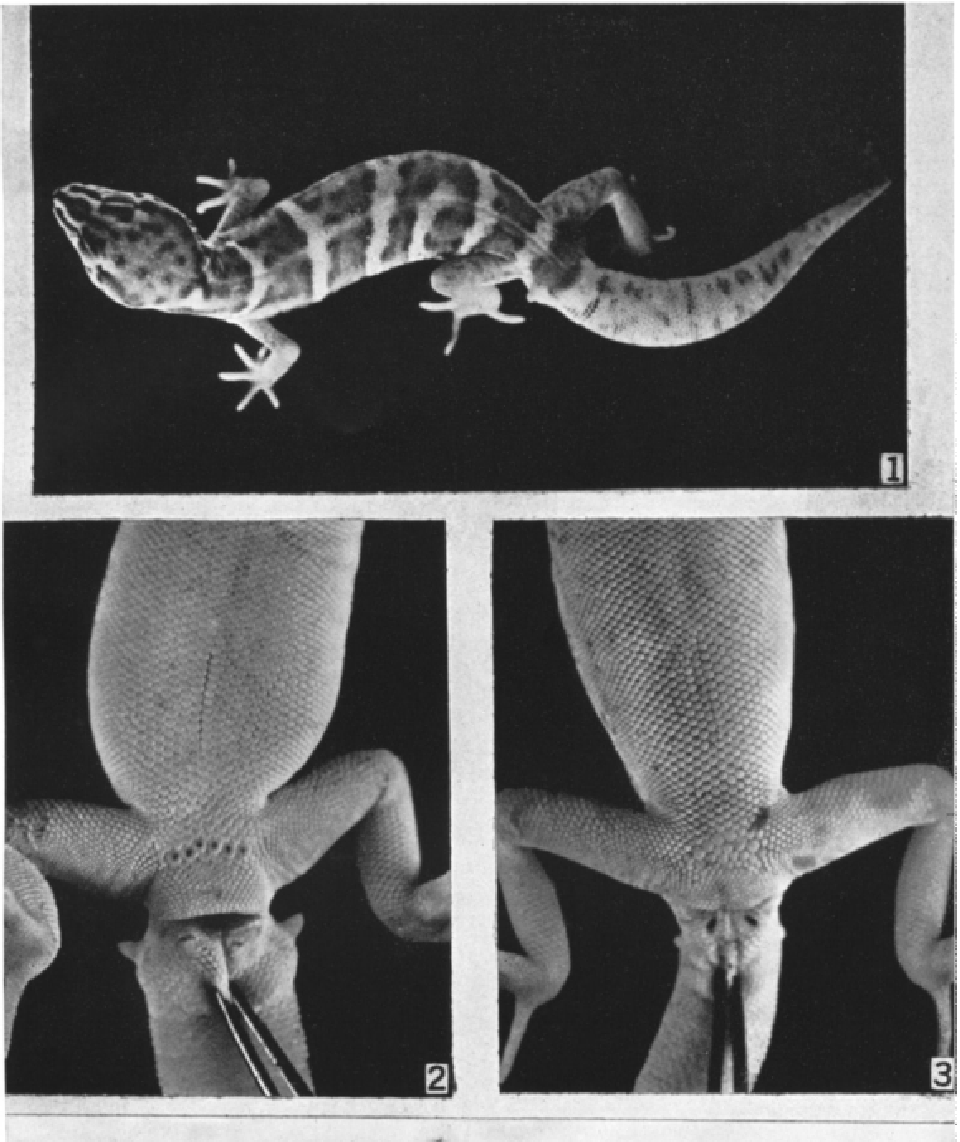
PLATE I

FIG. 1.—External features of the male gecko. Note markings and thick tail with spurs at base.

FIGS. 2 and 3.—Epidermal specializations at level of cloaca of male and female. Note the six enlarged preanal scales, openings of two postanal sacs over hemipenal swellings, and two dorsally projecting spurs. In the female (Fig. 3) the enlarged scales are not perforated by cones, spurs are represented by small epidermal elevations, but sacs are well formed.

FIG. 4.—Side view of a walking female, showing characteristic manner of holding head up, as contrasted with head-down, investigatory walk of the male (Fig. 1).

PLATE I



served, and a composite pattern may be described from these and also from the many unsuccessful courtships. The male begins an investigation of a female with nose to ground, body low, and tail waving (Fig. 1). He may poke with his snout or lick with tongue and then bite or immediately pounce from a short distance and bite at tail, leg, flank, shoulder, or neck (Fig. 5). Seizing hold, he pushes jerkily forward in a tempo which resembles the strut of the male *Anolis*. If the female does not struggle too much, the male lets go and moves up toward the neck, often biting at flank or shoulder on the way and repeating the jerky movements. As indicated by Table 1, the first grip is most frequently at the tail, while the final mating grip is at the neck. The basic elements of this pattern are (1) a preliminary grip, (2) jerky courtship movements, and (3) the mount and shift of grip to the neck region. Courtship differs from the fight pattern in that the latter involves tense body posture. The bite in fighting is not an attempt to hold on and is not followed by jerky movements typical of courtship.

TABLE 1

POSITION OF MALE'S GRIP ON THE FEMALE AT INITIAL COURTSHIP AND AT MATING

Grip	Tail	Flank	Shoulder	Neck
Initial	8	1	1	5
Final	0	0	3	12

The initial procedure is termed "courtship" because it is that part of the mating behavior which depends most directly upon the female's receptivity. A significant difference between the courtship of *Coleonyx* and that of diurnal species like *Anolis* is the dependence of the whole pattern in the former upon direct contact. *Anolis* males display at a distance and approach the female with a strut which consists of rapid bobbing movements of head and shoulders, continued as the male moves forward. This type of approach gives the female ample opportunity to escape *before* being gripped and anoestrous females are able to evade the male with ease. In the gecko, contact is the first essential element, after which the male performs strutlike movements. The female signifies willingness to mate by a minimum of resistance. She is as large as the male and easily escapes if anoestrous. Often she will reach back and bite her suitor, and the pair will whirl completely around before the male lets go. The female has never been observed to respond to courtship with the fighting pattern, but very occasionally she may rise high in a posture very like that used in fighting and maintain it only momentarily as an avoidance reaction. The courting male then may pass directly under her without touching.

Although no definite response indicative of oestrus has been noted, such as the neck-bend of female *Anolis* (Noble and Greenberg, 1941), there is other evidence of the necessity of co-operation. Anesthetized females cannot be mated with, although completely passive, since the male is unable to get his tail properly placed underneath. Such a baffled male has been observed to continue his courtship for long periods of time, even reversing position so that at times he gripped the tail region of the female and curled his tail around her neck. We repeated this experiment 20 times with the same result, namely, that the male cannot copulate with a female which does not respond. This critical response can be duplicated by simply lifting the prostrate female's tail and holding it up and against the male while he completes his pattern.

PLATE II

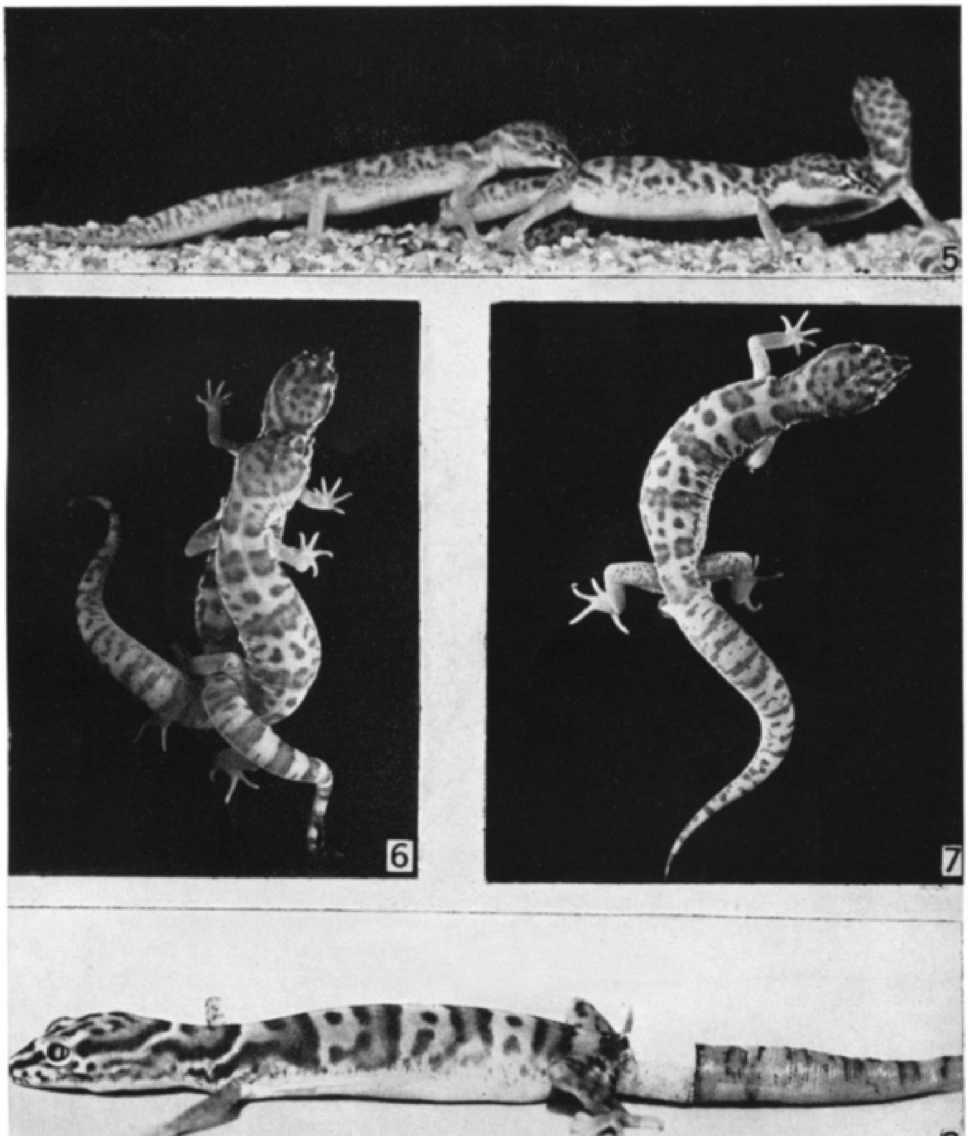
FIG. 5.—Initial courtship grip of the male. Female at extreme right is being gripped at shoulder by center male, who in turn is gripped by a second male. Note swollen cloacal region of the latter.

FIG. 6.—Dorsal view of copulation position assumed by a mating pair. The male maintains a grip on neck skin of female and a second grip on tail-base with left hind leg. The foot of this leg rests upon her thigh, while the left foreleg presses against her side.

FIG. 7.—This same male just after mating, showing the left hemipenis still everted. Note relationship between left spur and hemipenis.

FIGS. 8 AND 9.—Male and female with tails broken off and exchanged for the purpose of testing reactions of active males to them.

PLATE II



After a male *Coleonyx* has begun the courtship performance, little short of physical injury appears capable of interfering with him. It was found possible to get within very close range of a mating pair, throw spotlights upon it, remove obstructions, interpose objects such as a pencil, and even to pick up the pair and transpose them to the stage of a binocular dissection microscope without interrupting the mating. Often a particular position could be verified by turning them over. From direct observations at very close range, the copulatory pattern can be outlined as follows: Having mounted and taken a grip on neck or shoulder, the male begins to search with his hind legs for the mating position (Fig. 6). At the same time, the male's swollen cloacal region rubs transversely across the female's tail. The swelling consists of a portion in front and one back of the cloacal opening; the preanal part bears the enlarged scales and projecting comb, while behind are the subanal sheathed hemipeni. In response to the male's rubbing and palpating movements, the female raises her tail base. Thereupon the male brings his tail underneath, and this causes her tail to swing to the ipse-lateral side, pressing both close together. Then the male draws his *spur* or *hook* of the same side (Fig. 7) convulsively across her cloaca a number of times, in an attempt to secure a hold in the loose skin below it. Sometimes the hook lodges within the female's subcaudal sac but most often between and slightly below the two sacs. The pull of the hook draws the female's lower cloacal lip back and with a final thrust and pressing together by the male, the hemipenis everts, touches the lower cloacal lip, and causes it to reflex farther back, thus opening the cloaca to allow intromission.

Only one hemipenis enters the cloaca; the other remains swollen and sheathed, although there must be considerable pressure upon it. The male's subcaudal sacs now come into use. During the process of rubbing hook across cloaca, the sacs do not touch at all. Hence, traction upon the loose skin of the sac or any quieting effect due to suction are both entirely ruled out. When the hook has imbedded itself, the opening of the sac on the same side is completely obliterated by folding, but the one on the off side everts and becomes swollen. Therefore, it appears that the eversion of this sac acts to relieve pressure on the inactive hemipenis. It is also possible that the other sac provides freedom of rotation for the expanded base of the spur when the latter is swung back by the male's final copulatory thrust.

During the mating both are quiet and may be picked up and handled. If the female moves, the male performs a series of jerky and twisting movements of the head while maintaining the neck grip. These resemble the initial courtship movements and appear to quiet the female and prolong the mating.

Each of the male's copulatory reflexes evokes a reflex response on the part of the female. Rubbing the preanal comb and swollen cloacal region across her tail causes it to lift up. As his tail goes under, hers swings toward the ipse-lateral side. When the expanding hemipenis touches her lower cloacal lip, it reflexes back, and the cloaca gapes widely. That these responses of the female are actually reflex is easily demonstrated. Each can be elicited by mechanical manipulation. If a female is held loosely by the neck skin and the tail-base is gently stroked, the tail invariably lifts and can be caused to swing to left or right by touching the skin on the one side or the other. Similarly, touching the lower cloacal lip with finger or instrument elicits the gaping reaction. These responses were secured in oestrous females and some apparently not so receptive, but no attempt was made to correlate the ease of their elicitation with sexual receptivity.

It may be noted that the accessory structures are brought into play at definite places in the pattern. For example, it was observed that the preanal wax cones touch the female only during the transverse rubbing movements which elicit the elevation of the female's tail. When underneath her, the male's hind region is so twisted that only the dorsally projecting spur actually touches, and copulation follows immediately upon its successful anchoring. To test the function of the cones, anesthetized females were placed in the cages, and, upon securing mating attempts by active males, the observer placed his finger under the male in place of the female. The male was not interrupted and continued the palpating, rubbing movements which the observer was able to feel. It appears that the cones rub across the female's tail, and this seems to be their sole function. However, his swollen cloacal region also makes contact, and it is possible that this alone is sufficient for the purpose and the cones probably are accessory.

In order for copulation to succeed, the spur must take hold not far below the cloacal opening. If collodion is placed on that area, making it hard and smooth, the male is completely unable to mate. In one exception, however, the male mated with an anesthetized male in a most unusual manner. The hook imbedded itself in the angle of the subject's hind leg, and the courting male performed his thrust; the hemipenis expanded and came to rest on the former's undersurface without contact with his cloaca. Ejaculation without any observable movements followed while the pair was being examined. Apparently contact with the cloaca is not essential for ejaculation.

The presence of the spur and its action during the mating seems to have made possible a new mechanism of initiating expansion of the hemipenis. The male's final thrust rotates the spur, and its enlarged base, which lies under the skin over the hemipenal swelling, exerts pressure on the hemipenis, which then expands. Pressure is also exerted by the tight leg grip but this does not bear as directly on the hemipenis as that brought to bear by the spur.

SEX RECOGNITION

An interesting problem related to the courtship performance is the question of how a courting male distinguishes the female as a mating object. The term "sex recognition" has generally been employed by naturalists to denote this phenomenon. At some point of an encounter with another male or a female, the male lizard reacts to definite cues which release, in Lorenz' sense, either of his two main patterns of social behavior.

Lorenz (1935) postulates a lizard level of sex recognition on the basis of the work of Noble and Bradley (1933). At this level it is supposed that a male is recognized as such because he responds to challenge with fight, while a female does not fight and therefore is courted. Although response generally plays an important part, later studies have indicated that, at least in *Anolis*, it is far from the sole factor (Noble and Greenberg, 1939). In *Anolis* such physical differences between the sexes as the size and appearance of the adult lizards are sufficient to release the male's corresponding pattern, while behavior differences are not essential, although they are effective aids.

A peculiarity of the gecko, not characteristic of *Anolis*, was early noted. Once a courtship is begun, the male *Coleonyx* quickly becomes "overactive" if the mating sequence is broken by escape or removal of the partner. No discrimination is then observed. Dominance becomes momentarily thwarted, since a subordinate male will court the dominant until the latter reasserts his position. The courting male's reactions become quick and violent. A typical case may be cited:

7/12/39—Cage 4: Anaesthetized male and female placed in cage 4. Resident male investigates the female and promptly bites her in courtship, struggles to mate. He is temporarily removed, but immediately upon return to the cage, he makes for the female and bites her again. The male is taken off and bites my finger repeatedly, making courtship movements. Put near a group of males, he dashes at and bites two of them. He comes upon the anaesthetized male and grips him.

After the initial courtship, a generalized mating attempt persists for some time. This may be considered in the light of other elements of the life-cycle, namely, nocturnal habits, necessity for close contact before courtship begins, and the place of the "strut" in the courtship pattern. Unlike *Anolis*, the display of *Coleonyx* is not performed at a distance from the female, and strutting courtship movements do not begin until a grip is taken. Overactivity or persistence of mating attempt upon interruption during courtship may be considered an adaption to secure completion of the mating when contact with the partner is accidentally broken.

During the course of the study it was observed that, when not hyperexcited, male *Coleonyx* readily distinguish other males from females. A newcomer male, when approached and investigated by another male shows fight, whereas a female does not. All males which fight are thereby "recognized" or responded to with the fight pattern. Another difference is that the female, when moving past a male, has her head up (Fig. 4), while the male advances with head down and tail curling. The oestrous female does not run away at approach, and this receptivity and neutral walk might excite the male to courtship. The sex of the newcomer male, however, might be indicated by his investigative walk and fight pattern.

In order to test the extent to which behavior is essential to sex recognition, anesthetized subjects were introduced into the cages. Males and females treated with ether were used, either singly or paired. In 7 out of 12 cases prostrate males were investigated and courted; the other 5 trials resulted in indifference. It appears, therefore, that motionless males are not fought with but instead are most often courted. Eight nonresident females were etherized and placed in the males' cages. Seven of these elicited immediate courtship and prolonged mating attempts, but the remaining case was oddly different. The female had been placed on the sand with head lowered. One of the males encountered her from the fore and immediately bolted. A second male approached but did not court, and the dominant male of this cage, coming upon her from the rear, nudged her tail but did not court. Possibly the odd posture may have been significant.

Six anesthetized pairs (male and female) were placed at various times in the cages, about 6 inches apart and parallel to each other. A total of 12 reactions to these pairs by introduced males were recorded, and in 9 the female alone was bitten and courted while the male was ignored. In 4 of the latter 9 contacts the active male had first thoroughly investigated both, returning to court the female.

These observations suggested that the female might be identifiable as a mating object through touch or smell or other chemical stimulus whereby she differs from the male. To test this possibility, a further modification of the experiment involving discrimination between pairs was developed. Four different male and female pairs were anesthetized, and their tails were broken off near the base and interchanged; the female's tail was attached to the male and vice versa. Since a majority of the courtship approaches are from the rear and begin with a grip on the tail, it was thought possible to discover whether the female's tail alone, when borne by a male, would be attractive. The two were placed in the cage while still motionless but usually revived after a time and moved sluggishly around dragging the foreign appendage after them (Figs. 8 and 9). Although the anaesthetized pairs were investigated a number of times while prostrate, only 3 actual mating attempts were observed, in all of which the active male gripped the female tail attached to the male and courted with it in his mouth. Twelve positive reactions to the test animals were observed while they were moving around the cages. In 5 cases the female was gripped on some portion of the body above the false tail, while the tail itself was gripped only once. Significantly, the male was courted 5 times, and each time the "female" tail was gripped.

From these few cases it would appear that male *Coleonyx* respond to some chemical stimulus emanating from the skin of the female, which acts to reinforce such negative behavioral cues as absence of fight, neutral walk, and receptivity to courtship.

FIGHT AND DOMINANCE

The males of Old World species of geckos are known to be vicious fighters, in constant dispute over territories during the breeding season. Fischer (1887) described such home defense by male *Hemidactylus* and *Gymnodactylus* against newcomers placed within their terraria. Geckos have been reported to emit various cries while fighting and even during courtship (Loveridge, 1923). However, there is no clear evidence of a relation between these sounds and either behavior pattern.

We have 46 separate records which could be interpreted as fights. These were taken during 18 observation days between June 2 and August 10. During this time the subjects were 9–16 males and almost as many females. The small number of fights observed indicates that this particular gecko is much less belligerent than iguanids and probably less than the Old World geckos. A single male *Anolis* may fight that often in several days, when given sufficient contact with male rivals.

In the fight pattern of *Coleonyx*, the male rises high on all four legs and arches his back, with head held low and throat swelled. If the opponent does not immediately run or move away, the attacker stalks around, nudging at neck, flank, or tail. Both males may do this, and occasionally they are observed to stand side by side and touch each other, first with flank and then shoulders. The fights are of very short duration. Often an aroused male stands with head up and throat swelled, then dashes directly at his rival and bites him; he makes short rushes and stops and then rushes and bites again. Voice does not enter directly into the fight pattern but is only heard when one of the geckos is bitten. They will also squeak when handled by the observer. Thus *Coleonyx* rarely emits sounds and differs markedly in this respect from the Indian geckos, whose calls come so regularly that the natives wager upon their frequency during specified intervals (Barbour, 1926).

Males may rest close together without antagonism. Homosexual courtship is a frequent cause of fighting. The courted male retaliates with the fighting pattern, especially since courtship involves biting to secure a hold. Although fights are relatively brief and mild, dominance of one male over a group of males is the rule. In Cage II, one male won 25 out of 27 total combats. In another group 11 fights were recorded, all of which were dominated by a single male. The same situation was noted in the remaining cage containing males, although records of the fights were not kept. Since one male did all of the fighting, "pecking order," or relative dominance, could not be determined.

The females were never observed to fight. It is interesting that in this species where sex dimorphism is not very pronounced and the female may be even slightly larger than the male, the former does not fight during the breeding season. Dominance of male over female is essential to mating among lizards; and therefore, without a size superiority of the male, the aggressiveness of the female would be an interfering factor.

This type of dominance suggests the possibility of territory in the field. However, the conditions under which territories might be maintained by *Coleonyx* are very different from those of diurnal, arboreal lizards like *Anolis* or of fence lizards (*Sceloporus*). Unlike *Anolis*, there is no threat at a distance (dewlap), and fights occur only at very short range, depending upon contact. Since these geckos are not very pugnacious, territorial spacing of the males would seem to depend mainly upon size of population of a given area.

AGGREGATION

The survival of a nocturnal species is furthered by any mechanism which brings individuals together. Hence it was of interest to note a strong tendency of the geckos to form groups under shelters during the lighted period of their experimentally arranged day. This attraction was not merely sexual, since males were often found near other males as well as females.

To investigate this social factor under laboratory conditions, 25 stock animals (16 males, 9 females) were placed in a large cage with floor space of 32×67 inches. A variety of shelter was distributed over the sand floor of the cage: four large pieces of moss, five strips of hollow bark, several broken flower pots and assorted pieces, two large water dishes, and two smaller food dishes. The material was arranged symmetrically, with approximately equal positional value for similar pieces (Fig. 10). The geckos were maintained within a greenhouse under ordinary lighting and a constant temperature of about 28° C. Records were taken at 9:00 A.M., when none of the animals were on the surface. Eight such counts were made between October 28 and November 10, and another series of 7 from November 14 to December 12. Each piece of moss or bark was raised in turn, and all the geckos under it were identified. The animals reacted slowly and were easily secured without confusion. After the first eight counts, identification marks (paint spots) began to be lost as the result of shedding, and therefore toes were cut for a second trial.

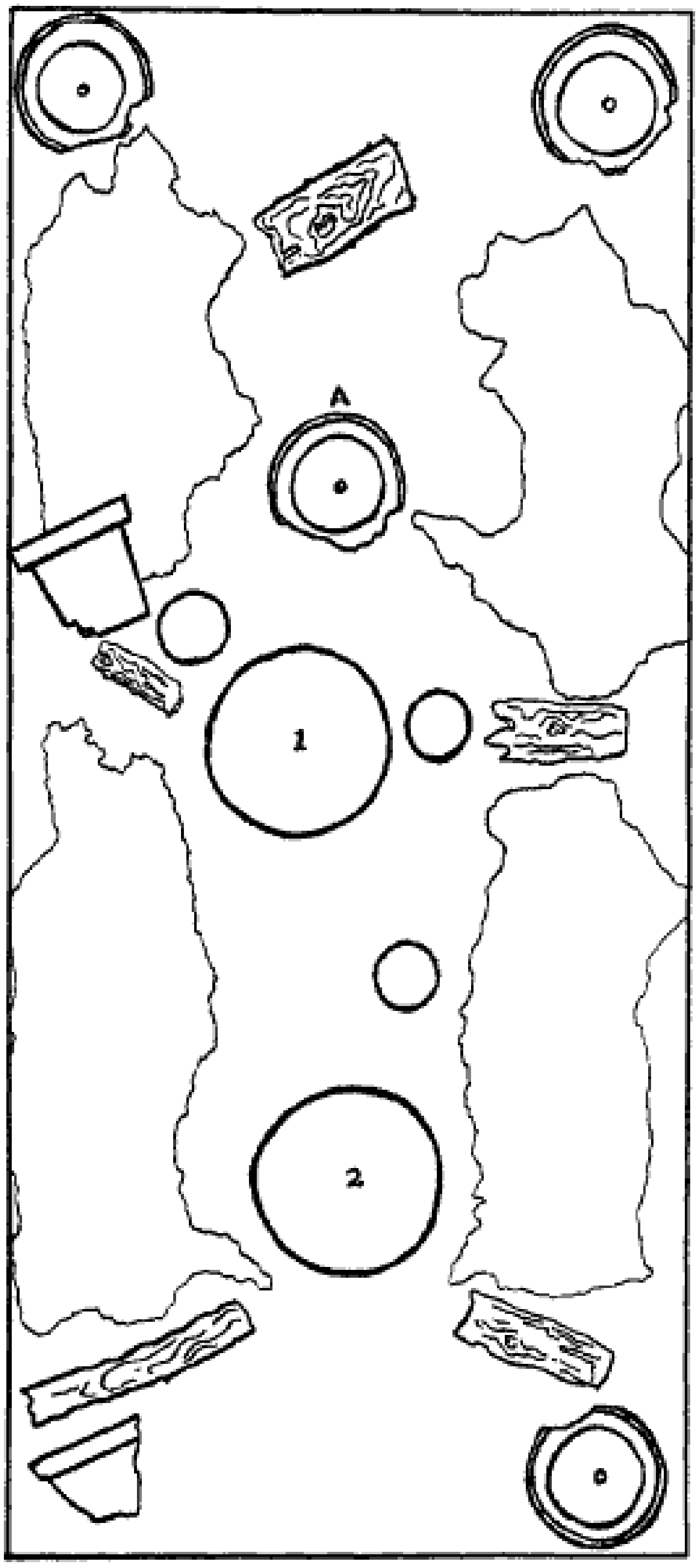


FIG. 10.—Scale drawing (14:1 inch) of the floor of the cage used in studying aggregation tendency. The cage had a floor space of 67×32 inches and contained 16 males and 9 females. Four large pieces of green moss, a number of up-ended flower pots with broken margins and several halves, five pieces of bark, two water dishes, and three small food dishes were symmetrically arranged to give equal positional value to similar pieces.

Table 2 presents the sizes of groups found during these fifteen counts. Almost invariably the majority of the animals were bunched together in several large groups. When the moss or bark was lifted, they were observed to be close together, not merely adjacent to one another. The evidence is clear that under the conditions of the experiment a strong aggregation tendency was manifested by the lizards. Only 1 animal was found alone more than once in succession. Our data applied equally to both sexes.

TABLE 2

AGGREGATION TENDENCY, AS MEASURED BY SIZES OF GROUPS UNDER VARIOUS DAYTIME SHELTERS

TRIAL 1

Oct. 28	Oct. 30	Oct. 31	Nov. 1	Nov. 2	Nov. 3	Nov. 7	Nov. 10
7	5	9	5	7	9	9	7
7	5	4	4	5	4	4	6
6	5	2	3	3	3	3	3
2	4	2	3	2	3	3	3
1	3	2	3	2	2	2	2
1	3	2	3	1	2	2	2
1		1	2	1	1	1	1
		1	1	1			
		1		1			
				1			

TRIAL 2

Nov. 14	Nov. 20	Nov. 24	Nov. 28	Dec. 5	Dec. 8	Dec. 12
8	11	6	8	7	8	8
4	4	6	5	6	8	6
3	2	4	4	5	3	3
3	2	2	3	3	1	2
2	2	2	2	1	1	1
1	1	1	1		1	1
1	1	1				1
1	1	1				
1						

Certain areas of the cage served as shelter for the great majority of the animals, while others of similar appearance did not have any groups. For example, under the large strip of moss at upper right of Figure 10 there often were two distinct groups, whereas the other three similar pieces of moss held few or none. Water dishes 1 and 2 seemed identical, but No. 1 never concealed any animals, while No. 2, when lifted, usually revealed a group. Of the two pieces of bark at the lower portion of the cage, the smaller right-hand piece almost always was the shelter for several or a group of geckos, but not so the similar and larger left-hand piece. The broken up-ended flower-pots were much-used locations, but even these differed in attractiveness. The center one at *A* was often used, while the others were seldom occupied by more than a single animal. This use of one site in place of others suggests persistent residence within a particular area. It may be assumed that a nucleus of each group was constant to one location and attracted the wanderers who were thus prevented from starting new groups at unfamiliar shelters.

In general, two opposing tendencies may be noted. *Dispersal* is furthered by courtship and dominance, since the males drive out other males and anoestrous females. However, *aggregation* as seen at daytime shelters is a factor even during the breeding season. Thus the gecko differs from strongly territorial species like *Anolis*, where a single male and a small group of females occupy an area during the breeding season but at other times isolation of individuals is the rule, except in crowded regions. *Anolis* are generally isolated, coming together for breeding periods, during which the males are widely spread over territories; but nocturnal *Coleonyx* are probably more gregarious when not breeding than during the breeding season, when dispersal factors come into action.

SUMMARY

1. The mating pattern of the male gecko is a timed sequence of events in which each of a number of epidermal specializations has a definite place. The male's copulatory reflexes elicit corresponding reflex reactions of the female, whose co-operation is essential for copulation.

2. "Sex recognition" in this nocturnal species depends primarily upon behavioral cues. Anesthetized males are treated as females, but experiments concerned with discrimination between a male or female member of an introduced pair suggest that other stimuli may be present which involve the chemical senses.

3. Absence of sex dimorphism of size and display characters has not favored the development in the female of fight, dominance, or territory. Thus *Coleonyx* differs from diurnal lizards, such as *Anolis*, in which dimorphism is present and is accompanied by fighting among the females resident within a male's territory.

4. Two opposing forces are seen to regulate the social system of the banded gecko. *Dispersal* during the breeding season is furthered by fighting among the males, which leads to dominance and perhaps territory and by courtship of anoestrous females. *Aggregation* as manifested under laboratory conditions is a strong factor even during the breeding season, when it probably aids reproduction, since the male's initial courtship performance is at close contact rather than at a distance.

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