

Some Observations of the Social Behavior of the Arizona Chuckwalla, *Sauromalus obesus tumidus* (Reptilia, Lacertilia, Iguanidae)

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ABSTRACT—The social behavior patterns of enclosed populations of the Arizona chuckwalla (*Sauromalus obesus tumidus*) were observed from 1970 to 1972. Field observations were conducted from June through August 1970 and 1974. In a challenge display a male chuckwalla compresses his trunk, partially extends his dewlap, orients laterally towards his opponent and performs rapid head nods. The head nodding follows a specific sequence: two complete up and down movements, two intermediate nods and two shorter nods. Dominant males in the enclosure and territorial males in the field are most active; they challenge and chase other trespassing males but tolerate females and juveniles. In the enclosure, subordinate males retreat from higher ranking males or assume a submissive posture. Female aggression is indicated by postural changes, chasing and biting. Sex recognition is based on posture and coloration. During copulation the male maintains a biting hold on the skin of the shoulder of the female. Under natural conditions males were territorial. Homing ability under natural conditions was observed to be accurate on sunny days. In the laboratory a dominance hierarchy and despotism developed. Supplanting behavior was not observed in the field but was common in the laboratory. The selective advantage of the lability of this social behavior is obvious in situations where limited food or other resources make it energetically unfeasible to defend a territory.

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INTRODUCTION

The social behavior of a number of iguanid lizards has been described (Brattstrom, 1974 and Carpenter, 1967 provides extensive bibliographies) and adaptive significance of territorial behavior in lizards has been discussed at length (Rand, 1967). The display-action-pattern (DAP) in certain contexts is species specific and has been described for a number of lizards (Berry, 1974; Carpenter, 1961a, 1961b, 1967; Ferguson, 1971). Although variations occur in the performance of the DAP, it is the most important signaling device in the social behavior of iguanid lizards (Berry, 1974; Crews, 1975; Stamps and Barlow, 1973).

In this study we describe the DAP of the Arizona Chuckwalla, *Sauromalus obesus tumidus*, and some aspects of the social behavior of this lizard in the field and in a laboratory enclosure.

MATERIALS AND METHODS

Laboratory Observations.—A group of 24 Arizona Chuckwallas, *Sauromalus obesus tumidus*, were observed in the laboratory from August 1970 until August 1972. All individuals were collected in the vicinity of Organ Pipe Cactus National Monument, Pima County, Arizona, during June and July of 1970.

The lizards were kept in an enclosure measuring 6 X 4 X 3 m high. The floor of the enclosure was covered with sand approximately 4 cm in depth. Several piles of cinder blocks, each consisting of three stacked blocks, provided basking sites; eleven boards placed along the

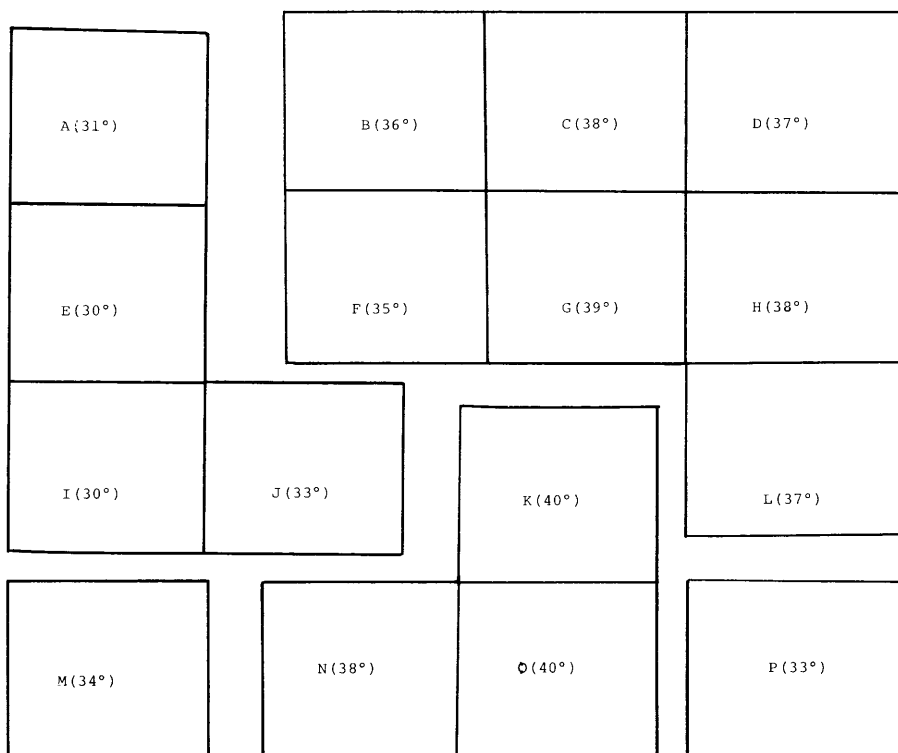
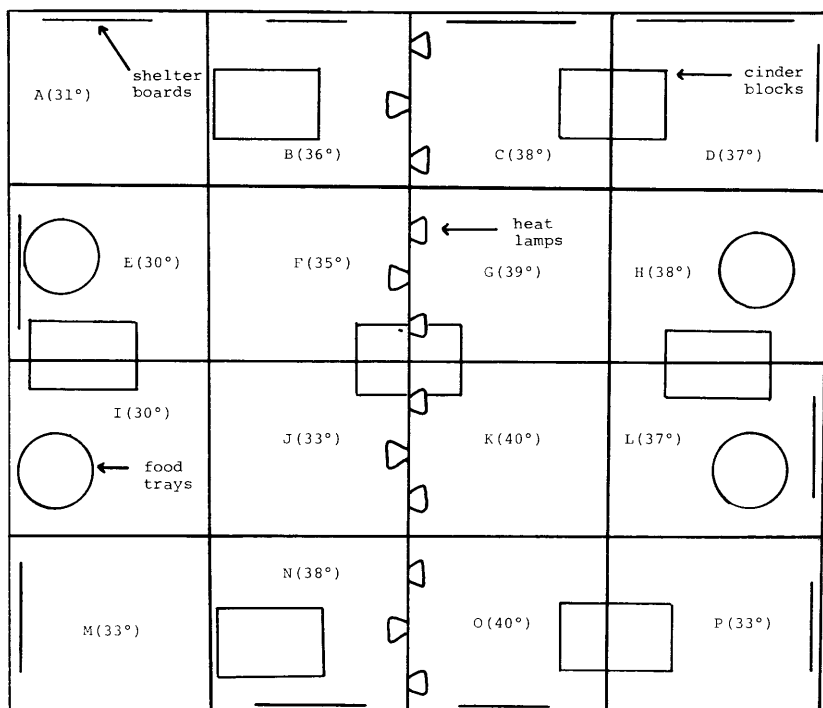


FIGURE 1. Schematic of the laboratory enclosure showing the location of heat lamps, food plates, cinder blocks, and shelter boards. Temperatures are the average ground temperatures in C° for each grid.

walls provided places for hiding and sleeping (Fig. 1). Air and surface temperatures ranging from 15 to 47 C were maintained by heat lamps of 300 watts each. A 12 h photoperiod was maintained. The lights were arranged in a straight line through the center of the cage 1.5 m above the floor. Each lamp could be rotated 360 degrees along the horizontal plane allowing specific areas to be thermally manipulated. Temperatures within the enclosure were continually monitored by a Northrop and Leeds Speedomax G 20 multiple recorder. Humidity was not controlled but was recorded daily.

Observations were conducted through a 30 X 30 cm one way window in the door of the enclosure. Each lizard was uniquely marked with a number on its back; a Sanford's Company red "magic marker" was used for females, black for males. Each lizard was also permanently marked by toe clipping as the numbers were lost with each molt.

The effects of removal and reintroduction of males was recorded. The response of the lizards to their mirror image was also observed. A 30 X 30 cm mirror was placed in the enclosure to afford the lizard the experience of seeing its reflection and the reaction of lizards was recorded. During these experiments only the lizard being tested was present in the enclosure.

Carpenter (1962) used eight categories for analyzing display behavior in iguanas. We used three categories in describing the challenge display of the chuckwalla under field and laboratory conditions.

Territorial boundaries were drawn by connecting points where lizards were observed to display from 3 or more times.

Field Observations.—Field observations were made on marked animals from June through August 1970. Some additional observations were made during the same months of 1974. All observations were conducted at the Organ Pipe National Monument, Pima County, Arizona. Data were permanently recorded by means of 35 mm slides and super 8 motion pictures. Sketches of the various displays and graphical representation of the DAP were constructed from still photographs and movie film.

The study area was a peninsular lava flow that extended approximately 400 m in a southeast direction from the Puerto Blanco Mountains. The flow was approximately 150 m wide with a central area 90 m wide and 240 m long, almost devoid of rocks. The rocks that were in the area formed "natural islands" in the desert (Fig. 2).

Homing behavior of the chuckwalla was studied by marking seven lizards and releasing

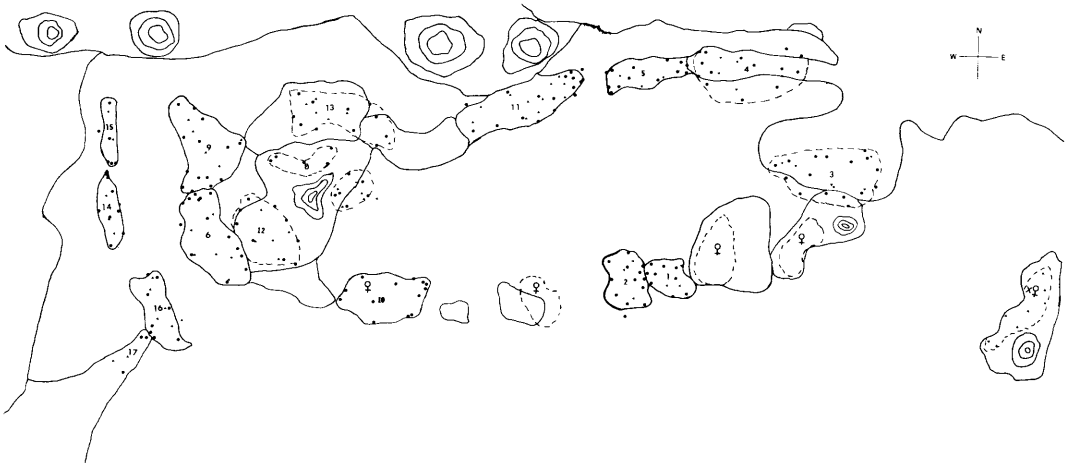


FIGURE 2. An outline drawing of the field study area showing the territories and home ranges of 18 Arizona chuckwallas. Key: Dashed line—territorial boundary not limited by a natural rock formation; solid circles—points where the males were observed three or more times; solid triangles—points where females were seen three or more times; numbers in center of territories—correspond to lizard's mark. Male and female of a mated pair were given the same number. The female symbol represents unmarked females.

them at varying distances from their original point of capture. Two animals were released 100 m from their point of collection in an area almost devoid of rocks. Three lizards were released in a rocky area 50 m from their point of capture and two individuals were released among large rocks and boulders 500 m from their original location.

All releases took place under sunny skies. The experiment was duplicated on a cloudy day using different lizards.

The response of resident males to introduced males was recorded. This was accomplished by capturing and marking males from a near-by population and introducing them into known territories of resident males. The effect of removal and reintroduction of males was recorded.

RESULTS

Challenge Display.—In a challenge display a male chuckwalla compressed his trunk, partially extended his dewlap, oriented laterally towards his opponent and performed rapid head nods with partial flexion of the front legs. The head nodding followed a specific sequence: two complete up and down movements, two intermediate nods and two shorter nods as determined by the distance the head was raised and lowered (Fig. 3).

Site.—In the field chuckwallas usually performed challenge displays from raised objects although the most intense challenge displays were performed on flat ground after a preliminary assertion display (see below). In the more intense displays the lizards repeated the DAP more often and was always complete. In displays of less intensity the DAP was seldom repeated and frequently the last two head nods were not performed. Under laboratory conditions the majority of challenge displays were performed at ground level, possibly due to lack of raised objects or to more intense display behavior in captivity.

Orientation.—The long axis of the body of the displaying lizard was parallel to the ground and lateral to the opponent. The challenging males maintained a "face-off" position each facing in the opposite direction (Fig. 4a).

Posture.—An "alert posture" was maintained by the lizard during challenge displays. In this posture the forebody was raised with the forelegs slightly flexed. The trunk was partially inflated and laterally compressed with the head horizontal or slightly lowered with the dewlap extended (Fig. 4b). The lateral plane of the trunk was tilted towards the opponent. This posture increased the apparent size of the lizard and exposed the brightly colored sides of the body.

Assertion Display.—This display involved the same head movements used in the challenge display, but was not necessarily directed at other lizards and was often performed in isolation. In the laboratory, 5229 assertion displays were recorded during 300 h of observation. More than one-half of these displays were performed by the two most dominant lizards, males 5 and 25 (Table 1).

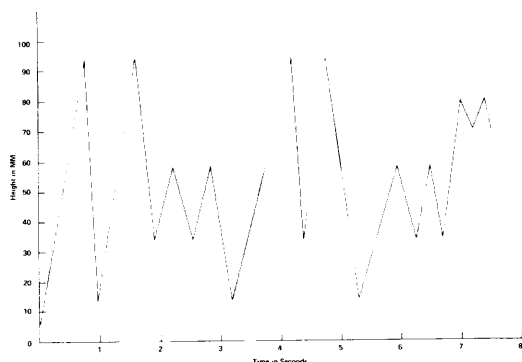


FIGURE 3. Display-action-pattern (DAP) of an individual *Sauromalus obesus tumidus*.

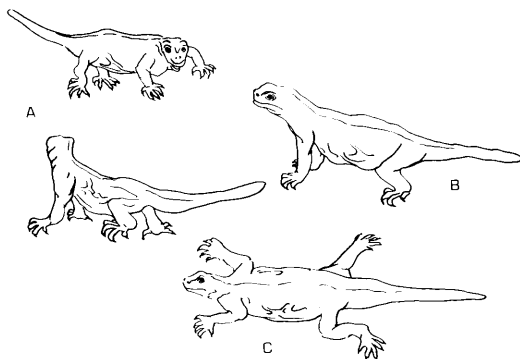


FIGURE 4. The face off (a), alert (b), and basking posture (c) of the Arizona chuckwalla.

TABLE 1. Dominance hierarchy among 18 individuals of *Sauromalus obesus tumidus* in a laboratory enclosure. Data based on number of bites, chases, challenge displays, fights, mounts, copulations and threats between March 1970 and May 1972.

		Dominant Interactions																Percent times Dominant		
		1	2	3	4	5	7	8	9	13	15	17	19	21	23	25	27	J ₁	J ₂	
Subordinate Interactions	1		6	2	1	1	4	5	1	3	1	4	2	1	1	1	1	5	5	1.3
	2	0		4	3	2	3	2	2	2	2	0	2	2	0	2	0	3	3	1.0
	3	1	3		0	1	0	1	0	0	2	1	0	0	0	0	0	3	1	0.3
	4	0	0	1		2	1	0	0	2	2	0	0	0	0	2	1	2	0	0.3
	5	31	17	13	26		22	130	77	23	49	27	12	64	32	101	44	0	0	20.5
	7	0	0	0	0	0		2	0	0	0	4	0	0	0	0	0	0	0	0.8
	8	0	0	0	1	5	0		0	0	4	0	0	0	0	4	1	2	0	0.5
	9	22	18	18	19	96	31	69		51	18	43	14	13	7	62	46	14	7	16.8
	13	0	1	0	1	16	0	24	11		2	2	2	3	2	33	20	7	0	3.8
	15	1	10	2	5	1	3	9	0	0		0	0	6	2	1	7	3	0	1.5
	17	0	2	0	8	0	0	0	0	0	0		0	0	2	2	0	0	3	0.5
	19	0	7	0	6	0	0	0	0	1	0	0		0	0	0	0	0	5	0.6
	21	10	34	50	69	28	7	37	10	66	40	87	6		19	35	10	0	8	15.8
	23	0	0	0	0	11	4	0	9	0	0	0	0	0		0	0	0	0	0.7
	25	8	52	40	20	56	69	110	20	117	25	55	7	98	31		40	3	0	23.0
	27	11	17	18	4	10	66	44	0	73	26	43	2	0	16	26		0	2	11.0
	J ₁	6	10	0	0	2	3	0	4	0	0	0	0	5	0	0	12		0	1.3
	J ₂	0	2	0	0	0	0	2	0	0	0	4	0	0	0	0	0	3		0.3

Courtship Display.—The courtship display was similar to the assertion display except that it was directed by a male towards a female.

Social Behavior.—Formation of Territories: In the field, all adult male chuckwallas established territories which were presumably marked by patrols, displays, threats and combat. Females and juveniles were tolerated inside the territories but trespassing males were aggressively challenged. The females did not participate in territorial maintenance. The boundaries of the home ranges during the study coincided with those of the territories.

In the field, during 1970, nine of the 11 fights observed took place during the first three weeks of June, even though observation periods were equally distributed from June through August. In a period of two months, 466 assertion displays and 213 challenge displays were recorded. It seems probable that the territories were actively maintained until the animals retreated for the winter months. By the end of June all males were observed within recognizable areas as defined by their patrols. In all but five cases the territories coincided with the natural islands formed by the rocks in the area (Fig. 2). The animals frequented the larger rocks and only descended during feeding (Prieto and Sorenson, 1975).

Adult males patrolled the perimeter of their territories at frequent intervals throughout the day. The stations chosen as basking, lookout and resting sites were raised areas within the territories. The males also displayed from these sites. Of the 466 assertion displays recorded, 271 (58%) were performed by the males that had the largest territories (3, 6, 9 and 11) (Fig. 2). More displays occurred along the boundaries than any other part of the territory. In the eleven instances of actual physical combat, seven were among males whose territories met along at least one boundary.

When the chuckwallas were first placed within the enclosure some individuals seemed more active and showed more assertion displays than their cohabitants. The most dominant lizard exhibited site fidelity within the enclosure. After the emergence of a dominant, this was the only animal to defend a specific area. It should be noted that these were not the same animals observed in the field but were collected from a nearby population.

Male 5 was the dominant animal in the enclosure from August to December 1970. During this time his preferred area was around rock site-3 and the wallboard directly behind it. This male wandered throughout the cage but always returned to this area to rest and sleep. The following manipulations were conducted to determine whether this area was chosen on the basis of temperature, topography or as an area of concealment. First the heat lamps were rearranged resulting in a decrease of temperature. As a result the animal basked elsewhere and then returned to the preferred area. The lamps were then rearranged to their original position and the wallboards removed. The lizard initially returned to this area and continually climbed up and down over the spot he had previously sought for shelter. The male's preferred site seemed to be determined by topography since he would chase any males that approached within one to two meters of this area.

Territorial Activities: In the field, daily activities within the territories included basking, feeding, displaying, courtship, mating and occasional defense.

Marking Behavior: There was no evidence that chuckwallas indicated their territories by means other than postural displays. Male chuckwallas, as well as other iguanids, possess well developed femoral pores on the inside of the thighs (Hunsaker and Burrage, 1969). The pores produce a prominent secretion during the breeding season. Two males were observed marking rocks with this secretion in the central area of their territories. Other males twice crossed these marked spots without any apparent recognition of the scent.

Homing: To avoid disturbance of the marked population, chuckwallas from adjacent localities were used in homing experiments. The approximate boundaries of the home ranges of four males and three females were plotted over an eight day period. The males were marked A, B, D, and F; the females C, E and G. On 20 July 1970, under sunny skies, lizards A, B and C were released in an area without rocks approximately 50 meters from their home sites. Individuals D and E were released in an area without rocks 100 meters from their original collection point and animals F and G were released 500 meters from their original location in an area with a number of rocks.

Individuals A, B and C were at their original sites on the morning of 21 July. Male D was observed 20 m from his territory on the afternoon of the same day. On the morning of 22 July female E was near the center of her home range. Later that morning, male F was sighted 85 m from the north boundary of his territory. Female G was never seen again. This experiment was repeated on a cloudy day with different animals; four of the five animals returned to their original sites.

Interactions Between Resident and Introduced Males: Marked animals (21, 23, 25, 27) from another area were introduced into the territories of males 6, 9, 11 and 17, in the field. The intruders were immediately challenged and driven from the area.

In the laboratory enclosure, male 5 was dominant from August through December 1970. During this time he defended a small area in the vicinity of rock site 3. If intruders invaded this area they were immediately attacked and chased. If the dominant male caught the intruder, and the latter assumed a submissive posture, the dominant would ignore the subordinate or stand on top of him while displaying. If the submissive posture was not assumed the dominant bit the subordinate and shook him until he managed to escape. Immediately after such an encounter the dominant became hyperaggressive, moved about while displaying and attacked any lizard, male or female, that was close by.

If lizards walked slowly by the dominant they were ignored; if they approached or walked by quickly they were immediately chased.

On two occasions in the laboratory the dominant male interfered with mounting which occurred less than two meters from him. After chasing the male he then attempted copulation himself.

Removal of the Dominant: On 13 September, male 5 was removed from the enclosure. Male 9 became very active and began displaying. Eight hours after the despot had been removed male 9 became the dominant animal. During this period male 9 displayed repeatedly but it was not observed to challenge or fight with any other male in the enclosure. This lizard had not previously shown any dominant behavior.

Male 5 was reintroduced into the enclosure on 18 September. Males 5 and 9 immediately challenged one another and then approached each other and presented laterally at a distance of 10 cm, faced off, threatened each other with wide open mouths and hissed, and then moved sideways toward each other in a jerky manner. Finally, male 5 lunged at male 9 and bit him on the side. Both animals rolled on the ground several times with male 5 maintaining a hold on male 9. Upon escaping, male 9 quickly retreated under one of the wallboards.

On 20 September 1970, male 5 was again removed from the enclosure and male 9 became the dominant after 10 minutes. Male 5 was returned on the same day and male 9 immediately fled upon being approached by male 5. Male 9 did not enter into any social interactions during the next four days. His social behavior underwent a sudden change; he ate only after all the other lizards had eaten and fled from the slightest contact with other males. Male 9 did not become dominant during the rest of the study. Two other males, 5 and 25, behaved in a similar manner after they had been defeated during a dominance period.

Male 5 was dominant longer than any other male in the enclosure. He was involved in 664 dominant interactions and was the despot 20.5% of the time he was in the enclosure (Table 1).

On the morning of 31 December 1970, male 25 began to display and showed increased aggressiveness. That same afternoon he challenged male 5 who fled. On 2 January 1971, male 25 was removed from the enclosure and male 5 became dominant within two hours. Male 25 was replaced on 3 January and immediately challenged male 5. After nine minutes of challenge displays, the animals approached each other and assumed the face off position. After two minutes in this posture male 5 turned and fled. Male 25 then turned and walked to his basking site where he displayed four times.

Male 25 did not defend any specific basking site in the enclosure, rather he moved about the cage displaying at frequent intervals. The sites he used for basking and resting were utilized by other chuckwallas but only in his absence.

Removal of Territorial Males: In the field, removal of territorial males resulted in only a slight increase in the size of the adjacent male's territory. The vacated areas were not colonized by other members of the population. When male 4 was removed from the area for three days, male 5 increased his activity in the domain of the removed male. When the latter was returned male 5 yielded the newly acquired territory without any apparent aggression.

Response to a Mirror Image: To test whether chuckwallas reacted to their mirror image a 30 X 60 cm mirror was placed on the floor of the enclosure and propped by rocks perpendicular to the floor. Females either ignored or passively moved away from the image. Male 25, who was dominant at the time, challenged his image and approached it with a lateral presentation. As he moved past the image he ceased displaying and jerked his head from side to side as if seeking the "other lizard." He then became hyperaggressive and when he walked past the mirror he once more challenged his image. Male 25 never attacked the image. In other encounters, lasting up to 11 minutes, male 25 moved slowly away from the image and partially displayed, as if tired of the stalemate. This could be the result of habituation.

Contactual Behavior.—In the field, adult male chuckwallas usually remained inside their territorial boundaries. The only exception was during feeding when up to three males were observed feeding together. On several occasions males basked within one meter of each other but each in his own territory.

The situation was quite different for females and juveniles, who would often bask in close proximity. Males and females occupying the same territory were often observed basking side by side. On two occasions a male, female and juvenile were collected under the same rock. Three juveniles, two females and one male basked together on at least three occasions. Once, two females residing in the territory of the same male were observed basking within 12 cm of each other. On 17 July 1970, female-X basked along side of an unidentified female. The marked lizard assumed the typical basking posture (Fig. 4C) but rested her head on the tail of the second female.

In captivity only dominant males maintained individual distances. The distances varied but usually the dominant males would challenge other males at a distance of one to two

meters. This distance was reduced to zero during feeding. The other lizards in the enclosure often rested and basked close to each other and made no attempt to maintain individual distances.

Grooming: This form of behavior was observed only under laboratory conditions. Male 1 groomed female 2 and male 25, the dominant male at the time. The dominant male assumed a crouched position in front of the subordinate animal (male 1) as the latter picked pieces of skin from his body. This grooming behavior was observed on four other occasions: female 4 groomed male 3, male 13 groomed female 2, female 4 and male 3. The lizard being groomed usually assumed a crouched position while the "groomer" bit off and swallowed pieces of skin from the "groomee." This behavior ended when one of the lizards walked away. Grooming occurred when the animals were shedding and losing large pieces of skin. The chuckwallas were never observed eating pieces of their own skin. A shedding animal frequently rubbed the side of his head back and forth against the rocks in the enclosure and would scratch the loosened skin with their hindlegs.

Licking: Chuckwallas often licked other lizards as well as inanimate objects. This sensory modulation presumably functions in association with the Jacobson's organ. In the laboratory, the licking of fecal pellets was common. Females in the enclosure were licked more often than males, usually by other males prior to mounting and copulation. When two lizards met, the dominant usually licked the subordinate. After a fight the dominant lizard might lick the subordinate if the latter assumed a submissive posture.

In the laboratory cloacal licking was observed 23 times. During this behavior a male lizard approached another lizard, male or female, from behind and pushed its snout beneath the tail and licked the cloaca of the lizard being tested. The recipient animal either raised its tail and remained still or quickly walked away.

Sleep and Rest Postures: In captivity all chuckwallas slept behind the wall boards in the enclosure. The posture was similar to that of a chuckwalla sleeping in a crevice, as they do under natural conditions, except that the body was not inflated. Males, 5, 21 and 25 always slept behind the same wallboards and usually alone. Other lizards slept together behind boards with as many as ten individuals per group.

In the field most chuckwallas had two to five crevices in which they were regularly located during the day. Presumably, these areas were used for sleeping although this was not verified.

Only two specific rest postures were noted outside crevices. In the first, the animal laid flat on the ground or on a rock with its head slightly raised and either the right or left fore- and hind-legs stretched out and pointed to the rear. In the second, and more common rest posture, the lizard perched flat on some object, with the legs of either side of the body overhanging the object. These postures were frequently observed in the enclosure but only twice in the field.

DISCUSSION

Chuckwallas use stereotyped displays to indicate aggressive intent. Displays are performed to declare a territory, challenge other males and as a means of assertion. In addition to color differences, behavioral displays may also help establish sex recognition. The assertion display advertises the presence of an individual in its immediate vicinity and is related only to the lizard and its immediate surroundings. It differs from the challenge display in that it is not necessarily directed at another lizard and is often performed in isolation. The assertion display is considered an expression of aggression, but not as a dominant interaction since only one individual is involved. In the field, assertion displays may function to mark territorial boundaries as indicated by the patrolling behavior of the chuckwalla. The display involves head movements termed bobs, nods and upward and downward movements of shoulder and chest region resembling pushups which were consistent in time and motion and are graphically

represented as the display-action-pattern (DAP). The DAP is a stereotyped behavioral action unmodified by age or experience and is species typical. When the display alone is not enough to bluff another lizard, other threatening postures follow in a predictable manner, sometimes resulting in combat. The displays and related postures are part of a behavior sequence used to produce or maintain an effective social system with a minimum of energy waste in physical encounters, by allowing individuals to assess the aggressive intent of conspecifics. The effectiveness of this behavior sequence was apparent in the enclosure where only nine fights were noted in 300 h of observations.

In the field chuckwallas showed accurate homing abilities. The simplest type of homing involved the return of animals to one of several home sites from some other part of their territory. Our field experiments demonstrate that chuckwallas also home when displaced considerable distances from their original sites.

Aggression plays a major role in the social structure of the Arizona chuckwalla, *Sauromalus obesus tumidus*. Male chuckwallas establish territories by means of patrols, displays, threats and combat. Females were tolerated in these areas but males were aggressively challenged. In our study all males were observed defending well defined territories. This differs from the social system of *Sauromalus obesus obesus*, in which Berry (1974) reports that only the tyrant holds territories while the subordinate adult males, females and juveniles align in a dominance hierarchy.

Rand (1967) states that successful defense of a territory enhances the possibility of: (1) securing a share of the environmental resources, (2) mating and (3) survival of the offspring. In the case of chuckwallas the environmental resources include adequate food, basking sites, crevices for sleeping and hiding places. Berry (1974) has reported harems in *Sauromalus obesus obesus* similar to the situation we have noted; that is several females residing in the territory of a single male. The reproductive fitness of the male is thus potentially increased by the greatest number of female home ranges without critically reducing the defendability of the territory. There is no reported parental care in chuckwallas and it is not demonstratable that the quality of the territory effects offspring survival.

As environmental conditions cause crowding, as in the laboratory enclosure, a dominance hierarchy or despotism is formed. In captivity, both social systems occur within the males, a situation similar to Berry's field observations. Choice basking and resting sites were claimed by the despot male and only used by other males in his absence. Females were tolerated on these sites.

When aggression can be appeased by retreat and there is a defendable resource, a territorial system may result from the aggression of specific individuals. Hunsaker and Burrage (1969) suggest that a continuum exists between territoriality and social hierarchy. It has been demonstrated in lizards that crowding will cause a territorial system to become a social hierarchy (Brattstrom, 1974; Carpenter, 1967). Our results show this to be true in *Sauromalus obesus tumidus*. The selective advantage of the lability of this social behavior is obvious in situations where limited food or other resources make it energetically unfeasible to defend a territory.

ACKNOWLEDGMENTS

We thank C. C. Carpenter, B. R. Koffler and an anonymous reviewer for their helpful comments and criticisms of the manuscript. We also thank Kate Bellis for the drawings of the lizard's behavior postures.

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Accepted 21 Dec 1977

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