Display and Communications in Reptiles: An Historical Perspective

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SYNOPSIS While the analysis of displays and communication in reptiles has accelerated during the past decade, much of the information has been anecdotal and gathered without focus. There are exceptions. In a few studies releasers and releasing mechanisms were analyzed. However, to date our understanding of the communication repertoire of even the best studied reptile, the lizard *Anolis carolinensis* is fragmentary. In a few other studies the quantitative nature of variation of particular display movements or acts has been elucidated but there are many more acts for all species whose quantitative and qualitative variations are unknown. Only a very few investigators have postulated adaptive reasons for observed patterns of variation between populations or species. There are no good tests of these hypotheses. Both broad comparative studies that rigorously measure environmental variables and in-depth studies on single populations are badly needed to relieve this deficiency.

Despite the lack of good data, recent techniques, some from studies with objectives entirely different from that of studying behavior, are likely to further our knowledge significantly. The projection image technique will enable the rigorous dissection of the signal value of various visually oriented acts. For the study of adaptive significance of display variation within a lizard population is presented an in-depth empirical approach that utilizes demographic analysis, behavioral observation and field experimentation.

INTRODUCTION

The study of reptilian social displays and communication has been sketchy during the last three to four decades. However, the few rigorous studies of reptilian behavior and the large number of anecdotal reports provide general descriptive models of display communication and its evolution in various taxonomic groups.

My purpose is 1) to paraphrase very briefly some of these models and 2) point out the current level of confidence regarding them. In this review I will emphasize what are, in my opinion, some of the more promising future lines of empirical investigation based on our current knowledge and technology. Many of the ideas of this paper are expanded in greater detail in Ferguson (1977) and Ferguson and Bohlen (1977).

This report will be divided into four sections: 1) anecdotal description and verbal models of reptilian communication; 2) studies of releasers and releasing mech-

anisms; 3) studies of stereotypy and species specificity; 4) studies of survival value and adaptive significance of display variation.

ANECDOTAL DESCRIPTION AND MODELS OF REPTILIAN COMMUNICATION

From the late 1800's until 1959, definitive studies of reptilian displays and communication were few. The contributions of D. Davis, L. T. Evans, B. Greenberg, G. Kramer, G. Kitzler, R. Mertens, and G. K. Noble and his co-workers are most widely quoted (see Ferguson, 1977 for citations). A perusal of the literature cited by Carpenter (1977) and Ferguson (1977) reveals that during this period about 570 publications contained information about reptilian displays and communication. Thirty-four of these (about 6%) published by 16 authors might be considered major contributions. The others were either anecdotal reports or major studies of subjects peripheral to reptilian communication and displays, but which contained some information on those subjects.

In contrast, from 1960 to 1973, a period of only 13 years, about 380 publications

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contained information on reptilian displays and communication. Of these, 72 (19%) published by 38 authors might be considered major contributions. Thus, like most fields of science, the study of reptilian communication has accelerated during the last decade. Yet, knowledge is still too general and hypothetical to say that we have good understanding of the details of how and why reptiles communicate.

The following is a brief example of the general verbal models of reptilian communication that are frequently encountered in textbooks; it is quoted from the summary and conclusions section of Carpenter (1977) and Ferguson (1977). "Lizards seem to have evolved the greatest visual display repertoire. Snakes and turtles with their highly specialized morphology still exhibit a wide variety of visual signals but rely more on olfaction and tactile communication than do most lizards. Crocodilians and *Sphenodon* . . . seem to rely mostly on olfactory, auditory and tactile communication." Table 1 summarizes the importance of various communicative modalities and displays within the class Reptilia.

The above statement is based on a few concrete studies on a small number of species and a large number of anecdotal reports. In the following sections portions of the models that are based on the soundest evidence are outlined in more detail; healthy progressions of ideas, promising problems and techniques, and gaps in our knowledge are emphasized.

STUDIES OF RELEASERS AND RELEASING MECHANISMS

Much of the early work on reptilian behavior attempted to identify the releasers and releasing mechanisms of Lorenz (1937) and Tinbergen (1969). Releasers are stereotyped sign stimuli that, when displayed by an individual cause a predictable and immediate response by another conspecific individual. A releasing mechanism includes the perceptual and response mechanism in the responding individual. Some of the authors who have considered

TABLE 1. *Importance of various communicative modalities and displays within the class Reptilia.*

Behaviors	Suborders and Orders				
	Crocodilia	Rhyncocephalia	Serpentes	Lacertilia	Chelonia
A. Visual					
Head movements	0?	0	2	4	3
Head shape change or mouth open display	4	4	4?	4	2?
Tongue extension and display	0	0	4?	2	2?
Limb display	0	0	0	2	4
Tail display	4?	0	4	2	0
Body coiling or posturing	4	4	4	4	0
Color change or presentation	0	0	4	4	2
Special appendages	0	4	0	4	1
B. Chemical					
1) All stages of encounter	4	?	4	4?	4
2) Terminal stages of encounter	4	?	4	4	4
C. Auditory	4	4	0	3	2
D. Tactual					
1) All or most stages	0	0?	4	2?	4
2) Terminal stages	4	4?	4	4	4

4 indicates widespread in more than one family within the taxon; 3 indicates widespread in one family within the taxon; 2 indicates obviously important for some species within the taxon; 1 indicates minor importance for some species within the taxon; 0 indicates no importance (from Ferguson, 1977).

these mechanisms are listed in Table 2.

In only a few instances have communicative systems been investigated in depth. A series of studies begun by Evans (1936) and culminated by Cooper (1972) and Crews (1975) shows a healthy progression of understanding of communication in the lizard *Anolis carolinensis*. The knowledge gained from these studies provides excellent background for even more detailed research at the neurophysiological level. That this species of about 7,000 extant reptile species has the best studied courtship and aggression communicative systems is testimony to our ignorance. The following outlines the studies on *Anolis carolinensis*.

Evans (1936) described a chain involving "8" responses during aggressive encounters of adult male *Anolis carolinensis* (Table 3) and suggested that these are invariant, *i.e.*, that the probability that act a follows act b (transition probability) is one, or

nearly so. Greenberg and Noble (1944) with additional data challenged Evans' views as too simplistic but did not treat quantitatively the subject of stimulus-response association. Cooper (1972) in a more extensive cinematographic analysis of *A. carolinensis* aggressive encounters defined 26 behavioral acts, and with a few examples pointed out that transition probabilities between the common acts between residents and nonresidents rarely approach one. Thus, whether a particular act of a resident follows the act of a nonresident has a certain probability. Reanalyzing portions of Evans' scheme, Cooper discovered that a challenge by the resident was followed by an answering challenge from the nonresident with a probability of 0.25 rather than 1.0. Seventeen other nonresident acts followed the initial challenge by the resident. The three most common after the answering challenge were withdrawing $(P = 0.18)$, head nodding $(P =$

TABLE 2. *Studies of releasers and releasing mechanisms in the Reptilia.*

Species studied	Subject	Investigators
Chelonia		
several species	visual and olfactory mechanisms	Granda and Hayes (1972)
Geochelonia carbonaria	visual cues	Auffenberg (1965)
Gopherus berlandieri	olfactory cues	Weaver (1970)
Terrepene carolina	visual cues	Evans (1956)
Crocodilia		
Alligator mississippiensis	auditory cues	Beach (1944); Evans and Quaranta (1949)
Caiman sclerops	auditory sensitivity	Wever and Vernon (1957)
Lacertilia		
Agama agama	visual cues	Harris (1964)
Amblyrhynchus cristatus	visual cues	Carpenter (1966)
Anolis auratus	visual cues	Kästle (1963)
Anolis carolinensis	visual cues	Evans (1938) Greenberg and Noble (1944); Noble (1944); Cooper (1972) Crews (1975).
Anolis nebulosus	visual cues	Jenssen (1970)
Anolis trinitatus	visual cues	Gorman (1968)
Coleonyx variegatus	olfactory and tactile cues	Greenberg (1943)
Crotaphytus wislizini	auditory cues	Wever et al. (1966)
Cophosaurus texanum	visual cues	Clarke (1965)
Sceloporus torquatus	visual cues	Hunsaker (1962)
Sceloporus undulatus	visual cues	Noble (1934); Carpenter (1962a).
Sceloporus virgatus	visual cues	Vinegar (1972)
Lacerta	visual and olfactory cues	Kramer (1937)
Lacerta	visual and olfactory cues	Kitzler (1941)
Uta stansburiana	visual and olfactory cues	Ferguson (1966)
Serpentes		
Thamnophis sirtalis	olfactory cues	Noble (1937)
Thamnophis butleri	olfactory cues	Noble (1937)

TABLE 3. *Agonistic sequences of male chameleons* Anolis carolinensis *(From Ferguson, 1977).*

challenger	challenged	challenger
dewlap reflex ⟶	⟶ ignore	
	⟶ retreat ⟶	pursuit
	⟶ dewlap reflex	
	⟵	
dorsal crest reflex ⟶	⟶ dorsal crest reflex	
⟵		
sidewise approach ⟶	⟶ sidewise approach	
⟵		
lateral flattening ⟶	⟶ lateral flattening	
⟵		
biting ⟶	⟶ biting ⟶	biting
	⟵	
	⟶ retreat	
⟵		
pursuit		

0.10), and looking about ($P = 0.10$). Quantitative analyses such as these suggest that stimulus-response control during aggression is considerably more complex than previously considered. (See also Barlow, 1968; Stamps and Barlow, 1973).

Some of the most common or "more probable" stimulus response sequences have been investigated experimentally.

The extension of the red dewlap (throat-fan) of the male lizard *Anolis carolinensis* was originally postulated to be the basis of sex recognition, *i.e.*, dewlap extension of a non-resident male was thought to cause the resident to challenge rather than court the intruder, that of a resident, to attract the female to the male, and to stimulate her to be receptive (Evans, 1938). Greenberg and Noble (1944) tested these hypotheses experimentally. In one experiment females with an attached artificial red dewlap were challenged and attacked by males, but when a nonresident male and female of similar size were blindfolded and placed in the resident's cage, the resident attacked the male preferentially even though the dewlap of the nonresident male was not exposed. In another experiment sexually receptive females were placed between two males each of which was displaying about 1 m from the female. The dewlap of one male was painted green. The females chose the most active male regardless of the color of his dewlap. When the distance at which the females were placed from the two males

was increased to 4 m the females showed a slight preference for a male with the red dewlap versus a male whose dewlap was prevented from extension with collodian (28 females attracted to normal males; 8 females attracted to altered males). Greenberg and Noble suggested that the red dewlap along with other aspects of a dewlap display and certain subtle morphological proportions of the male shape releases an aggressive response from resident male. The red dewlap might have increased the conspicuousness of the male to a distant female but the behavioral aspects of courtship were more important in attracting females to males.

Crews (1975) assessed experimentally the relative contributions of dewlap extension and dewlap color of courting male *A. carolinensis* to the stimulation of female receptivity. He subjected females to males, 1) whose dewlap had been artifically colored blue (vs. the normal red) by injecting India ink into the throat, 2) whose dewlap was prevented from extending by partial hyoidectomy, 3) whose dewlap was unaltered. The courtship pattern of the three classes of males was identical in all other respects. Most of the 12 females that proved receptive to a normal male both before and after being subjected to the altered males were receptive to the blue-dewlapped males but were non receptive to the hyoidectomized males. Thus, dewlap color seemed unimportant for stimulating female receptivity (defined by the

female behaviors, "courtship stand" and "neck bend") but the configurational changes proved critically important. All of the *A. carolinensis* studied by Crews and Greenberg and Noble were from Louisiana. Crews suggested that dewlap color may be more important for stimulating receptivity in localities where *A. carolinensis* is sympatric with other species of *Anolis* (e.g., southern Florida).

Greenberg and Noble (1944) studied other stimulus response mechanisms in *A. carolinensis* such as the function of the "head nod" performed by females and subordinate males but the above is sufficient to illustrate a first step in the careful dissecting of a communication system at the level of behavioral analysis. A complete understanding of how such a mechanism works for any species involves coming to grips with questions at the neurophysiological level. Such questions to my knowledge are virtually unexplored in visual communicative systems of *Anolis* or, other reptiles (but see Granda and Hayes, 1972; Wever *et al.*, 1966; Wever and Vernon, 1957). Ontogenetic and geographic variation in such systems are also unknown.

A recent technique has been developed and should result in important breakthroughs in the study of visual communicative systems in reptiles. Jenssen (1970) developed the projection image technique. His apparatus consisted of a 2 m long cage with a movie projector positioned outside of the cage and at each end. The two projectors were timed to project images of displaying lizards alternately through the screens which comprised the ends of the cage. The lizard whose response was to be tested was introduced into the middle of the cage. The projectors were activated and the response of the introduced female was noted. In his experiments the response of the lizard *Anolis nebulous* to normal versus altered movies of displaying males was studied. Females chose the normal displaying image significantly more often than the altered display when the alteration was major. Jenssen clearly demonstrated an experimental technique whereby visual cues can be isolated from those of other modalities and the visual input can be rigidly controlled.

STUDIES OF STEREOTYPY AND SPECIES SPECIFICITY

While studies like the previous ones are critically important for understanding the proximate communicative mechanism or the function of displays, the question arises "How stereotyped is a particular display and how does it vary between populations and species?" Perhaps the first to emphasize that there was some degree of "species specific" stereotypy or discontinuity of the variance of particular social displays between species of reptiles were Noble and Bradley (1933).

The first to quantitatively measure species specificity of displays were Carpenter and Grubits (1960). They originated the display action pattern graph to emphasize the predictable nature of push-up movement sequences of iguanid lizards. In several papers beginning in 1962 (see Carpenter, 1976, for references) Carpenter demonstrated using cinematographic techniques that the variation of the timing of up and down display movements could be precisely described and that differences between closely related species existed. In one study (Carpenter, 1962b) he concluded that the push-up movements of the species *Uta stansburiana*, *Urosaurus graciosus*, *Urosaurus ornatus*, and *Streptosaurus mearnsi* were species specific.

His samples of each species were small but represented in some cases individuals from several conspecific populations. Although some intraspecific variation was observed in *Uta stansburiana*, it was clearly less than the interspecific variation. Carpenter speculated that the intraspecific variation was probably related to motivation of the animal. Thus, in his study the adult males, the only ones to participate in highly aggressive interactions, had the greatest number of up and down units in the display sequence.

Ferguson (1971) hypothesized on the basis of the preliminary data of Carpenter and a pilot study by Aubert (1966) that

genetically based geographic differences existed between the displays of populations of *Uta stansburiana* and between closely related *Uta* species. He tested this hypothesis by analyzing samples of push-up movements of from 8 to 25 individuals from each of 13 populations of *Uta* and demonstrated statistically significant quantitative differences between the variations of timing and relative heights of the push-up and nodding movements of different populations. He corroborated Carpenter's findings of species differences but added the dimension of intraspecific geographic differences pointing out that for some species these might be too great to characterize a species by its display. Although he did not investigate the genetic basis of the differences, he summarized indirect evidence that observational learning is probably not a factor in the variation and that intergrades show the intermediacy expected of a heritable feature. Thus, the intraspecific variation originally pointed out by Carpenter was probably due to different geographic origin of his specimens.

Ferguson (1971) did not investigate the amount of variation of successive push-up displays of the same individual but assumed that it was slight. McKinney (1971) detected within-individual variation in three particularly variable intergrade populations of *Uta stansburiana*. Griffith (1966) critically analyzed the between and within-individual variation of the push-up displays of populations of *Sceloporus undulatus* and demonstrated that between individual variation (presumably genetically based) was significantly greater than within-individual variation (presumably motivationally based). Berry (1974) demonstrated significant variation between individuals of head-nodding movements of the Chuckwalla *Sauromalus obesus*.

Jenssen (1971) analyzed the displays of the lizard *Anolis nebulosus* and demonstrated not only geographic variation but confirmed a relatively low within-individual variation. He also demonstrated significant ontogenetic "slowing" of the display cadence in some individuals.

In short, statistical data show that sig-

nificant differences exist between some analogous display movements of different species, of different conspecific populations, of different individuals within a population, within the same individual at different ages, and within the same individual at different motivational states. However, comparative research in the past has emphasized only restricted aspects of displays and has been confined to a few lizards and turtles. While push-up movements may vary considerably between populations of lizards, other communicative acts may not. Conclusions regarding push-up and nodding movements of nonanoline iguanid lizards may not apply to the genus *Anolis*, many species of which have complex display repertoires (Ruibal, 1967; Jenssen, 1977). Only a few detailed behavioral inventories of lizards exist and none compare different species or populations (*e.g.*, Brattstrom, 1971; Greenberg, 1977). Future comparative studies of reptilian social displays should be more holistic and emphasize complete social repertoires.

A knowledge of variation of displays is biologically significant for at least the following reasons 1) variation of display intensity or type within an individual may reflect variation of communicative information and must be considered to fully understand the communication systems, 2) display variation between taxa can provide important taxonomic clues for discrimination of similar taxa or for showing their phylogenetic affinity, 3) display variation between populations can provide clues to the potential rate of evolutionary change of displays, 4) correlation of interpopulational display variation with environmental variation can provide important clues to the selective bases for divergence and pave the way for experimental studies of natural selection.

STUDIES OF SURVIVAL VALUE AND ADAPTIVE SIG-
NIFICANCE OF VARIATION

One of the more difficult, yet exciting, frontiers of display investigation involves reason 4 above, the elucidation of the adaptive significance of variation of reptile

communicative mechanisms. Several general approaches can be taken. One involves correlation of interpopulational variation with ecological variation; this can be a powerful approach if the variations of both display and ecological parameters can be quantified and enough populations can be analyzed to allow a rigorous correlation analysis. This approach has not been undertaken in studies of reptilian displays but has to some degree for social structures and displays of birds (Crook, 1964). Various factors have been proposed to be ultimate causes of variation (Ferguson, 1977). For example, both Rand and Williams (1970) and Ferguson (1971) suggested that visibility to predators and conspecifics is an important ecological parameter influencing display evolution in lizards but neither provided critical analyses of their hypothesis.

A factor probably influencing display evolution is similar or closely related sympatric species. The analysis of character displacement differs from that described above and should involve the analysis of communication systems of several populations of each of the two or more important species where they are sympatric and allopatric. There are a few documentations of character displacement of communicative signals and their responding mechanisms for vocalization in a few species of amphibians (e.g., Littlejohn, 1965; Littlejohn and Loftus-Hills, 1968) and for visual signals of gulls (Smith, 1966); but only one good example of behavioral character displacement has been demonstrated for reptiles. This involves the dewlap color of sibling species of the *Anolis brevirostris* group (Webster and Burns, 1973). Behavioral aspects of the displays and responding mechanisms of these species is currently being investigated by Jenssen (personal communication).

Another more in-depth approach sacrifices broad applicability of its finding, but uncovers better the complexity of the workings of natural selection. It involves the correlation of relative fitness of display variants within a single population with ecological events throughout the life history of individuals. A combination of observations, demographic and experimental techniques are used. This approach has not been taken to analyze the fitness of types of displays, but in the lizard *Uta stansburiana* it has provided unique insight into 1) the complexities of interaction of food quality, aggressive behavior of lizards, activity patterns of lizards, and predation and 2) the influence of these parameters on survival probability (Fox, 1973).

Iguanid lizards are probably the easiest vertebrates to study from a point of view that combines demographic monitoring, behavioral observation and field manipulation (Ferguson and Bohlen, 1977). Table 4 outlines a general empirical in-depth approach for studying the adaptive significance of signature display variation. The signature display (Stamps and Barlow, 1973; Ferguson 1977) is a display movement sequence performed in several social contexts throughout the ontogeny of an individual iguanid lizard. It is defined more on the basis of species or population specificity than its presumed communicative information content which may be complex and vary. The push-up display movements described previously are signature displays.

The methods outlined in the table are for the most part based on well established quantitative procedures (See Ferguson and Bohlen, 1977, for documentation). Objectives I and II would be easiest to accomplish. Perhaps the most difficult phase of a study would be objective III. Because, unlike birds, most iguanid lizards conceal eggs underground and do not remain near them for long, it is difficult to assign parentage to hatchlings (see Tinkle, 1965). However, by intensively observing females near the time of oviposition, one can locate nests. Incubation times can be estimated, and nests can be fenced to prevent dispersal of emerging hatchlings before they can be marked. Parentage may be easier to assign in ovoviviparous species.

Objective V is apt to be more difficult to achieve for lizards than for plants or sessile invertebrates but studies by Turner *et al.* (1973), McKinney (1969) and Fox (1973)

TABLE 4. *A general empirical approach for studying the adaptive significance of signature display variation in temperate, oviparous iguanid lizards. (fitness = ability of an individual to contribute to the next breeding generation).*

OBJECTIVE	METHODS
I. Determine contribution of prebreeding survival to relative fitness	1) Characterize display variation of hatchlings 2) Compare demographic survival of variants

II. Determine contribution of mating and oviposition success to relative fitness	1) Monitor social structure during breeding season of individuals marked as hatchlings
	2) Determine for each male of known display type:
	  a) breeding territory establishment success
	  b) number of females in his territory each breeding season
	  c) his survival through first breeding season
	  d) number of breeding seasons he survives
	  e) survival each season of his females to first oviposition
	  f) number of ovipositions his females survive each season
	3) Determine for each female of known display type:
	  a) whether or not mated
	  b) resource quality of her home range or territory
	  c) her survival to first oviposition
	  d) number of ovipositions

III. Determine contribution of production of offspring to relative fitness	1) For males of known display type determine number of eggs produced by his females and their hatching success. 2) For females of known display type determine number of eggs produced and their hatching success.
IV. Determine contribution of offspring survival to fitness	1) Determine contribution of prebreeding survival to relative fitness
V. After determining life history stages where natural selection is operating, determine the factors responsible for differential fitness by experimental manipulation of suspected environmental variables and monitoring the behavior of the lizards and the variables.	

show it to be feasible. I predict a bright future for the study of the adaptive significance of display variation in iguanid lizards.

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