

The Evolution of Reptilian Social Behavior

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SYNOPSIS. Reptiles display a diversity of behavior that is reflective of their evolutionary heritage from fish and amphibians and their ancestral contribution to the diversity found in birds and mammals. Much of the behavior observed in reptiles seems specific to the ecological setting within which they live. As a result, a diversity of behavior is found in each of the groups of modern reptiles. Recent studies on the social behavior of lizards have proved them capable of a variety of behavioral postures, sequences, and sociality that exceeds that found in some mammals and birds. While many species of lizards are territorial, others are hierarchial and some have harems. For all those territorial species studied, crowding results in increased social interaction, increased aggression, and a switch to hierarchial behavior.

While smell and sound may be important stimuli for social behavior in some reptiles, posture, actions, and especially color appear to be most important in diurnal lizards. Temperature and energy studies suggest that the large extinct dinosaurs probably fought considerably less than commonly portrayed in movies and stories, but were also probably much more brightly colored than commonly shown in reconstructions.

INTRODUCTION

In contrast to fish, birds, and mammals, reptiles are generally considered to lack complexity in all aspects of their behavior. This view is due in part to the fact that many of the early behavioral studies on these forms were carried out at ecologically unrealistic temperatures so that social behavior often did not occur. The view is also due to the phylogenetic orientation of many of the studies which has had a tendency to limit observations to only certain aspects of reptilian behavior.

The view that reptiles were less intelligent and showed less behavior than other vertebrates is based in large part on early learning studies which tended to show that lizards were stupid! In some studies most

lizards took over 300 trials to learn a simple T maze (see review in Northcutt and Heath, 1971). In all these studies, ambient or radiant heat was usually not sufficient so that the lizards could not heat up to normal efficient body temperatures, and therefore the studies were really measuring metabolic inactivity rather than learning ability. Based on a background of thermal data (Brattstrom, 1963, 1965), studies were independently begun by Vance (Krekorian et al., 1968) and by me using temperatures, situations, and reinforcers that were ecologically relevant to amphibians and reptiles. These studies showed that these animals have complex social behavior, behave best at optimum temperatures, learn mazes and similar tasks rapidly (1-15 trials; also see Northcutt and Heath, 1971), and respond best to environmentally relevant cues (heat as reinforcement for diurnal basking lizards, dark boxes as reinforcement for nocturnal lizards, etc.); lizards could even be trained to press a bar to obtain more heat for reinforcement (Stevens, 1974). Further, when field or laboratory cages or aquaria were set up in proper design and effective environmental controls were used (correct temperature or moisture, consideration of microhabitat preference,

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etc.), then a wide variety of behavior was observed.

Almost all of the studies on amphibian and reptilian behavior have been in the evolutionary context of the behavior as a premating species isolating mechanism. Thus, the majority of amphibian studies have been on the mating calls of frogs and toads or on the complicated courtship patterns of salamanders. Reptilian studies have been primarily with diurnal lizards (iguanae, agamids, varanids) and have described species differences in courtship or aggressive displays. They include the pioneering studies of Carpenter and his students (Carpenter, 1961, 1963, 1966, 1967, 1969; Carpenter et al., 1970; Clarke, 1965) and others interested in the evolutionary context of displays (Hunsaker, 1962; Ferguson, 1966, 1969, 1970, 1971a, b; Ruibal, 1967; Garcea and Gorman, 1968; Gorman, 1968; Tinkle, 1969).

In addition there have been isolated studies on field, laboratory, or zoo animals, often on some of the more spectacular kinds of amphibians and reptiles. These studies often suffer by not being brought into some behavioral framework, thus represent interesting, but perhaps unusual behavior.

It is the major purpose of this paper to describe ways in which herpetologists study social behavior in reptiles, to indicate those basic conclusions thus far considered valid, to describe some of the more interesting social systems, and to give an overview of the evolution of social behavior within each of the groups of reptiles. Though the literature has been reviewed (also see "Lizard Ecology, A Symposium" especially papers by Carpenter, 1967; Evans, 1967; Rand, 1967; Ruibal, 1967), the following will largely describe studies going on or completed in our laboratory.

MATERIALS AND METHODS USED IN REPTILIAN BEHAVIORAL STUDIES

Animals

Most reptiles used in behavioral studies are first observed in the field and are then collected and returned to the laboratory or outdoor cage for further studies. Our studies

are usually on males only, females only, and then mixed male/female groups. Most animals are studied immediately upon return to the laboratory, as even under the best of conditions some species of reptiles do not do well in captivity. With poor health, many reptiles become inactive and do not interact socially.

Marking

Historically, amphibians and reptiles were marked for field and laboratory studies by clipping toes. Recent studies (Clarke, 1972) have shown that this technique adversely affects the behavior of salamanders, frogs, and probably also lizards. Tattoos, removal of clips of scales, and drawing individual color patterns are other techniques often used. Most workers have found that marking with paint, marking pencil, nail polish or similar substance is adequate for individual identification and distant observation and does not appear to interfere with the lizard or its behavior. Markings are placed on the back of the lizard since most of the visual signal stimuli in lizard behavior are lateral or ventral (Greenberg and Nodle, 1944; Ferguson, 1966; Kästle, 1967; Petry, 1971; Cooper and Ferguson, 1972); however, the critical experiments on the effect of additional dorsal markings have not been done.

Experimental situations

In Figure 1 are diagrams of different types of aquaria, cages, or outdoor pens used in our studies. In general the enclosures are simple and are provided with water, food (usually *Tenebrio* larvae), and one or more heat sources (usually a red or white bulb, infra-red lamp). Placement of heat sources is critical as their position can influence social behavior. A dominant lizard may defend a rock under a heat lamp and exclude other lizards from the heat (Regal, 1971). Subordinates may therefore not obtain an adequate amount of heat for digestion of food (Regal, 1971). The placement of the rock and the heat lamp may also dictate that a hierarchical, rather than a territorial, social system will be estab-

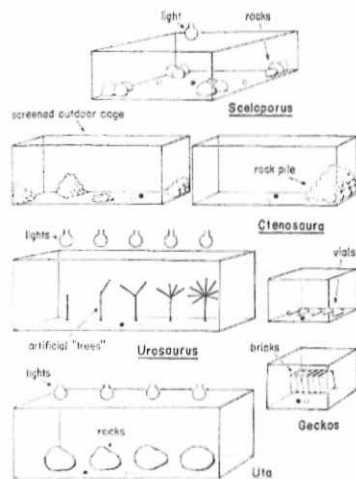


FIG. 1. Typical experimental situations used in lizard behavior studies. Black and white dots show location of food and water dishes.

lished (see below).

Rocks or rock piles are moved or changed in number in the experiment. Rocks are set up according to the microhabitat preferences of the animal. Thus, night-lizards and geckos are given bricks with cracks between them or darkened tubes or vials (Fig. 1). Diurnal lizards are given rocks, and big iguanids such as *Ctenosaurus* are given rock piles. For studies on tree dwelling lizards, such as *Urosaurus*, we have made "tinkertoy" trees with various numbers of branches. Each tree is placed under its own heat lamp. Nocturnal lizards are observed at night, usually under red incandescent light with the observer hidden behind a visual barrier with a peep hole. Nocturnal lizards can be observed at night or during the day by switching their internal clocks around so that their subjective night is during the observer's day.

Behavioral postures and positions

For reptiles, basic postures and positions have only been adequately described for

courtship and fighting behavior (Carpenter, 1961, 1962, 1969; Kästle, 1963, 1967; Blanc and Carpenter, 1969; Ferguson, 1970) and fully analyzed for only a few species (Carpenter, 1962; Gorman, 1968; Jenssen, 1970b, 1971; Ferguson, 1971a, b; Purdue and Carpenter, 1972a, b). Only recently have there been attempts at describing the entire repertoire of behavioral postures and positions found in any one species of reptile (Kästle, 1967; Brattstrom, 1971). In our laboratory we are currently describing behavioral postures for a variety of common amphibians and reptiles. Brattstrom (1971, 1973) discusses problems in describing and defining postures, motivational levels, sequences of behavior, and the contextual roles of a single posture. Though the number of postures per species may be of interest from a general evolutionary point of view (Brattstrom, 1973), the more important comparative studies may be within a group of closely related species. In Australian geckos, for example, some species have more than 65 postures, while others have considerably less. Many postures are shared, but others are unique to each species.

BASIC ASPECTS OF REPTILIAN SOCIAL BEHAVIOR

Many reptiles, especially snakes and turtles, have home ranges or activity ranges that are undefended and within which one individual seldom meets another (Fitch, 1958; Moll and Legler, 1971). These reptiles apparently meet only during the mating season, and thus, social behavior is limited to these times. Social behavior is especially prominent in diurnal basking lizards. Typical diurnal lizard territories have been described by Fitch (1940, 1958), Stebbins and Robinson (1946), Tanner and Hopkin (1972), Tinkle (1969), Tinkle et al. (1962), to mention only a few. Lizard territories in open country (grassland or desert) are often evenly spaced and almost equal in size (Tinkle et al., 1962), but as the habitat becomes more diverse and complex, territory distribution becomes uneven and unequal in size (Jenssen, 1970b; Tanner and Hopkin, 1972). This is usually due to the relation of territories to the presence of

rocks, trees, perching, or basking sites (Rand and Rand, 1966; Blanc and Carpenter, 1969; Jenssen, 1970b). Indeed basking sites are sometimes more important in determining territory size and shape than social behavior (Jenssen, 1970b), and often social behavior is stopped for thermoregulatory behavior (Brattstrom, 1971). Further, the more complex the habitat, the more kinds of lizards that can occur in it. These species often have overlapping territories but different food-utilization or food-getting strategies (Pianka, 1967).

In lizards the territory serves as an area for feeding, mating, egg-laying, survival and protection of the young, and spacing (Table 4) (Rand, 1967). Territorial behavior in crocodilians and in the only known territorial snake, the King Cobra, serves to protect egg-laying sites (Oliver, 1956; Shaw, 1960; Cott, 1961).

Hierarchies or dominance relationships in lizards have been described by Greenberg and Noble (1944), Carpenter (1961, 1967), Carpenter and Grubits (1960), Clarke (1965), Honegger and Heusser (1969), Hunsaker and Burrage (1969), Brattstrom (1971), and others. Most of these hierarchies have been induced by crowding. Hierarchies may be linear, dendritic, or mixed. Hierarchies may involve complex fighting and submission, as seen in many iguanids and agamids, or very subtle behaviors such as sounds and mutual licking as seen in geckos and night lizards.

At present, reptilian behavioral studies seem to indicate that the various relationships shown in Figure 2 are valid. Many of these generalities are common to other vertebrates. Thus, when population size (or density) increases, aggressive interactions increase. When aggressive interactions increase, dispersal increases (leading to increase in spacing or, if confined, to a greater distance moved about a cage) (Brattstrom, 1973). If dispersal is impossible, then territory size per individual generally decreases until the social system switches to a hierarchical system. Hierarchical position is usually dependent upon size (also see Table 1, 2) and strength of the signal sys-

tem. In a confined situation, the amount of aggressive interaction is greatest at first and declines with time. The dominant animal makes the greatest number of displays ("push-ups," "bobs," "DAP's" = Display Action Patterns). The possible relationships of size of territory to size of territory, of size of territory to food habits, or of sexual dimorphism to social structure have not yet been demonstrated for amphibians and reptiles, though Turner et al. (1969) have shown a positive relationship between body size in lizards and size of the "home range."

DENSITY DEPENDENT RELATIONSHIP BETWEEN TERRITORY AND HIERARCHY

It is a common observation that lizards that are territorial in the field become hierarchical in the laboratory (Carpenter, 1967; Brattstrom, 1971). Presumably, this results from the inability of any but one lizard to obtain and defend a territory in a crowded situation. To explore the interrelationship between territory and hierarchy we have used two methods: observing field territorial animals and placing these same animals under crowded laboratory conditions, and manipulating variables (numbers of lizards, rocks, heat lamps, and total space

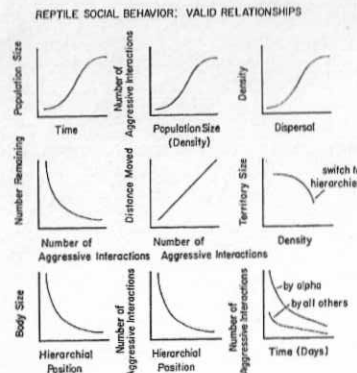


FIG. 2. Relationships which seem valid for reptilian social behavior.

TABLE 1. Relationship of hierarchical position to body size in several laboratory hierarchies of male lizards.

Species	Hierarchical position							
	1	2	3	4	5	6	7	8
<i>Sceloporus occidentalis</i>	8.2	8.2	8.1	7.4	7.9	7.6	5.7	5.3
<i>Phrynosoma platyrhinos</i>	7.5	6.8	6.6	6.3	6.8	5.5	6.4	5.1
<i>Ctenosaura hemilopha</i>	26.2	25.6	25.7	22.4	21.0			
<i>Coleonyx variegatus</i>	7.1	6.5	7.2	6.7	6.2	5.3		
<i>Coleonyx variegatus</i>	7.2	6.5	6.5	5.8	6.5	6.3		

Measurements are snout-vent lengths in millimeters.

available). Thus, large Spiny-tailed Iguanas, *Ctenosaura hemilopha*, common in the Sonoran thornscrub of Mexico, are typically found on large rock walls, cliffs, trees, or piles of rocks. A territory is defended by a male against other males by threat postures and bobs. A male's territory may contain the territory or home range of a female and a juvenile. Five male territorial lizards of this species (Table 1; Fig. 1) were brought back to the California State University, Fullerton, campus and placed in a large outdoor cage (Fig. 1) with four rock piles. All lizards, except the smallest, could still successfully defend separate rock piles. The smallest was accepted as a subordinate into the territory of another male. When the rock piles were combined into one (Fig. 1), a hierarchy developed that was related to size (Table 1).

In the crevice-dwelling night lizards and geckos (*Xantusia henshawi*, *Phyllodactylus xanti*, several Australian species), one generally finds only one lizard per crevice in the field (except during the mating season and except if the crevice is unusually large) (Leavell, 1971). If placed in a large aquarium with enough bricks to provide one crack per lizard, the lizards are territorial and defend cracks to the exclusion of others. If bricks, hence cracks, are systematically removed, the lizards are forced into a hierarchy, with subordinate showing submissive postures and usually living in lower part of the vertical crack with a dominant lizard at the uppermost part of the crack. Bricks can be removed until all geckos are within a single crack.

Data for two field and laboratory studies on the Western Fence Lizard, *Sceloporus occidentalis*, are shown in Figures 3 and 4

and Table 2. In a study by Carlson (Fig. 3), the territories of male fence lizards were mapped in two situations, a rock wall of a dam (Loc. A, Carbon Canyon Dam, Brea, California, May 4-7, 1969) and on a large woodpile (Loc. B, Yorba Linda, California, May 19-26, 1969). Table 2 shows the relative size of each lizard, size of territory, and level of aggressiveness of each lizard. Four of the lizards from Loc. A were later placed in a small aquarium (Fig. 1, 3). Lizard A was dominant and could walk about the entire aquarium. Lizards B, C, and D were successfully territorial over their own rock pile, but were submissive when approached

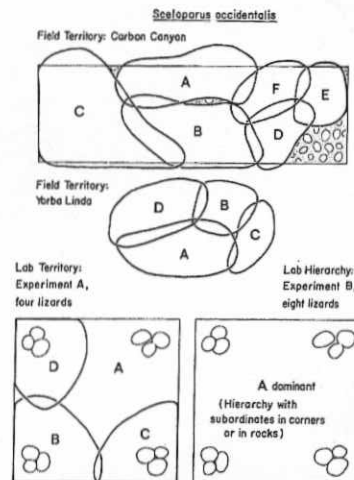


FIG. 3. Results of a field and laboratory study on the Western Fence Lizard, *Sceloporus occidentalis*. See Text and Table 2.

TABLE 2. Relationships among body size, territory size, and aggressive level in the two field and two laboratory situations shown in Figure 3 for the Western Fence Lizard, *Sceloporus occidentalis*.

Location or experiment	Lizard	Lizard size (rank)	Relative territory size	Relative level of aggression	Number of aggressive interactions
Loc. A.	C	1	1	1	19
	B	2	2	2	14
	A	3	2	3	10
	F	4	4	4	9
	D	5	4	6	2
Loc. B.	E	6	4	5	4
	A	1	1	1	37
	D	2	2	2	26
	C	3	3	4	15
Expt. A.	B	4	3	3	19
	A	1	1	1	
	B	2	2	2	
Expt. B.	D	3	2	3	
	C	4	2	4	
	Hierarchical position				
	A	1	1	1	63
	B	2	2	2	56
	C	3	3	3	49
	D	6	4	4	20
	E	4	5	5	17
F	5	6	6	15	
G	7	7	7	6	
H	8	8	8	1	

by A. On May 26-28, a total of eight male lizards (from both localities) was placed in a similar-sized aquarium and a hierarchy resulted in which no lizard could maintain a territory and subordinates restricted their activities to corners or under or adjacent to rock piles (Fig. 3).

In another experiment with this species Bayer mapped the territories of several males (Fig. 4). The males were then collected and placed in an outdoor patio 22 ft sq. The lizards quickly set up a hierarchy. On day one, all lizards were active, displaying, bobbing. Within a few days this activity was reduced and most of the bobbing was done by the dominant male. Later, almost no bobbing occurred, except by alpha, and most lizards indicated their hierarchical position by adopting a submissive posture when any lizard higher in the hierarchy approached. The hierarchy was linear at the upper levels and interacting and dendritic at lower levels (Fig. 4).

In a related study, Bielat observed the behavior of the Side-blotched Lizard, *Uta stansburiana*. Four males were placed in a 110 gal aquarium with four rocks and four

heat lamps (Fig. 1). Two lizards defended

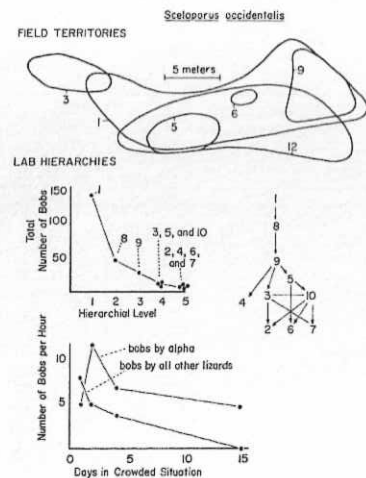


FIG. 4. Results of a second field and laboratory study on the Western Fence Lizard, *Sceloporus occidentalis*. See text.

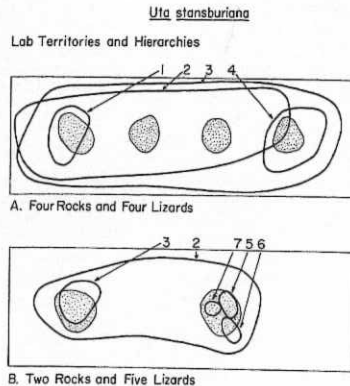


FIG. 5. Laboratories and hierarchies in the Side-blotched Lizard, *Uta stansburiana*. See text.

small territories restricted to individual rocks (Fig. 5). The two other lizards were each most commonly found on the other two rocks, but their territory included the entire cage. They were dominant over the other two lizards but seldom approached their rocks. The two lizards with large territories had overlapping territories (except for some exclusion on rocks) but seldom encountered each other. Later two rocks were removed and five male *Uta stansburiana* (numbers 2 and 3 from previous experiment plus 3 new males) were placed in the aquarium. Figure 5 shows that three lizards had restricted territories on one rock, one lizard had a restricted territory on another rock, and another lizard (number 2 from previous experiment) had the entire cage and both rocks as a territory and was dominant over the other lizards when he occurred on their rocks.

SPECIAL ASPECTS OF REPTILIAN SOCIAL BEHAVIOR

Submission

Since overt aggression is energetically expensive, many animals have reduced extended displays and fighting to only those times that either is absolutely necessary.

The energetics of ectothermic amphibians and reptiles (heat source from without, high fatigue rate, good ability to use anaerobic respiration, low ability to repay lactate debts) (Brattstrom, 1965; Bennett, 1972a,b; Bennett and Dawson, 1972; Bennett and Licht, 1972) makes it especially important that the information associated with various social stimuli is sent, received, and responded to quickly. Further there is an energy savings to the individual if this response is made at some low rate of energy expenditure. Thus, many lizards can do a variety of things to indicate subordination; most often the lizard adopts a submissive pose with the belly adpressed to the substrate. In addition, complicated display behavior is soon dropped after hierarchies are established (Fig. 4). Even during the establishment of hierarchies, challenges, displays, and complicated fights account for only a small percent of male-male behavior. As Evans (1951) noted in his studies on normally territorial *Ctenosaurus* crowded by fire onto a rock wall, hierarchies are size-related and determined in large part by the subordinate "recognizing the higher status or size" of the dominants. Subordinates often assume a submissive posture or retreat before a dominant displays. Thus, dominants may largely gain their status by action of the subordinates, not by their own successful displays and fighting. The submissive posture of adpression to the substrate allows females and young males to exist within the realm of a dominant with little expenditure of energy. The submissive behavior of "escape" or "running" allows for escape from further aggression and for dispersal and spacing.

Two unique submissive behaviors occur in Australian agamid lizards. In the Bearded Dragon, *Amphibolurus barbatus*, submission is indicated by the adpressed posture and by an overhand wave or circumduction (Carpenter et al., 1970; Brattstrom, 1971). Dominants have head bobs and aggressive up-and-down waves, but subordinates can stop all aggression toward them by waving. They can, therefore, freely move about within the realm of a dominant. The wave is a slow overhand wave and is

directed towards specific dominant individuals and is given by either hand, depending upon the location of the aggressor. The wave is common to several species of *Amphibolurus* and is successful in stopping interspecific as well as intraspecific aggression.

Another unique example of submission was reported to me by the late F. John Mitchell who had been studying a small desert lizard, the Lake Eyre Dragon, *Amphibolurus reticulatus*. Females of this South Australian lizard emerge from underground nocturnal retreats under the crust of this dry lake and go towards shore to feed. Males emerge and go away from shore and develop territories around ant mounds (sometimes shaped into mushroom-like forms for shade) that emerge onto the surface of the dry lake bed from below the crust. When territories are being established or when the lizards are placed in a cage in the laboratory, subordinate males indicate their status by flipping over on their backs. When the dominant lizard moves away, the subordinate rights itself, only to return to the same vulnerable position should the dominant return.

Presenting

Harold Cogger (1967) has reported a curious behavior found in the small desert dragon, *Amphibolurus maculosus*. These lizards are patchy in their distribution, but when found are aggregated and abundant. During the breeding season females wander about among the males presenting their blue-colored vent regions. Males often lick the vent region of the females. Specific olfactory cues may trigger male mounting behavior.

I have subsequently seen ripe female horned lizards, *Phrynosoma platyrhinos*, presenting to males in laboratory aquaria, and it may be that reproductive behavior in lizards is more complicated than the mating sequences described in the literature.

Harems

Eibl-Eibesfeldt (1955) has reported harem

formation in the Galapagos marine iguana, *Amblyrhynchus cristatus*. As pointed out by Carpenter (1967), an unbalanced sex ratio is favorable to harem formation and polygamy but does not necessarily cause this social organization. Thus, Carpenter's observations, with which I concur, suggest that the marine iguana is polygamous but males do not collect and defend harems. In my opinion, harem formation is established only when a male collects or defends several females and only he mates with these females. Since most lizard territories overlap with or are adjacent to only one female territory or home range, most lizards are monogamous, at least seasonally. There are two good examples of polygamous or incipient harem systems reported in lizards. For the Madagascar iguanid, *Chalarodon madagascariensis*, Blanc and Carpenter (1969) report that male territories are normally distinct and contain a single female, but that some male territories include two or three females and sometimes small juvenile and subordinate males. Stebbins et al. (1967), reported that the Galapagos Lava Lizard, *Tropidurus albemarlensis*, is territorial, though occasionally males tolerate juveniles and immature males in their territory. The sex ratio in this situation favored polygamy and most males had territories which included two or three families. One very large, aggressive male had 11 females within his territory.

The Chuckawalla, *Sauromalus obesus* (Berry, 1971) is the only lizard known to have harems. In this species, large tyrant males defend large territories within which good-sized but subordinate males are restricted by the tyrant's action to mini-territories about rock piles and basking sites. Females have feeding and basking site territories generally larger in area than those of the subordinate males. Tyrants patrol their territories daily, restricting the activities of subordinate males and visiting the females within their territory. Patrolling occurs before, during, and after the breeding season. Only the tyrant mates with the females, but most mating is initiated by the female (Berry, 1971).

TABLE 5. Types of social behavior found in reptiles.

Group	Non-aggressive behavior				Aggressive behavior			
	No social behavior except mating	Aggregation behavior	Home range	Territorial	Hierarchical	Harems	Tyrants	
Turtles	Some	Mating, feeding, egg-laying, basking, winter retreats	Many, as feeding areas	A few over retreats, food	Over mates, in captivity when crowded, ? in wild.	0	0	
Crocodilians	Some?	Basking	As feeding areas	Males, calling sites; females, by nest.	When crowded as in captivity	0	0	
Sphenodon	?	?	+	0	0	0	0	
Snakes	Some burrowing forms	Mating, egg-laying, food seeking, temp. responses, winter retreats	Most active snakes as feeding area	Nesting King Cobras; ? Eua vipera?	"Combat Dance"	0	0	
Lizards	Some burrowing forms	Mating, feeding, egg-laying, temp. responses, winter retreats	As feeding area in non-breeding season	Most species as feeding, mating and egg-laying.	Most forms when crowded; Chameleons over mates; others?	A few species	One species, Chuckawalla	
Large dinosaurs	Some	Mating, feeding, egg-laying	Most forms as feeding area	Rare in carnivores as feeding area	Rare, perhaps over mates.	0	0	
Small extinct reptiles (Thecodonts, Therapsids, Eosuchians, Corylosaurs)	Some forms	Mating, feeding, egg-laying	Some	Most common, as mating, feeding and egg-laying	Rarely	0	0	

THE EVOLUTION OF SOCIAL BEHAVIOR
IN REPTILES

Social behavior is most complicated or perhaps only best observed and studied in the conspicuous diurnal lizards and in a few nocturnal lizards in laboratory studies. Social behavior, other than that associated with courtship and mating, may not be well developed in some groups of reptiles. Table 3 summarizes the types of social behavior found in each of the groups of reptiles.

Turtles display limited interaction with other individuals and tend to aggregate only for mating, basking, and egg-laying. Bustard and Tognetti (1969) and Rand (1967) have described the population control mechanisms associated with aggregated nesting on isolated beaches in turtles. Most turtles wander about a home range in search of food and seldom defend territories (Moll and Legler, 1971). Marking of territories with urine and feces is known in captive Desert Tortoises, *Gopherus agassizi* (Patterson, 1971a), and there is occasional fighting in turtles over retreats, hiding places, or food (Evans, 1961). Hierarchies are reported for several species in captivity (Evans and Quaranta, 1951; Evans, 1961; Boice, 1970; Harless and Lambiotte, 1971), and males are known to fight, usually over a female, in many of these same species of tortoises and box turtles (also see Auffenberg, 1965, 1969). Hierarchies are related to size (hence age) and are often based on subtle behaviors, such as order of entry into a nocturnal retreat. Often the dominant tortoise is the last to enter (Patterson, 1971a). Fighting between male tortoises may be spectacular and fights often end when one tortoise retreats or is turned over by the winner (Evans, 1961; Auffenberg, 1969). The losing turtle may have difficulty righting itself. Several mechanisms in the Desert Tortoise assure the survival of the defeated tortoise. Among these are the ability to urinate in an arc to cool the head if overheating, and the use of a unique sound which stimulates the winner to turn the loser turtle right-side up (Patterson, 1971b). Size, fights, sounds, odors, and head

bobbs are important stimuli in turtle social behavior (Auffenberg, 1965, 1969; Patterson, 1971).

Little is known about crocodylian social behavior, but new interest in crocodylian conservation and ecology have spawned many recent studies (Cott, 1961; Bustard, 1970). Male alligators are apparently territorial when they defend small inlets or wallows by calling. The bellowing of male alligators, besides being one of the loudest of animal sounds, reveals a fairly even spacing of animals throughout a large swamp and suggests territoriality (Kellogg, 1929; McIlhenny, 1935; Shaw, 1960). Female crocodylians defend their nests, and their presence may be essential to proper incubation and release of the young (Evans, 1961). Most of the territorial defense of the nest may be against predators, not conspecifics, hence nest defense may be parental behavior rather than true intraspecific territoriality. In crowded situations, as in captivity, crocodylians are often aggressive and cannibalistic against smaller individuals of the same or other species (Shaw, 1960; Evans, 1961). Sound, smell, and perhaps overt fighting are apparently the important stimuli in crocodylian social behavior.

Many aspects of lizard social behavior have been described above. Some forms may have no social behavior other than mating. Others may aggregate for feeding or egg laying or in winter retreats (Table 3). Many lizards have undefended home ranges associated with retreats and feeding areas during most of the year. Most lizards are territorial during the breeding season, some (true chameleons) (Rand, 1961; Bustard, 1965; Parcher, 1971) are hierarchical, most are hierarchical under crowded conditions, several species are polygamous, and one species (the chuckawalla) has harems and tyrants. Postures, actions, colors, and sounds (especially in nocturnal forms) are the most important stimuli in lizard social behavior.

Snakes may be the most asocial of all reptiles. This may be a function of their elongate bodies (with few structures of the body for utilization for display) and largely se-

cretive nature, or it may only be a function of the difficulty of studying these forms. Courtship, mating, and aggregation (for mating, egg laying, or thermoregulation and in winter retreats) (Evans, 1961; Myres and Eells, 1968) behaviors encompass the greater portion and function of social behavior in snakes. Courtship may be simple, but mating may be complicated. There is a species-specific hemipenial-cloacal lock-and-key isolation mechanism which apparently restricts interspecific mating (Dowling and Savage, 1960). Most snakes wander about a home range, feeding and resting after feeding. Some migrate to winter den sites where aggregation and sometimes mating occurs. In the King Cobra both sexes help build a nest of leaves among bamboo stems and then guard the nest. Whether this is really intraspecific territoriality, parental behavior, or a response to passing humans is not clear (Oliver, 1956). The European Viper has a restricted home range which may be a defended territory (Evans, 1961; Naulleau, 1966a,b). Male snakes of several species (especially copperheads, rattlesnakes, and some colubrids) engage in a "combat dance." A female is usually, but apparently not always, present. In a typical pit viper combat dance, males raise the anterior parts of their bodies off the ground and face each other swaying. One male wraps its body around another and throws the other solidly to the ground. This may be repeated numerous times. Attempts at mating between the two males during combat have been reported and suggestions as to the function of the combat dance run from homosexual behavior to sex recognition behavior (Bogert and Roth, 1966; Smith, 1968; Rigley, 1971). If the latter, then these snakes could be referred to as hierarchical. Intra- and interspecific cannibalism is fairly common in snakes and visual and especially olfactory cues may be the most important for social behavior. Other than the studies on aggregation behavior (Dundee and Miller, 1968; Watkins et al., 1969), nobody has, in my opinion, designed the appropriate experiments to study social behavior in snakes properly. The prevalence of spectacular threat (de-

fensive) behavior in snakes and numerous isolated observations (head-swaying in racers, trail following, tail displays) suggest that there is more to snake social behavior than has been assumed.

Little is known about the social behavior of the sole surviving Rhynchocephalian, *Sphenodon*. It lives in burrows which it shares with a bird (petrel) in loose colonies. It is active at low temperatures and at night.

Herpetologists have had a long interest in the ecology, behavior, and physiology of the large extinct reptiles such as the dinosaurs. New studies (Bakker, 1971; Spotila et al., 1973) now allow us to speculate on dinosaur biology with greater confidence. Though we now suspect that due to their size, the larger forms had a fairly constant body temperature and hence were homeothermic (Bakker, 1972), we also suspect, because of reptilian energetics (Bennett, 1972a,b; Bennett and Dawson, 1972; Bennett and Licht, 1972), that the classical picture of long sustained fights between large dinosaurs was probably not possible. In addition, ecosystem energy dynamics would also predict that there would only be a few of the top "super carnivores" anyway. As expected, only five specimens are known of the large carnivorous *Tyrannosaurus rex*, and other large carnivores are much less common in the fossil record than their contemporaneous herbivorous species. I would suspect that the large herbivorous dinosaurs had aggregation behavior for feeding (such as large herding herbivorous mammals today) and this facilitated mating. Such herds would have had a home range, but probably didn't defend it against conspecifics or others. Though hierarchies may have occurred, and they are suggested in those duck-billed dinosaurs that had "false crests" (i.e., large crests without elaborate nasal passage-ways and enlarged nasal bulbs), most were probably non-aggressive. Large carnivores may have had large feeding territories associated with moving herds of herbivores. Hierarchies, if they occurred, were probably short-term, non-fighting dominance relationships by males over mates. Small herbivorous and carnivorous reptiles from lizard-sized therapsids and eosuchians

to medium-sized pelycosaur, thecodonts, and small dinosaurs, probably had a gamut of social behavior similar to that found in modern lizards. In any event, overt fighting was probably minimal and especially so in the larger forms. This would suggest that odor (especially in the "true-crested" duck-bill dinosaurs) and especially color were the important cues used in social behavior. Thus, many of the large extinct reptiles may have been even more brightly colored than is commonly shown on reconstructions and in pictures.

CUES AND STIMULI IN SOCIAL BEHAVIOR IN REPTILES

While sound may be especially important to crocodilians and some nocturnal lizards, and scent important to snakes, visual cues, including color markings, appear to be the most important stimuli used in sex discrimination and social signaling in diurnal lizards (and perhaps dinosaurs). These colors are associated with postures that maximize exposure of the colored area to the receiver, thus bobs, dew-lap extensions, and lateral compression of the body to expose belly and throat colors are common behaviors or displays. A few experimental studies have been done on painting out or enhancing visual stimuli on real or model lizards (Greenberg and Noble, 1944; Hunsacker, 1962; Harris, 1964; Ferguson, 1966; Kästle, 1967); a more important question may be to ask what quality of a stimulus elicits a specific response and what quality of stimulus or internal physiology makes an animal more aggressive, more dominant, or

more responsive. Most studies on reptiles have indicated that male aggressive behavior is hormonally related and that hormone levels are due to temperature and photoperiod responses (Evans, 1961; Licht, 1972). No studies have been done, however, on hormonal levels of lizards of different social status nor with changing social status as a function of hormonal injections (though induced breeding, fighting, and similar behavior has been brought about experimentally by hormone injections, proper photoperiod, and temperature). Size, age, and experience (Greenberg and Noble, 1944) are important variables and stimuli in hierarchial and harem social systems in lizards. Color (Petty, 1971) and color intensity may also be important. Scores on a subjective and arbitrary scale for several color markings that may be important in the social behavior of the Side-blotched Lizard, *Uta stansburiana*, are shown in Table 4. These data correlate well with the hierarchial position of these lizards based on laboratory studies.

Colors associated with social behavior seem to be more useful as social stimuli in open areas than in dense forests. It may be that territorial and hierarchial behavior is less prevalent in tropical lizards and that social behavior is limited to mate-seeking and limited largely to occasional chases and flights. Habitat, microhabitat, and niche specialization may reduce the need to defend an area. Two exceptions to these generalities must clearly be the New World anoles and the African True Chameleons. Both groups are largely tropical and both use color, color change, and body move-

TABLE 4. Subjective qualitative value scores on a scale from -1 to +3 for various colored areas on the Side-blotched Lizard, *Uta stansburiana*, and the relationship of these scores to hierarchial position.

Lizard number	Number of blue spots on back	Size and intensity of side blotch	Chin color	Tail color and intensity	Average	Hierarchial position based on laboratory studies
1	+1	+1	+1	+1	+1	4
2	+3	+3	+2	+3	+2.75	1
3	+1	+3	+3	+1	+2.0	2
4	-1	-1	+1	+1	0.0	5
5	+2	+2	+1	+1	+1.5	3
6	-1	+1	-1	+1	0.0	5
7	+1	-2	-1	+1	-0.25	6

ments in their social behavior. Anoles have brightly colored dewlaps and dewlap extension displays and body bobs (Ruibal, 1967; Gorman, 1968). Chameleons have bright sexual colors, body movements, and body ornamentation (Kästle, 1967; Parcher, 1971). In both groups these colors and displays are largely species-specific isolating mechanisms which appear to be necessary for proper species identification in these two groups of lizards associated with their tropical diversity (Rand, 1961; Bustard, 1965; Ruibal, 1967; Gorman, 1968; Parcher, 1971). Further, my interpretation of Parcher's (1971) extensive motion pictures is that some chameleons may have a kind of lek behavior.

A FINAL COMMENT

Numerous questions remain unanswered about current and past studies on reptile social behavior, and almost nothing is known about the social behavior in some reptile groups such as crocodilians and snakes. Further, studies on sensory physiology, learning, and genetic aspects of the behavior of reptiles are in their infancy. The interrelationship of color, body size, sexual dimorphism, territory size, feeding strategies, predation, thermoregulation, and reproductive strategies in reptiles has not yet been fully explored. Recent trends in reptilian and ecological research and the results of a systems approach to ecological studies (as with the IBP program) suggest that a new era has begun in reptilian ecological studies, and we may soon have some important clues as to the ecological and physiological determinants of social organization of reptiles.

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