VARIATION OF AGGRESSIVENESS OF THE COLLARED LIZARD (CROTAPHYTUS C. COLLARIS)

by

IRA NATHAN YEDLIN

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Approved by:

Gary W. Ferguson

Major Professor

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Aggression and the factors influencing it have been studied in a laboratory (artificial) situation (see, for example, Emlen and Lorenz, 1942; Evans, 1935; Gibson, 1968; Greenberg, 1945; Marler, 1955; Ulrich, Wolff, and Azrin, 1964) but few experiments have been done with animals in field (natural) situations (Bronson, 1964). Proximate causes of variation in aggression have been discussed (Brown, 1963; Guhl, 1953; Harris, 1964; Marler, 1955), but the ultimate or adaptive functions of this variation have been neglected by these authors. Proximate factors are the physiological or environmental factors controlling behavioral expression while ultimate factors are the environmental events that cause differential mortality leading to evolution of behavior (Fretwell, pers. comm.). Because most work on this subject concerns birds and mammals and lizards are better than these for field studies of aggression it seemed important to investigate this problem in lizards to broaden our understanding of the nature of aggression and the factors which influence its variation.

Preliminary observations of free-living collared lizards revealed variations in the level of their aggressiveness. Males seemed more aggressive in some areas of their home ranges than in others, more aggressive at some times of the day than others, and more aggressive at some seasons than others. Because no quantitative verification of these variations was in the literature, I decided to examine the effect of the position of an individual in its home range (location effect), the time of day (diel effect), and the time of year (seasonal effect) on the level of aggressiveness of male collared lizards; while with females I examined the effect of the time of year (pre and post-parturition effect).

Because female collared lizards have smaller home ranges than males and are more sedentary, the location effect was not studied with females. Also the diel effect was not studied with females. Instead, females were observed during the same time period each day to obtain more accurate data on seasonal variation.

I hypothesized that the location and seasonal distribution of male aggression would indicate defense of breeding females; while the seasonal distribution of female aggression would indicate defense of nest sites.

In addition, the social behavior of the collared lizard in a natural situation was described in detail to augment the more general accounts in the literature (Greenberg, 1945; Fitch, 1956; 1958; Mosley, 1963).

MATERIALS AND METHODS

The collared lizard (*Crotaphytus c. collaris*) is a medium-sized lizard of the family Iguanidae. The subspecies under study (*C. c. collaris*) occurs from southern Missouri and northern Arkansas west through Kansas, Oklahoma, Texas, and western New Mexico (Fitch, 1956). Adults are approximately 80 to 110 mm in snout-vent length; males are about 10 to 15 mm larger than females at maximum adult size. The tail of both sexes is commonly twice as long as the snout-vent measurement. The collared lizard exhibits obvious sexual dichromatism. The body color of Kansas males ranges from turquoise blue to bright green with scattered light or dark spots along the back; the throat is bright orange. In contrast, the body color of females is usually brown or tan and the throat is white. Males have considerably broader heads than females and males usually possess enlarged postanal scales. Both sexes have a double black bar which almost completely encircles the neck; hence the name, collared lizard. Collared lizards generally frequent rocky areas.

The present study was carried out on the limestone rock fill comprising the southeast corner of Tuttle Creek Dam and adjacent area (Pottawatomie Co., Kansas). The study area was approximately 1.5 acres. The study area was divided into 20 foot-squares, to enable accurate location of lizard's positions. Dominant vegetation on the study area included: *Melilotus officinalis* (L.) Lam. (Yellow sweetclover) and *Sorghastrum nutans* (L.) Nash (Indiangrass).

Aggressiveness of the lizards was measured by recording the number of charges made by a free-living resident (male or female), towards an introduced nonresident of the same sex during a two minute test period. The nonresident was tethered at the end of a ten foot fishing pole. The length of the restraining string was approximately one foot at the start of the tests but it was subsequently lengthened to about four feet when the resident lizards reacted negatively towards the close proximity of the pole. The nonresident was placed about three feet from the resident. A charge was scored when the resident ran towards the nonresident and attempted to bite it. The nonresident was moved prior to the bite of the resident and placed again about three feet from the resident. Harris (1964) used models of lizards made of wood and Mosley (1963) used models made of latex and clay and all three model types elicited aggressive responses from residents. I made models from freeze-dried collared lizards, but these were not effective in eliciting aggression from residents. Fitch (1956) used a method similar to mine (introducing tethered nonresidents) and elicited aggressive responses from collared lizards. The frequency and latency of male aggressive displays directed towards a nonresident, and the frequency of lizards chasing other lizards in natural encounters were thought to be potentially significant in assessing variation of aggression and were recorded. Nonresident lizards used in my study were collected from other local populations, at least two miles distant from the one under study. To minimize habituation towards a particular nonresident the same nonresident was never used for two successive trials nor for more than five trials total. Eighteen different nonresidents (ten gravid females and eight males) were used as models.

The study occurred between 25 April and 28 August 1971. Eighty hours were spent in the field. Time periods spent in the field did not vary seasonally. Introduction tests were conducted between 26 May and 30 July. Introduction tests with females were conducted between 1300 and 1500 hours; those with males, between 1000 and 1900 hours at random times daily. Only one trial per resident per day was performed. Of several lizards on the study area, adequate trial data were collected for only one resident male and three resident females. Only two of the three females resided in the territory of this particular male.

To facilitate identification of individuals all lizards on, and adjacent to the study area were marked both by toe clipping and by painting distinguishing numbers or letters on their backs (Tinkle, 1967). Snout-vent measurements were to the nearest millimeter. The gravid state of females was determined by three criteria: 1) orange "post-nuptial" markings along her sides, 2) a distended abdomen, and 3) eggs felt by palpation. Post-parturant females appeared thin and wrinkled. Ambient air temperature was recorded daily.

RESULTS AND DISCUSSION

AGGRESSIVE BEHAVIOR OF MALES: The resident adult male collared used for the introduction trials was located approximately one-half of his time within a restricted area of his home range: the "core area" (Rand, 1967), (Fig. 1; Table 1). Within this core area all but five of the aggressive responses towards the nonresidents occurred. The male's home range encompassed that of five females, whose home ranges were largely non-overlapping. Interestingly, the area of overlap of four of the female home ranges coincided with the small area of high aggression of the male (Fig. 1). This supports the hypothesis that males are defending females. Rand (1967) reported that each adult *Anolis lineatopus* spends approximately one-half of its time in a very small area compared with that it visits each day. This small area overlapped least with the activity ranges of other conspecifics of the same size. He did not point out, however, any relationship between the core area of adult males and proximity to a number of females. The association of several female home ranges within that of a single male is called a harem (Ferguson, 1971a; Rand, 1967). The harem arrangement occurs in many iguanid species and allows a male to service several females in a minimum amount of time during a presumably short receptive period. Fitch (1956) spoke of male and female collared lizard pairs, but I observed no evidence of monogamy. However, Ferguson (1971a) suggested that the number of females per male may vary in some lizard populations.

The small high-aggression area contained a large prominent rock, from which the resident could command a wide view. These may be analagous to the "display posts" of *Agama agama* (Harris, 1964). Both Rand (1967) and Harris observed that Anolis lineatopus and Agama agama, respectively, were particularly aggressive on and around their usual perches.

The resident male seemed to be least aggressive during midday (Table 2). Similar periodicity has been observed for the activity of other iguanid species (Irwin, 1965; Ferguson, 1971a). Although I have no quantitative data, the collared lizards also seemed less active at midday. The decrease in midday activity and aggression was probably due to high ambient temperatures (37°-41°C) which prevented lizards from exposing themselves on the probably hotter substrate, or participating in any activity which might raise their body temperature above their critical maximum (probably >45°C, Fitch, 1956). The low reading of 40% for the 1600-1800 hours period in Table 2 was due to the fact that no introduction trials were attempted at that time during June; the month of peak aggression.

Fitch (1956) stated that adult collared lizards become more secretive after the breeding season, but gave no supporting data, nor did he discuss the level of aggressiveness of individuals after the breeding season. Seasonal variation of the aggressiveness of the male on my study area was evident. Eighty percent of the male-male aggressive encounters occurred in June (Fig. 2). The peak of male aggressiveness coincided with that of the females. The observed quantitative variations in aggressiveness support the general statements in the literature that male aggression in iguanids is usually highest during the breeding season (Fitch, 1941). This tends to support the hypothesis that males are defending females even though the peak of male aggressiveness did not coincide exactly with the probable mating period. Ferguson (1971a) stated that male Sceloporus graciosus defended territories against other conspecific males as frequently in August (post-reproductive condition of females) as during the breeding season in May. Rand (1967) stated that fighting in male Anolis lineatopus is not seasonal but exists at a fairly uniform level year round. The discrepancy between seasonal variations of male aggressiveness of collared lizards and that of Sceloporus might result from the possibility that collared lizards defend only females and nothing after the breeding season while the Sceloporus defend a resource, such as food, after the breeding season. For Anolis, the breeding season may extend over most of the year. Thus for that species it would be more difficult to ascertain the function of the aggression.

According to Mosley (1963) male collared lizards exhibit typical iguanid aggressive patterns. Initially, a resident male raises high off the ground by extending all four legs, arches his back, extends his dewlap, and compresses his sides laterally. From this challenge or aggressive display, the resident male directs a series of bobs at the intruder. The bobs result from a rapid extension and flexion of the forelegs. By this time both lizards have moved to about one or two feet apart and are facing in opposite directions: the "face off" position (Carpenter, 1967). Then, the resident male charges and attempts to bite the intruder in the head region. From my observations, I conclude that behavioral sequences during aggressive interactions between males are much more variable than the above general description. A total of 33 introduction trials were performed and in 17 of these trials (52%) the resident male made no aggressive response (charge or display) towards the nonresident. There were a total of 34 aggressive responses (charges and displays) made during the remaining 16 trials. In five of these aggressive responses (15%) the resident charged the nonresident without prior displaying; in 10 (29%) the resident displayed and then assumed a normal "alert position" (Mosley, 1963) without charging. The remaining 19 aggressive responses (56%) involved charges with prior displays. Of the 16 trials in which aggressive responses occurred, the resident charged the nonresident in 8 trials (50%) and displayed without charging in 8 trials (50%). Those displays which were measured varied from 6 to 6.8 seconds in duration (n=15, $\bar{x}$=25.6). The intensity of the display also varied. In some, the back was highly arched and the throat quite extended; in others, the back was slightly arched and the throat slightly extended. Latency of the initial aggressive response (charge or display) by the resident towards the nonresident varied from 2 to 110 seconds (n=16, $\bar{x}$=56.6). Of those trials in which the resident charged the nonresident (n=8), four trials (50%) included one charge, three trials (38%) included two charges, and one trial (12%) included three charges.

After a male collared lizard changed location he performed an assertion display that consisted of a series of two or three bobs. Carpenter (1967) stated that assertion displays may indicate to other lizards in the immediate area "to keep their distance." Displays were more intense during the breeding season and less so during July and August. An intense assertion display was characterized by a greater inflation of the throat and higher bobs than a weak display. Fitch (1956) and Mosley (1963) described a similar display in collared lizards, but did not mention variations in strength. Assertion displays were not seen in females.

AGGRESSIVE BEHAVIOR OF FEMALES: There was striking seasonal variation in the aggressiveness of the three resident females. Aggressiveness increased markedly just after egg laying and persisted at a high level for several days (Fig. 3a,b; Table 3). Both the number of charges made during introduction tests and the number of chases observed between females increased. I believe that the significant post-parturition increase in female aggression supports the hypothesis that females are defending nest sites. A female who repels other nesting females would prevent her nest from accidentally being dug up and would increase the likelihood of her clutch hatching. Increases in female aggression during the period of nest construction and egg laying have been suggested by Carpenter (1966), Ferguson (pers. comm.), and Rand (1968), however, these authors present no quantitative data demonstrating the change.

Female collared lizards are thought to be less aggressive than males, but female-female pursuit and attack has been observed (Fitch, 1956; 1958; Mosley, 1963). From my observations I conclude that the aggressive displays of females are not as elaborate as those of males. During a typical female aggressive display, the lizard inflated her throat, extended all four legs, and flattened her body laterally--all components of the male aggressive display. However, the display was never as strong as that of a male; i.e. the throat was not extended as greatly, the body not arched as highly, nor the body flattened as pronouncely. Unlike males, females did not bob. Females were closer than males to an intruder before they charged or displayed (about one foot of separation for females versus as much as 10-15 feet for males). This suggests higher aggression in males.

Females engaged in a type of aggressive behavior directed only towards males. This was termed the rejection response (Carpenter, 1967; Fitch, 1956; Mosley, 1963) because it usually followed the approach of a male, seemingly intent on copulation, toward a female who behaved in a generally non-receptive manner. The female extended her throat, compressed her body dorso-ventrally, raised high off the ground by extending all four legs, and raised her tail. Mosley (1963) described an additional rejection response where a female hopped jerkily with her tail directed towards the head of a courting male. Such a display has been reported in several iguanid species (Carpenter, 1967), but I never observed this in collared lizards.

Female collared lizards develop bright orange spots on their sides prior to parturition. Cooper and Ferguson (In Press) induced spots in non-pregnant females with massive doses of progesterone and implied that high levels of blood steroid following ovulation may cause the spots under normal circumstances. Fitch (1956) and Mosley (1963) stated that spots develop three to four days after a successful copulation and Mosley (1963) stated that the spots gradually fade and are barely noticeable two weeks after laying. I did not observe the latter in all of the females on my study area. One female emerged from hibernation in April 1971 with very bright orange spots. I believe that her spots had been elicited the previous season and had failed to fade. Ferguson (pers. comm.) observed some captive females that retained bright orange markings many weeks after egg laying. Fitch (1956) and Mosley (1963) hypothesized that the orange spots might be a visual sign that prevents males from mating with gravid females. The males on my study area did not behave differently towards females with orange spots than they did towards females without them. Gravid females prevented copulation with behavioral postures. It is not clear what the signal value of the orange spots may be if, in fact, they have any signal value.

SOCIAL BEHAVIOR: I observed 75 male-female interactions during the study. During 47 courtships a male approached a female with his head held low. He moved quickly towards the female, pausing intermittently for a second or so. The male usually nodded his head rapidly up and down, but there were three interactions with no nodding. Nodding is typical of the courtship of many iguanid species (Ferguson, 1970). The single receptive female that I observed allowed the male to take hold of the skin of her neck with his jaws and copulation followed. In 46 interactions the female rejected the male. Generally, females exhibited the typical rejection posture described above but there were exceptions. In some interactions a female allowed a male to take hold of the skin in her neck or shoulder region but then rejected him by rolling over onto her back. During the latter part of June and early July, females performed the aggressive displays typical of female-female encounters to approaching males. These displays indicated the general increase in female aggressiveness during the post-parturition period. Fitch (1956) and Mosley (1963) stated that male collared lizards initiate courtship activity. I did not always observe this. Females sometimes approached males and nudged them with their snouts. Male courtship followed immediately. Blair (1960) stated that female Sceloporus olivaceous may initiate courtship. Twenty-eight male-female interactions involved a curious type of "circling behavior" during which a male and female simultaneously crawled around and over each other. Mosley (1963) stated that circling is included in the rejection behavior of other female iguanids, but I found no other mention of such in the literature. Fitch (1956) interpreted circling behavior as courtship but the circling that I observed could be distinguished easily from typical "male courtship-female accept or reject interactions" and, in contrast, occurred both during and after the egg laying period (June 9-16). In short, courtship was typical of the pre-parturition period; circling, the post-parturition period. I would rather interpret circling as "pair forming" behavior. Ferguson (1971a) suggested that pair bonding occurs throughout the growing season in some lizard species. Behavior associated with pair bonding would convey definite advantage to species where a male and female might share the same area in successive years. Several collared lizards marked during the 1970 season were present on the study area in 1971. Fitch (1956) stated that adult collared lizards live several years. It is not known whether male and female collared lizards typically share the same mates from year to year.

To date several studies have utilized the technique of introducing tethered nonresident lizards into the vicinity of a more or less free-living resident lizard (Ferguson, 1969; 1970; 1971b; Fitch, 1956; Harris, 1964; Mosley, 1963; Rand, 1967; and Ruibal, 1967). Various of these authors argued that the technique does not seem to affect display behavior and is useful for observing a relatively large number of interactions involving a free-living animal in a "natural" setting. However, six factors that may limit the value of the technique for collared lizards should be mentioned.

1) Presence of the Experimenter: This had a demonstrable effect on the movement of the residents; especially males. Lizards would not move towards me when I was sitting within their home ranges.

2) Abnormal Behavior of the Nonresident: When introduced, all nonresidents lay against the substrate and moved their heads around; behavior not normally seen in free-living lizards. This could possibly affect the behavior of the resident towards the nonresident.

3) Method of Nonresident Introduction: A nonresident was simply lowered down onto a rock, through the air, about three feet from the resident. This may have affected the resident's behavior because lizards normally don't approach other lizards like that. The resident occasionally retreated after such an introduction.

4) Nonresident Tied to a String: The presence of the string and its restraint on the nonresident sometimes resulted in unusual postures and movements by the nonresident.

5) Negative Reaction of the Resident Towards the Pole: Early in the study, residents reacted negatively towards the fishing pole when it was moved too close.

By using moveable blinds behind which an experimenter could operate, factor (1) could be controlled. Lengthening the string from one to four feet seemed to alleviate the problems cited in (5). The remaining three factors are difficult to control using the technique, but can be overcome in laboratory and field experimental enclosures where the meeting of two or more lizards can be controlled without restraining either. The most fruitful studies of lizard social behavior in the future will include data obtained from:

1) Observations of natural encounters in the field.

2) Introduction of tethered nonresidents into the vicinity of free-living residents.

3) Controlled meeting of nonrestrained lizards in laboratory or field enclosures.

Fig. 1. Location of aggressive responses and activity of the resident male.

The area within the dotted line is the core area. Arabic numerals indicate the number of females typically found within that particular area. Two of the three females located in the peripheral areas were also found in the core area. (X) indicates location where charge occurred during introduction trials, (●) indicates position where only a display occurred, and (O) indicates position where no aggressive response occurred. Scale: 1 inch = 27 feet.

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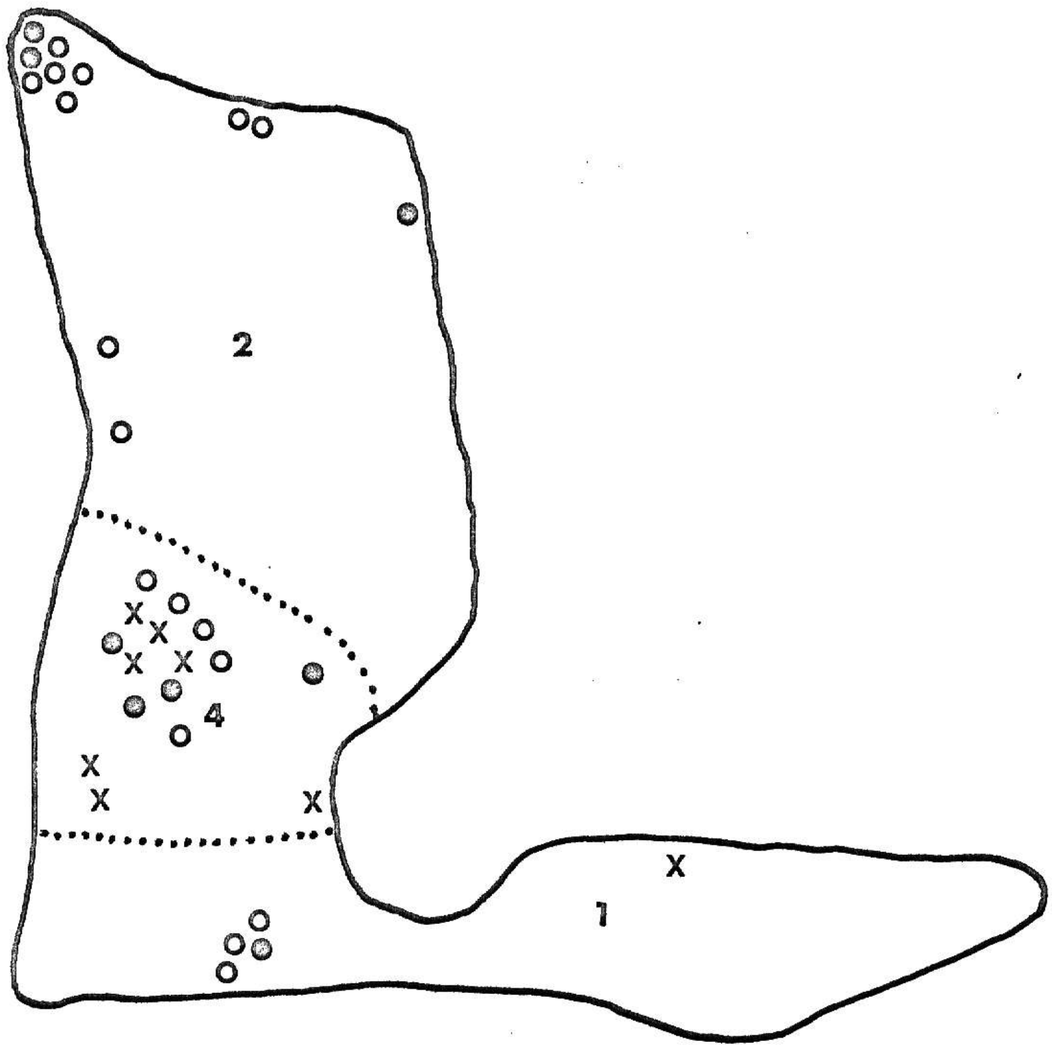
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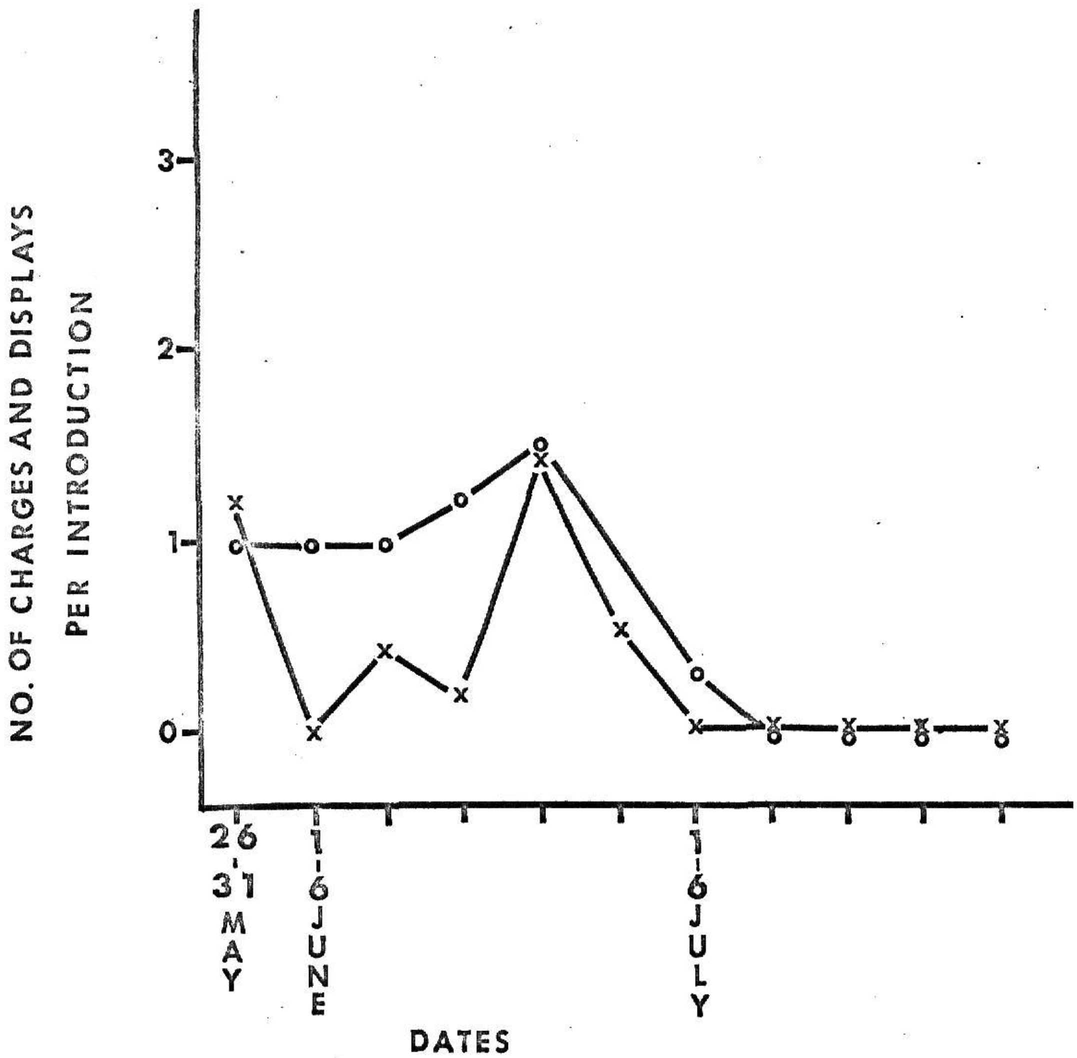
Fig. 2. Seasonal variation of the aggressiveness of the resident male. (x) = charges, (o) = displays.


NO. OF CHARGES AND DISPLAYS PER INTRODUCTION
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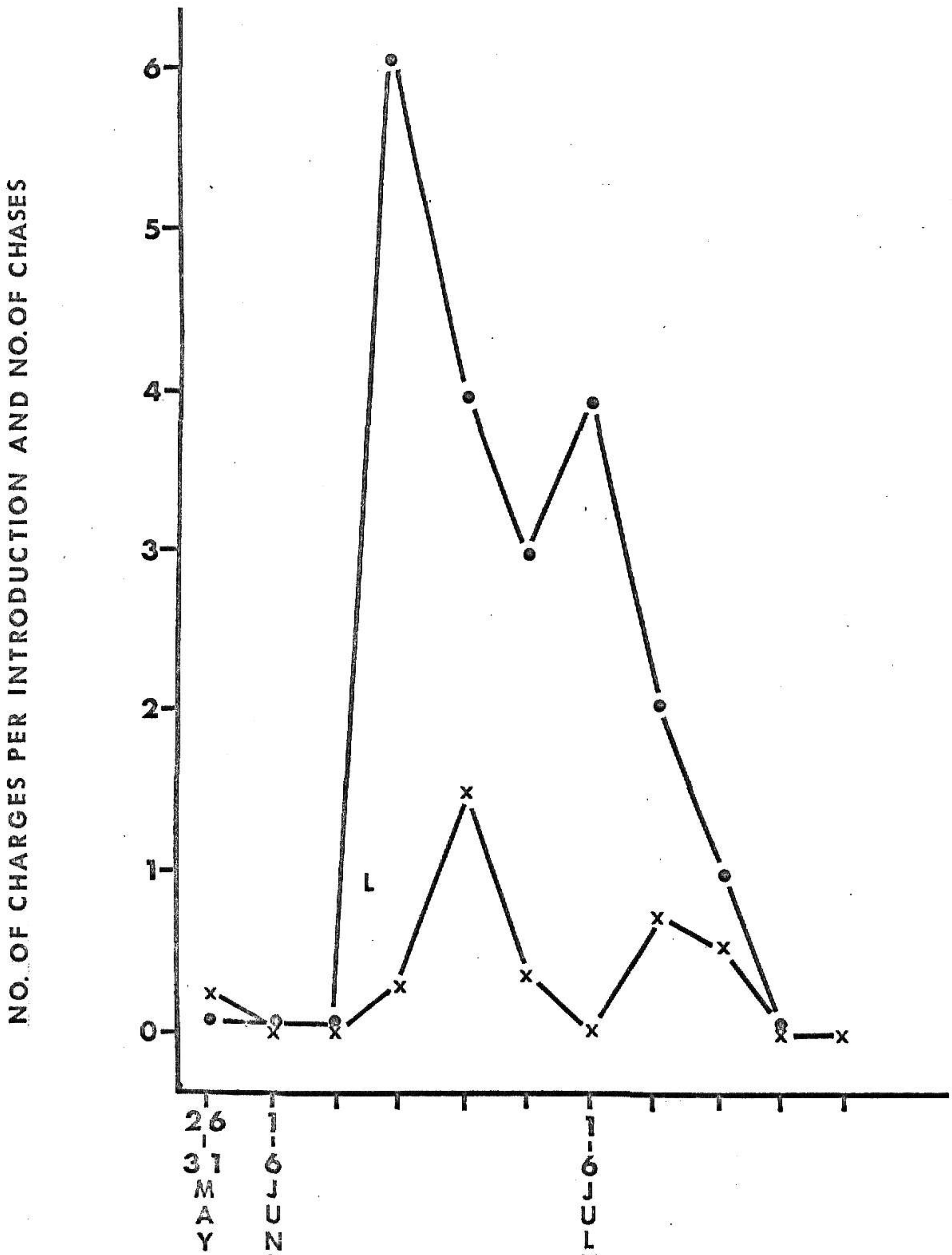
26-31 MAY
1-6 JUNE
1-6 JULY
DATES

Fig. 3. Seasonal variation of the aggressiveness of each of three resident females. (L) indicates approximate time of egg laying.

a. Female 1; b. Females 2 and 3. (x) = charges, (•) = chases.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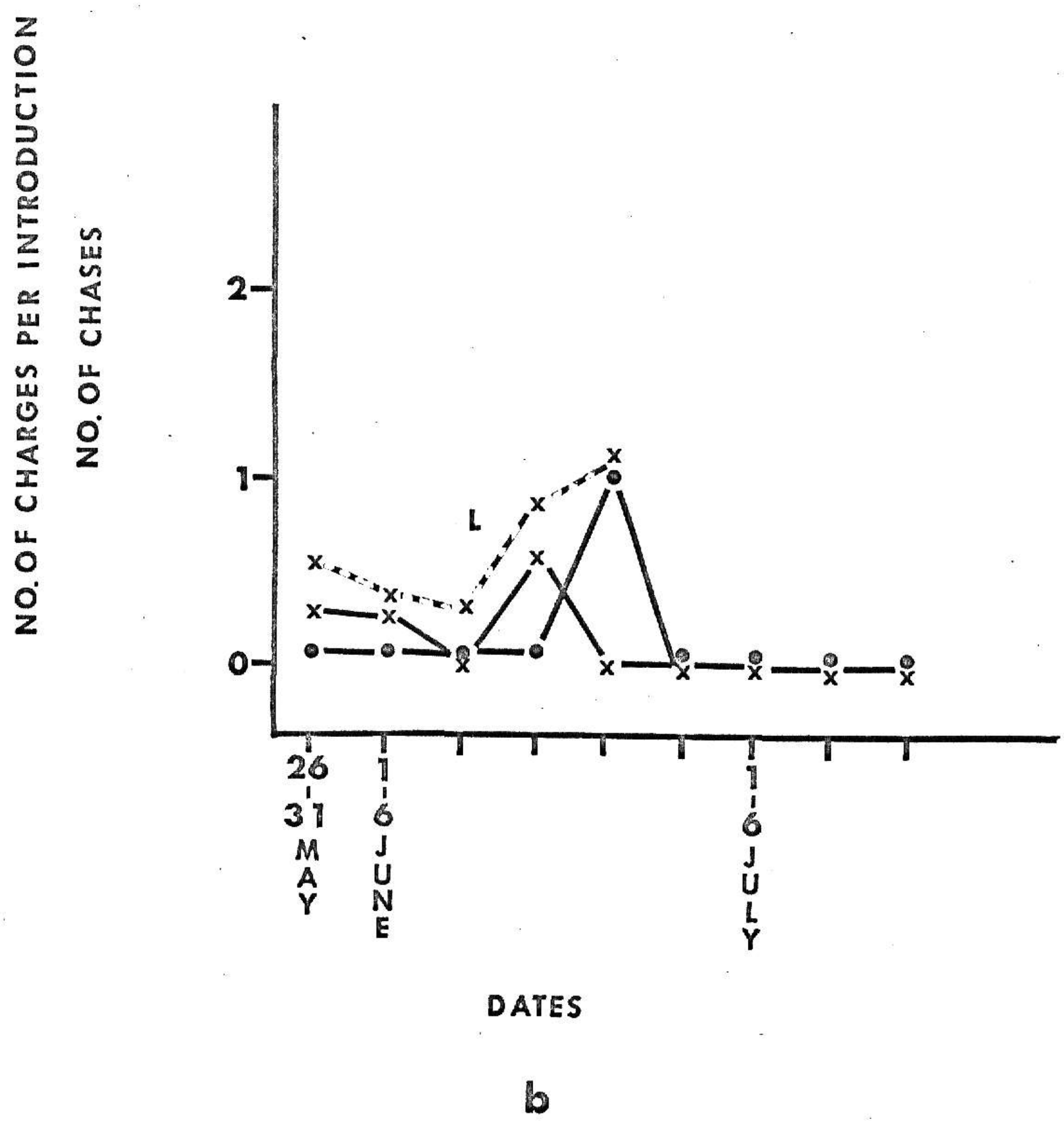
a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1-6 JUNE
1-6 JULY
DATES

b

Table 1. Location effect of the resident male. (N) is the number of introduction trials and (n) is the number of observations on days with no trials. Location of lizard for each (N) or (n) was the initial position recorded on a given day.

	CORE AREA	PERIPHERAL AREAS
Percent of Total Area	25 (10,500 sq. ft.)	75 (31,500 sq. ft.)
Percent of Time Spent in Area	49 (n=25)	51 (n=26)
Percent of Aggressive Responses to Introduced Nonresidents	69 (N=16)	29 (N=17)

Table 2. Diel variation of the aggressiveness of the resident male. Percentages indicate introduction trials in which charges or displays occurred. (N) is the total number of trials.

Time Period (hours)	1000-1200	1200-1400	1400-1600	1600-1800	1800-2000
	71%	33%	46%	40%	75%
	(N=7)	(N=6)	(N=11)	(N=5)	(N=4)

Table 3. Sum of number of trial and observation days with zero vs. one or more aggressive encounters (charges and chases) for each of the three resident females before and after egg laying. Chi-square = 5.36, significant at 0.025 level. (observed/expected). Expected was determined from the total number of trial or observation days.

	0 Aggressive Encounters	$\geq$ 1 Aggressive Encounters
Before Egg Laying	26/22.4	6/9.6
After Egg Laying	9/12.6	9/5.4

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The effects of location, time of day, and season on the level of aggressiveness of male collared lizards; and season on the level of aggressiveness of female collared lizards were studied. The resident male exhibited a small area of his home range in which the majority of his aggressive responses occurred. This area coincided with the area of overlap of the home ranges of several females. The resident male was least aggressive during midday (1200-1600 hours) and was most aggressive during morning (1000-1200 hours) and evening (1600-2000 hours). The resident male was most aggressive during June with the peak of aggressiveness coinciding with the time of female egg laying and the time of peak female aggressiveness. Female aggressiveness increased markedly after egg laying. Social behavior was described.