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Ethological Considerations in the Experimental Study of Lizard Behavior

Neil Greenberg

University of Tennessee - Knoxville, ngreenbe@utk.edu

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Neil Greenberg*

Laboratory of Brain Evolution and Behavior
National Institute of Mental Health

SUMMARY. The importance of an ethological approach to the experimental study of an unfamiliar species is described and several of its problems discussed. The selection of units of behavior is a crucial first step in the development of a behavior inventory. The correlation of a behavioral unit with a particular context is necessary to ascribe function to that unit and to develop an ethogram. Methods of studying lizards under controlled conditions are described and discussed. Constraints on behavior that must be considered in an experimental study include the microclimate and its thermal qualities, food and water, shelter utilization, and social behavior. Ritualized display patterns are proposed as sources of hypotheses about the neurophysiological control of social communications.

INTRODUCTION

This report will first discuss some issues in an ethological approach to the study of an unfamiliar species and will then describe some observations that bear on the development of an experimental design for the study of lizard behavior in the laboratory.

The observations described, both my own and those gleaned from the literature, are presented to indicate the complexity of the environmental constraints on lizard behavior. They constitute something of a guide for researchers—be they students of reptiles devoted to a favorite group or those who see lizards as a possible model for experimentally testing hypotheses about the causation and function of behavior.

THE ETHOGRAM AND UNITS OF BEHAVIOR

Naturalistic observation is the essence of ethology and the fountainhead of hypotheses about the causation and function of behavior as well as the foundation on which experimental tests of these hypotheses must be built.

*Present address: Department of Zoology, University of Tennessee, Knoxville, TN 37916.

The importance of the ethogram in the interpretation of an experimental study of a species is stressed by most ethologists (e.g., Lorenz, 1935, trans. 1970:111; Tinbergen, 1951; Thorpe, 1973). Failure to consider all aspects of normal behavior has diminished the usefulness of many experimental studies (Adams, 1973; Eibl-Eibesfeldt, 1970; Thorpe, 1973).

Units of Behavior

A problem in developing ethograms has proven to be the objective delineation of separate units in what is a continuum of behavioral patterns. To minimize the arbitrary nature of behavioral classification, the investigator attempts to identify reliable, easily recognizable diagnostic features. Ideally, behavioral units should be of the type that a neurophysiologist could deal with. Barlow (1968) asserts that, in this regard, only quantifiable behavior is of interest because the behavior must be mathematically modeled if it is to be considered in neurophysiological terms. But preoccupation with quantification can be hazardous, interfering with the Gestalt perception of a phenomenon

that is crucial to generating creative hypotheses (Lorenz, 1971). For example, time sampling can often be misleading unless the environmental or social context is considered, and that is not always possible (Driver, 1968). As Vowles (1975) points out, a preoccupation with quantification may be an understandable response to the subjective and introspective approach of early psychology.

The selection of units of behavior must be suitable to the questions being asked. The hard decisions of "lumping" and "splitting," familiar to taxonomists, must also be made when behavior patterns are to be organized into manageable groups. This is true at the level of individual units in a coordinated sequence as well as in more complex behavioral categories. It is often helpful to begin with a broad overview of general activity patterns and then subdivide them until the appropriate "resolution" is achieved (Fig. 1). A neurophysiologist may profitably deal with units as fine as a muscle group and its associated actions (e.g., the "functional unit" of Liem, 1967, cited by Barlow, 1968: 217), while a population biologist may be concerned with a complete communicative act and its consequences.

While too fine a preliminary analysis can obscure a behavioral pattern with trivial details, if the units of behavior utilized in the study of a species are too broad, difficulties may emerge that could not have been anticipated until the comparative perspective was brought to bear on a problem. For example, details of behavior that might suggest a physiological mechanism or the evolutionary sources of signal behavior can be overlooked. This can be a problem in studies of display behavior where the individual components of the display and/or their time course are often not as clearly delineated as the general form of the display. A notable exception is the comparative study of the vertical "bobbing" movements of displaying males of the genus *Sceloporus* by Purdue and Carpenter (1972). Such analysis is useful because the body movements in the ubiquitous bobbing displays of iguanid lizards have generally

been treated as a single unit, when they may, in fact, represent multiple behavioral patterns which have coalesced; neck and limb movements may represent two alternative mechanisms which have become combined to effect a display. Some species have several bobbing movements for different displays which utilize limb and neck movement to different degrees or even dispense with one type of movement.

Another difficulty in defining units of behavior is that motor patterns and sequences are too easily defined in functional terms which combine explanation and description. This can interfere with comparative interpretations and replications of the original study.

The Evolutionary Perspective

One goal of comparative studies is the development of the evolutionary perspective that leads to an appreciation of the genetic (and to that extent "innate") contribution to behavior (Brown, 1969). Comparative studies are also useful to investigators in suggesting hypotheses and in analyzing the adaptive aspects of natural units of behavior. Both analogy and homology are important considerations in thinking comparatively about behavior.

In evolutionary biology, Mayr (1969) asserts that only homologous characters are of taxonomic importance. Homology originally referred to an anatomical correspondence between structures in two animals sharing a similar body plan, but, in current use, the evolutionary explanation for homology has usurped the original meaning of the term (Beer, 1974).

Two characters under consideration by a biologist may differ markedly in form or function and yet be related through derivation from a common ancestral precursor. Such relatedness may provide valuable insights into the causation of dissimilar behavioral patterns and the manner in which animals evolve.

The idea of behavioral homology, however, is a continuing source of confusion. The con-

FORAGING ⟷ STALKING

walking

body-lean
and
head tipped down

lunge

walking

assertive
display

pause

scanning

head-cock

head tipped-down

food-nudge

EMERGENCE → BASKING ⟷ PERCHING

head exposed

cautious walk

fully emerged
at threshold

COVERT BEHAVIOR

negative
perpendicular
orientation
facilitated by
oblique stance
and
lateral expansion
and (cold substrate)
body-up low-mod
(or warm substrate)
ventral adpression

posterior adpression

as
substrate
warms

anterior
body up
low-mod

scanning

head cock

body-down
head-down
(freezing)

FEEDING

sleeping
covert activity
covert basking
(dorsal adpression)

covert feeding
covert perching
hiding

RETREAT

predator escape
social retreat
thermal retreat
feeding retreat
nocturnal retreat
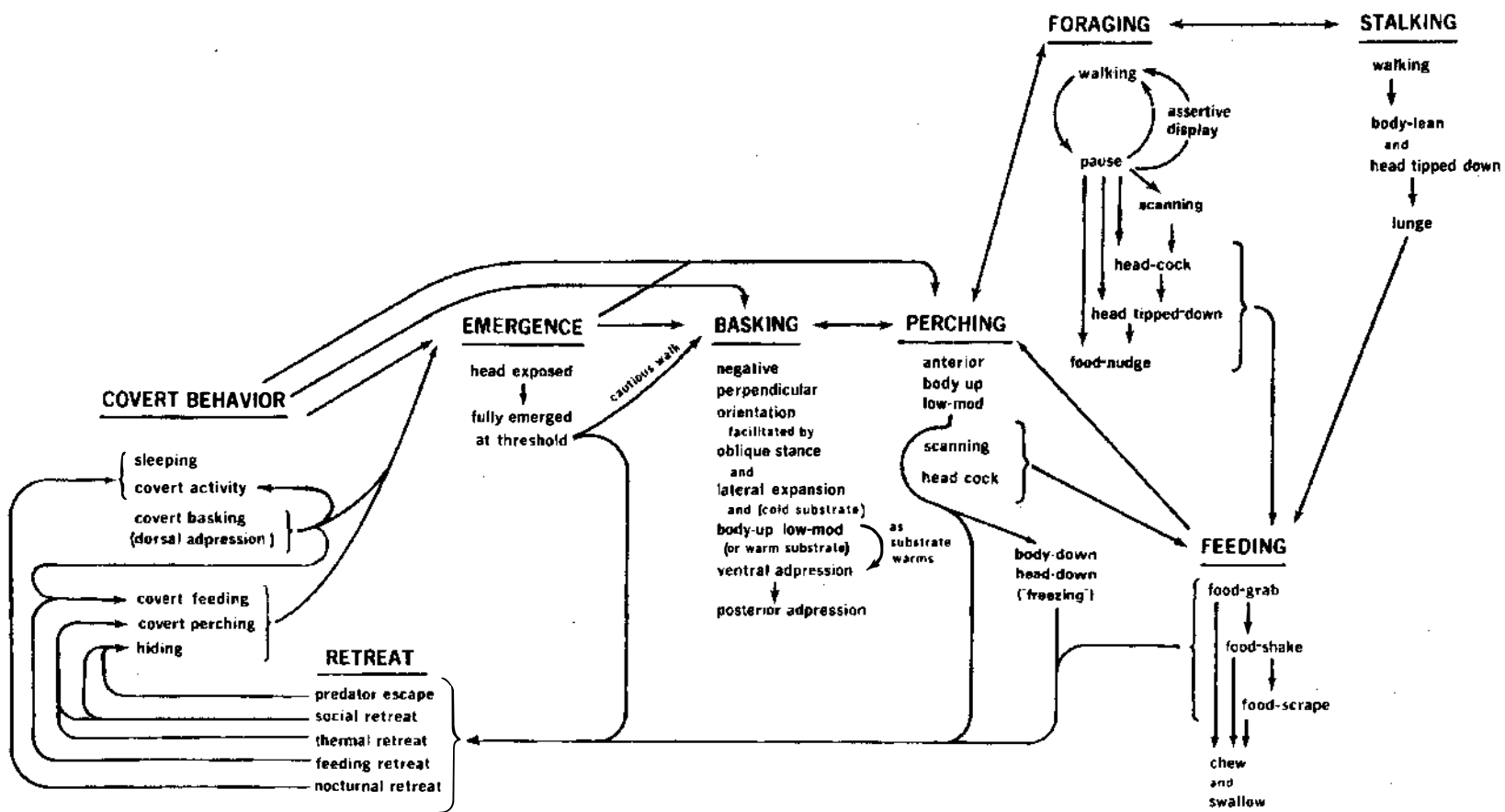
food-grab

food-shake

food-scrape

chew
and
swallow

Figure 1. A preliminary ethogram of the blue spiny lizard, *Sceloporus cyanogenys*. Such a broad overview of daily maintenance patterns may be used as a baseline against which subsequent manipulations may be contrasted to indicate distortions in behavior induced by experimental or maintenance regimens.

cept resists attempts at rigorous definition and yet is of obvious use. Atz (1970) examined the criteria used to recognize homologous behavior and argued that only morphologically defined behavioral patterns could be properly homologized.

Hodos (1977) extended Atz's ideas and concluded that behavior patterns may be regarded as homologous only to the extent that their morphological substrates can be traced back to a common ancestral precursor. He proposes a morphocentric definition of behavioral homology:

> Behaviors are considered homologous to the extent that they can be related to specific structures that could, in principle, be traced back through a genealogical series to a stipulated ancestral precursor irrespective of morphological similarity.

According to this definition, two behavioral patterns would be homologous if they are associated with homologous structures, no matter how different the functions of the behavioral patterns might be. Such morphocentric definitions of behavioral homology rightly regard behavioral patterns as evanescent extensions of anatomical structures into evolutionary time. But, it is the very disjunction of behavior and morphology that Atz regards as the crucial problem in considering behavioral homology.

Strictly applied, a morphocentric definition creates a difficulty if two different behavioral patterns associated with homologous structures have arisen independently. To avoid using the term in a misleading sense, perhaps the definition should be amended to include a stipulated ancestral behavioral pattern. Such a condition would also satisfy the definitions of behavioral homology ventured by Baerends (1958) among many others (Atz, 1970). Of course, "stipulated ancestral" behavioral patterns are derived from the comparative study of closely related extant species, and thus all proposed homologies must be regarded as hypotheses that ultimately are untestable (but see Evans, 1959a, 1959b, 1959c). The

heuristic value of such considerations, however, is uncontested.

Hodos also suggests that any statement about homology must specify the basis on which it is adduced, that is, precisely what the ancestral precursor structure might be. The level of analysis depends on the detail of anatomical structures considered, and their specification is a necessary part of a statement of a homology or proposed homology.

To further clarify the issue, Hodos recommends the use of the terms "homoplasy," referring to similar behavioral patterns, associated with nonhomologous structures, and "analogy" to refer to behavioral patterns which are functionally similar.

Analogy is important to many researchers, particularly comparative psychologists who are searching for simplified models for human behavior. This anthropocentric selection of research problems has been criticized by Beach (1960), but, nevertheless, functionally analagous behavioral patterns in different species are useful for suggesting causal mechanisms (Zeigler, 1973). Wickler's (1973) analyses of convergent behavioral adaptation provide excellent examples of particular behavioral functions which are the outcome of different internal mechanisms in distantly related animals. Under such circumstances we may be more confident that similarities in the behavioral patterns of species that are not evolutionarily related are necessary to the solving of a particular ecological problem. Indeed, Lorenz (1971, 1974) regards the study of analogy crucial to an understanding of the survival function of a behavioral pattern.

Regardless of the more useful perspective for approaching a specific problem, an excellent case can be made for the presentation of behavioral data in two complementary forms: a *behavior inventory*, in which behavioral patterns are defined in morphological terms with minimal, if any, regard for function, and an *ethogram*, in which the context and apparent functions of behavioral patterns are described.

Laboratory and Field Studies

For contextual information and confirmation of the "naturalness" of behavior, field studies are valuable but present certain problems. Field conditions may vary considerably from area to area and from year to year, necessitating many years of observation before an investigator might be confident that he has inventoried the complete range of behavior. Further, field studies may be prejudiced by the presence of the observer (Cowles and Bogert, 1944; Schneirla, 1950), partly because the observer may be perceived as a potential predator (Edson and Gallup, 1972).

Laboratory studies, on the other hand, generally rely on a specific behavior performed out of context by animals in an ecologically impoverished environment. Deprivation of outlets for some activities may profoundly influence other behavioral patterns in unexpected ways (Hediger, 1955; Morris, 1964; Kavanau, 1964, 1967). For example, general activity may increase, depending upon the nature of the opportunities (Hinde, 1970). Compulsory regimes and the constraints of small habitats may also lead to distortions of behavior that cause contradictory or paradoxical results (Kavanau, 1964, 1967).

Giving the animal some control over its habitat or initiative in environmental manipulation may be illuminating in some respects, but there is the danger that the search for "good performers" or tractable animals may find only subjects that demonstrate principles peculiar to themselves (Breland and Breland, 1961). When an animal is required to make arbitrary associations, the principles explicated may be peculiar to those associations and not necessarily applicable to the animal in nature (Morris, 1964; Seligman, 1970).

Ideally, the experimental ethologist dealing with an unfamiliar species would have a thorough knowledge of the habitat in which the animal's behavioral patterns were forged. Indeed, without such knowledge, Hediger points out, there may be contradictory impressions of the abilities of an animal (1950: 84). Furthermore, without the intimate and continuing experience with a species that the development of an ethogram requires, there may be contradictory interpretations of function (Hediger, 1955:140).

Lorenz (1935, trans. 1970:111–112) has pointed out the difficulties of objective communication of "pure" observations as opposed to experimental results. In a recent review of observational sampling methods, Altmann (1974) has contrasted internal and external validity, corresponding in each case to the consistency of laboratory research and the generalizability of field studies. A critical aspect of any experiment is the presence of controls. These, of course are not absent in the field, but are nonmanipulative. According to Altmann, it is the observer's sampling decision that influences the relative internal validity of the observations.

According to Seligman (1970), the premise of equipotentiality that underlies much psychological investigation (general learning theory) is limited in its usefulness because of its emphasis on arbitrary associations, events, and its avoidance of "contamination" by an animal's biology or experience (Seligman and Hager, 1972). He proposes a "preparedness continuum" that is recognized, for example, by the ease with which an animal can make an association (acquisition). The point along the continuum at which an animal functions in a given situation is significantly influenced by its evolutionary and developmental history. This suggests that a behavioral pattern readily demonstrated or easily elicited in the laboratory is a response that an animal is "prepared" to make, and that its causation and function are probably not significantly different from that found in nature (Jenssen, 1970a). As Hediger points out, however, a captive animal that is no longer subject to the constraints of its natural environment may behave in unpredictable, even unprecedented ways (Hediger, 1950:91).

The ability of lizards to learn is attracting considerable attention (Brattstrom, this volume; Peterson, discussion). As Lorenz

and others have observed, some things are more easily learned than other by a particular species. Mayr (1974) regards this as a situation reflecting the ease with which a genetic program manifesting itself in behavior may be modified and refers to more or less "open" or "closed" genetic programs. An "open" program is highly susceptible to ontogenetic experiential influences, whereas one which is "closed" is not subject to subsequent modification—it is "fixed."

Laboratory and Field Perspectives Combined

From the ethological perspective, experiments are regarded as most useful when animals are unencumbered by apparatus, unaffected by handling, not subject to unnatural constraints, and free to interact with their environment and with each other. A satisfactory research method is one that provides a simulation of a field habitat under laboratory control. The use of ecologically relevant cues in learning paradigms has been effectively utilized by Brattstrom (1974) and others (Brattstrom, this volume).

For conducting neuroethological experiments on display behavior in lizards (Greenberg et al, 1976; Greenberg, 1977b), my first concern has been to obtain behavior inventories and ethograms for lizards that are likely subjects for laboratory experiments. To do this, I have tried to create as complex a habitat as possible to provide lizards with a variety of natural stimuli and behavioral options. Such habitats are adjusted until benchmark aspects of the animal's behavior estimated from field observations and the literature are approximated. Then, types of behavior that are less amenable to field study can be monitored (Figs. 2, 3).

In this way, I have developed preliminary behavior inventories and ethograms of the blue spiny lizard, *Sceloporus cyanogenys* (1973a, 1977a); the rainbow lizard, *Agama agama;* and the green anole, *Anolis carolinensis.*

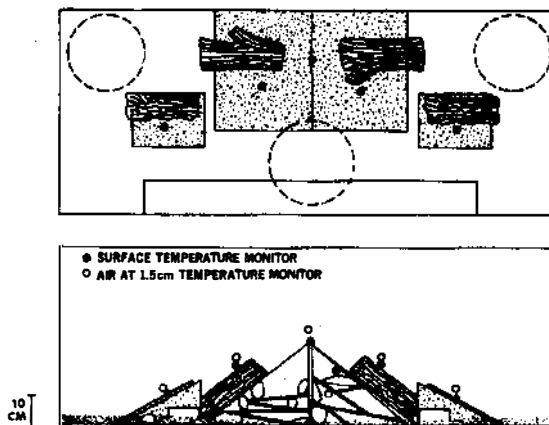Once contextual constraints on behavioral patterns are revealed from observations

Figure 2. A complex laboratory habitat and its microhabitats. In an attempt to elicit natural behavorial patterns, a variety of perches and substrates, crevices, and feeding sites are provided. Diverse prey forms are provided on an irregular schedule in order to compel lizards to maintain a natural level of alertness.

① 25 WATT INCANDESCENT
② 250 WATT INFRA RED
③ 3X250 WATT INFRA RED PLUS 2X15 WATT "Vita-lite"
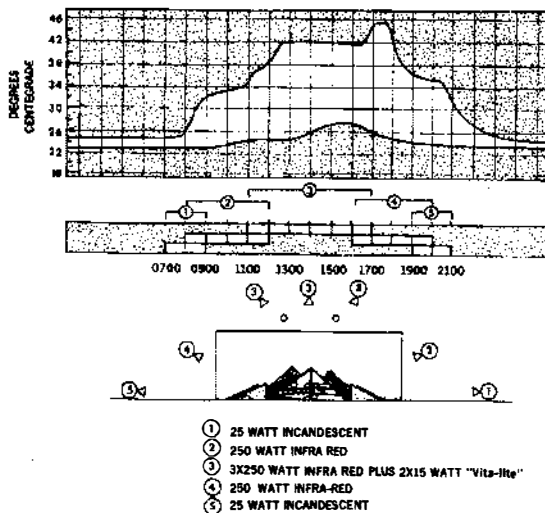④ 250 WATT INFRA-RED
⑤ 25 WATT INCANDESCENT

Figure 3. A complex laboratory habitat and its photothermal regimen. The diversity of thermal levels simultaneously available is indicated above.

made on subjects in complex habitats, different kinds of behavior may be teased out by providing the relevant stimuli in relatively restricted habitats which are more appropriate for tests on experimentaly treated animals.

An effective way of doing this is to obtain a preliminary ethogram (Fig. 1) and then to concentrate on a specific portion of it.

Such preliminary work contributes to one's confidence in the "normality" of behavior when a laboratory habitat is modified to emphasize behavioral patterns or to facilitate observations of behavioral patterns of special interest.

Observations

The techniques employed in making behavioral observations must be adapted for each species of lizard in their experimental habitats. *Anolis carolinensis* seems less subject than many other lizards to the observer effect, and it is possible to record their activity while seated a few meters away in a darkened room. Blue spiny and rainbow lizards are another matter. There is no one ideal way to observe them, but a balanced use of direct observations through a blind fitted with a one-way window and closed circuit television is effective.

The video monitoring system I employ consists of two monitors attached to a zoom lens capable of very close focus (e.g., Dage model RGS–50) and a third monitor attached to a wide angle camera so that an animal can be quickly located and peripheral activity followed (Fig. 4). The use of a time-lapse videotape recorder (e.g., GYYR model VTL 300) also allows relatively straight-forward analysis with resolution of up to 60 frames per second in replay. The tongue touching of the substrate commonly associated with the *Agama's* display may be revealed clearly in only one frame. By recording in the time-lapse mode, up to 99 hours may be compressed onto a 1-hour tape.

The Esterline-Angus pen-writing event recorder controlled by on-off-momentary switches continues to provide a reliable means for the recording of continuous states (e.g., postures, color, territorial sites) as well as momentary events (e.g., motor acts).

For extended observation of large numbers of delineated behavioral units, Dr. Richard Radna and I are developing a system that converts any conventional communications terminal into an event recorder by the use of
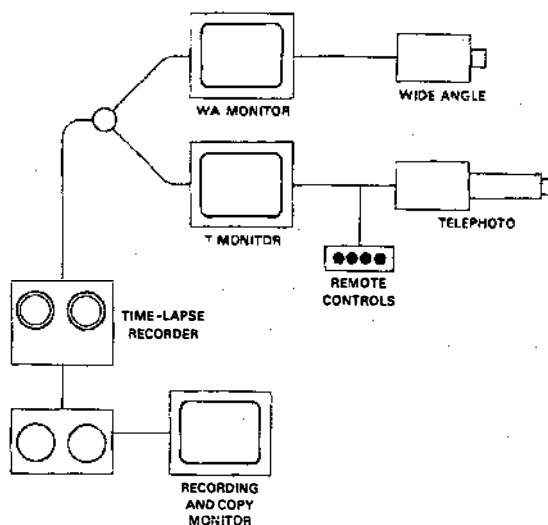

Figure 4. Separate closed-circuit television monitors are connected to (1) a zoom camera capable of extreme closeups and (2) a wide-angle camera so that peripheral action can be followed or an animal quickly located. The picture on either monitor can be recorded and events of interest can be quickly copied onto an adjacent recorder.

a system of FORTRAN programs called CABER (programs and user's guide available). CABER permits us to enter any two-digit alpha-numeric code as one would type. The internal clock of an IBM 370 is accessed, and the time, to whatever precision desired (up to one-hundredths of a second) is entered whenever the return key is hit (Fig. 6).

CONSTRAINTS ON BEHAVIOR

Microclimate

The quality and quantity of light are not only of importance for thermoregulation in ectothermic lizards, but influence behavior in other ways. Photoperiod length has been associated with gonadal regulation (Fox and Dessauer, 1958), appetite and growth (Fox and Dessauer, 1957). Species differences in response are apparent (Mayhew, 1964), and the response to photoperiod may be substantially altered by the ambient temperature (Licht, 1973), humidity (Crews et al., 1974), and possibly population density. In my study

Figure 5. Closed-circuit television closeup. The CCTV system has a timebase generator to record the date and time to one hundreths of a second on each frame.

of blue spiny lizards (1973a), individuals maintained in a large habitat (Fig. 2) spontaneously resumed a seasonal pattern of social activity after more than a year under constant conditions. Those in much smaller habitats did not.

Dim light is of little thermal significance, but simulated twilight transitions have been shown to have a potent effect in normalizing the activity patterns of animals in the laboratory (Kavanau, 1962, with mice; Regal, 1967, with lizards). Dim light may cue a lizard's shelter seeking so that it will not be caught far from its shelter when night falls (Regal, 1967). In the morning, some lizards may be cued by light to emerge (Greenberg,

1976a), while others apparently rely on the penetration of morning warmth into their shelters (McGinnis and Falkenstein, 1971; Bradshaw and Main, 1968).

An endogenous circadian rhythm was posited by Heath (1962) to account for the emergence of *Phrynosoma* in apparent "anticipation" of the onset of laboratory heatlamps, but McGinnis (1965) has argued that such a rhythm could be an artifact of the consistency of the laboratory habitat.

The importance of ultraviolet light for some species is apparent both with respect to metabolic needs (Reichenbach-Klinke and Elkan, 1965) and the expression of normal behavior (Moehn, 1974). Licht (1973) has

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20: 8:26  79 ES 53 OD BD HL FD RB YO DB
20: 9:20  73 22 OD BD HM FD RE YO BN
20: 9:34  99 ES 23 OU BD HD FD RC YO DB
20:10:22  79 ES PA
20:10:36  79 ES 53 OD BD HD FD RC YO DB
20:10:41  73 NC
20:11:42  99 ES 23 OU BD HD FD RC HP DB YO
20:11:46  99 ES MV PA
20:11:58  99 ES 23 OD BD HL SC FD RE YO DB
20:12: 3  73 SC
20:12: 5  99 ES TT
20:12: 9  79 ES NC
20:12:32  73 HA HC
20:13:36  73 HA PA
20:13:52  73 22 OD BD HD FD RC YO BN
20:14:24  99 ES 23 OD BD HD FA RE YO DB
20:14:35  79 ES 53 OD BD HD FD RC YO DB
20:15:20  NC
20:16: 1  NC
20:16:58  73 HA HL
20:17: 3  79 ES
20:17: 6  99 ES
20:17:21  73 22 OD BD HL FD RC YO BN
20:17:31  79 ES 53 OD BD HD FD RC YO DB
20:18:52  99 23 OD BD HD FA RE YO DB ES
20:19:44  79 PA
20:19:47  99 PA
20:20:21  73 22 OD BD HL FD RB YO GB
20:20:52  99 HA SN
20:20:58  79 NC
20:21: 8  99 PA MV 23 OD
20:21:23  73 PA MV 23 OU
20:21:38  99 PA MV 23 OD SN
20:21:41  99 AD
20:21:52  73 HA HM AD
20:21:54  99 AD
20:22: 2  73 TT
20:22:11  99 23 OD BD HD FD RE DB ES
20:22:43  73 22 OU DB FD RB YO GN
20:22:45  79 HA
20:22:55  79 53 OD BD HD FD RB YO DB ES
20:22:58  99 — ES
20:23: 7  99 23 OD BD HD FD RE YO DB
20:23:22  73 22 OU BD HD FD RB YO GN
20:23:25  99 HA HC
20:23:31  99 PA MV
20:23:42  99 23 OU BD HA AD
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Figure 6: Examples of data as stored and formatted by CABER. On a data line, the first six numbers are the time, the next two represent an animal, and subsequent entries represent behavioral patterns. The computer indicates the time whenever the carriage-return is depressed.

found evidence of an influence of the spectral quality of light on testicular recrudesence in *Anolis carolinensis*. Other possible influences of the spectral quality of visual light are discussed by Regal (this volume).

The influence of wind gusts on the activity of *Sceloporus* was observed by Jackson (1974). He suggests that these lizards change perching sites to increase their predatory surveillance area and that they make these site changes during gusts of wind when they may be less subject to predation because their movements would be less conspicuous.

Thermoregulation

Since the landmark study of Cowles and Bogert (1944), reptilian thermoregulation has been intensively studied. It is clear now that most lizards, given an environment with some thermal diversity, are capable of regulating their body temperatures at levels appropriate to their individual physiological or ecological circumstances. Few biologists today would ignore this aspect of an experimental setting. Nevertheless, there are studies which have mistaken metabolic inactivity for an inability to learn (Brattstrom, 1974; this volume). A similar potential source of error may be encountered in neurobehavioral investigations. Damage to the parietal eye, an often-used surface landmark overlying the forebrain of many lizards, may cause aberrations in behavioral thermoregulation (Roth and Ralph, 1976). Berk and Heath (1975) have cautioned investigators that, since there is an elaborate central neural network involved in thermoregulation, lesion studies might confound behavioral deficits with thermal torpidity.

The thermal requirements of lizards are not simply satisfied by keeping them at any "ideal" temperature. As Regal (1968) has observed, keeping some lizards cool for extended periods does not necessarily compromise their health. Given a diversity of thermal gradients, they will demonstrate circadian thermophilic tendencies. Wilhoft (1958), however, has demonstrated that housing lizards at their "preferred" temperatures may lead to thyroid hypertrophy and eventually death.

The thermal biology of lizards is sufficiently understood to allow the laboratory maintenance of many species. There are, however still serious deficits in our knowledge about the differential effects of heat and light, time sharing of thermal resources, and the relationship of heat seeking to energy budgets, arousal and activity (see Regal, this volume). In *Lacerta* freshly received from the field and in those kept at low temperatures in the laboratory, Boycott and Guillery (1959) have observed cerebral changes that resemble those noted by Cajal in the brains of hibernating reptiles. These changes take 1 to 4 weeks to develop and are reversible, and it is not certain that the cytological effects

of cold can be dissociated from the effect of cold on activity (Boycott, Gray, and Guillery, 1961). Daily variations in low temperature tolerance (indicated by a loss of the righting reflex) were described by Spellerberg and Hoffmann (1972), who attributed the changes to short-term acclimation during the cold night hours as well as an endogenous daily rhythm.

Cabanac (1971) observed that body temperature and arousal are so intimately related as to require a knowledge of the animal's internal state when considering its responses to various stimuli. He has ventured the term "alliesthesia" for the phenomenon of changing stimulus value with variations in the animal's internal state. For example, Garrick (1974) has observed that the selection of body temperature by two species of lizard is affected by the animals' reproductive and hormonal state. Other species respond to bacterial infection by selecting warmer microhabitats and effectively developing a "fever" (Kluger, Ringler, and Anver, 1975) which may be important to survival (Bernheim and Kluger, 1976).

In a study of blue spiny lizards, thermal radio transmitters were used to monitor the lizards' body temperatures during various activities (Greenberg, 1976a). It was of interest that these lizards basked until their body temperatures attained the maximum voluntary level, after which they were relatively passive in regard to the thermal qualities of their microhabitats (Fig. 7). This suggested that after an initial "warming up," behavioral thermoregulation would not compete with or complicate an interpretation of subsequent activities. Such a eurythermic species seemed at first to be an ideal laboratory subject, until the body temperature correlates of feeding and foraging were analyzed (Fig. 8).

Feeding occurred across a wide range of body temperatures, but foraging occurred in a relatively narrow range of elevated body temperature. It is reasonable to assume that a lizard would be both a better predator, as well as a less vulnerable prey, if it limited forays to times at which body temperatures
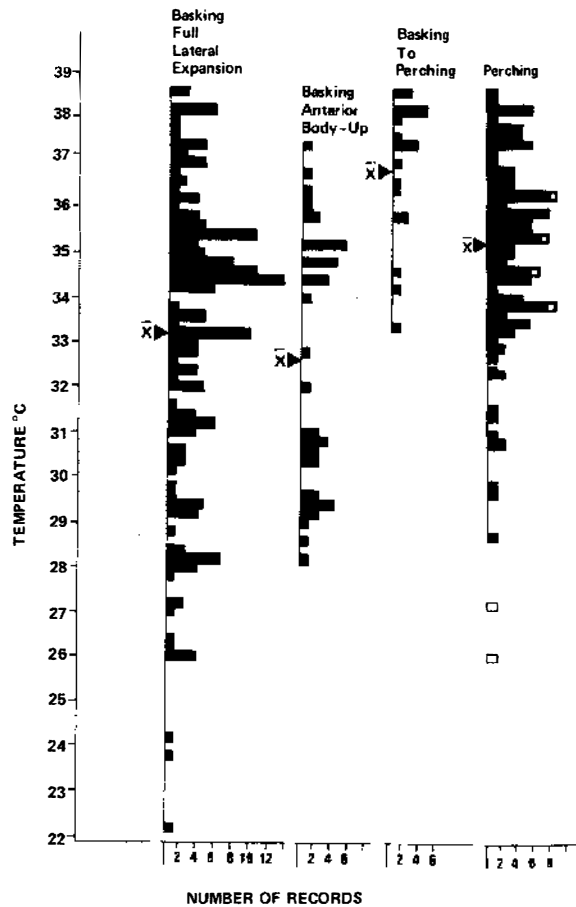

Figure 7. The body temperatures associated with two basking postures, the transition from basking to perching, and the perching "range." Most basking and all other temperatures were obtained by use of temperature sensitive miniature radio transmitters implanted in three lizards. (Adapted from Greenberg, 1976a).

are elevated to levels conducive to both maximum alertness and action.

These observations suggest that if one provided only the minimum conditions necessary to keep a lizard feeding well and apparently healthy, one might be misled in an interpretation of spontaneous activity.

Basking and Perching

Basking is a commonly employed thermoregulatory behavior among diurnal lizards. It can be defined as an activity in which
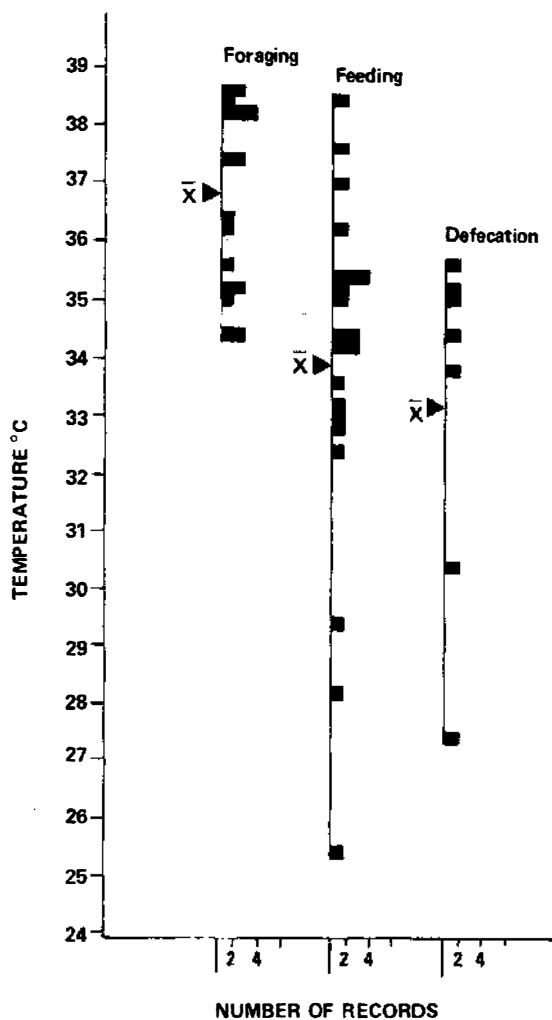
Figure 8. The body temperature correlates of sit-and wait feeding (predation from the perch) and foraging.

tures when orienting to a photothermal source—clinging, for example, to rock prominences or shelves to expose their dorsum to the light.

The postures employed when perching are more suggestive of readiness for rapid action than those of basking. A relative insensitivity to stimuli in basking lizards was noted by Rand (1964) for *Ameiva*, Bartholomew (1966) for the Galapogos marine iguana, *Amblyrhynchus*, and Anderson (personal communication) for two species of *Sceloporus*. That lizards respond to stimuli more readily when in the perching posture is indicated by an analysis of the feeding and foraging episodes that occurred during basking or perching (Table 1) (Greenberg, 1973b), During basking, relative immobility would make exposed lizards less attractive to predators.

The postural distinction between basking and perching may vary considerably among species, but familiarity with the differences may be useful in making observations on levels of arousal, activity, and alertness.

Food and Water

Most knowledge of lizard feeding habits is derived from gastric or scat analyses (for example, Fitch, 1954; Knowlton, 1938; Blair, 1960) and occasional observations of predatory encounters. There is only scant information about the drinking habits of lizards. One suspects that these aspects of a lizard's life are among the most sensitive to the "observer effect." The cues that may draw a lizard into a drinking or feeding situation are not understood, but prey movement, sound, odor, or the feeding activity of congeners are probably important. *Anolis carolinensis* typically requires a dew-like coating from which water may be licked, while *Sceloporus cyanogenys* may learn of available water only by moving drops or ripples.

Freedom from the need to search for food has been implicated as a factor contributing to abnormal behavior in some small captive

lizards expose themselves to the sun (heliothermy) or some other thermal source and assume postures or orientations which maximize the rate of heat gain. Since basking behavior can vary with the habitat and with the lizard's physiological requirements, it is unlikely that all lizards must necessarily bask in order to become active (Regal, this volume).

The blue spiny lizard and rainbow lizard use distinctive postures when they find sources of thermal reinforcement (Figs. 9, 10). They sometimes get into awkward pos-
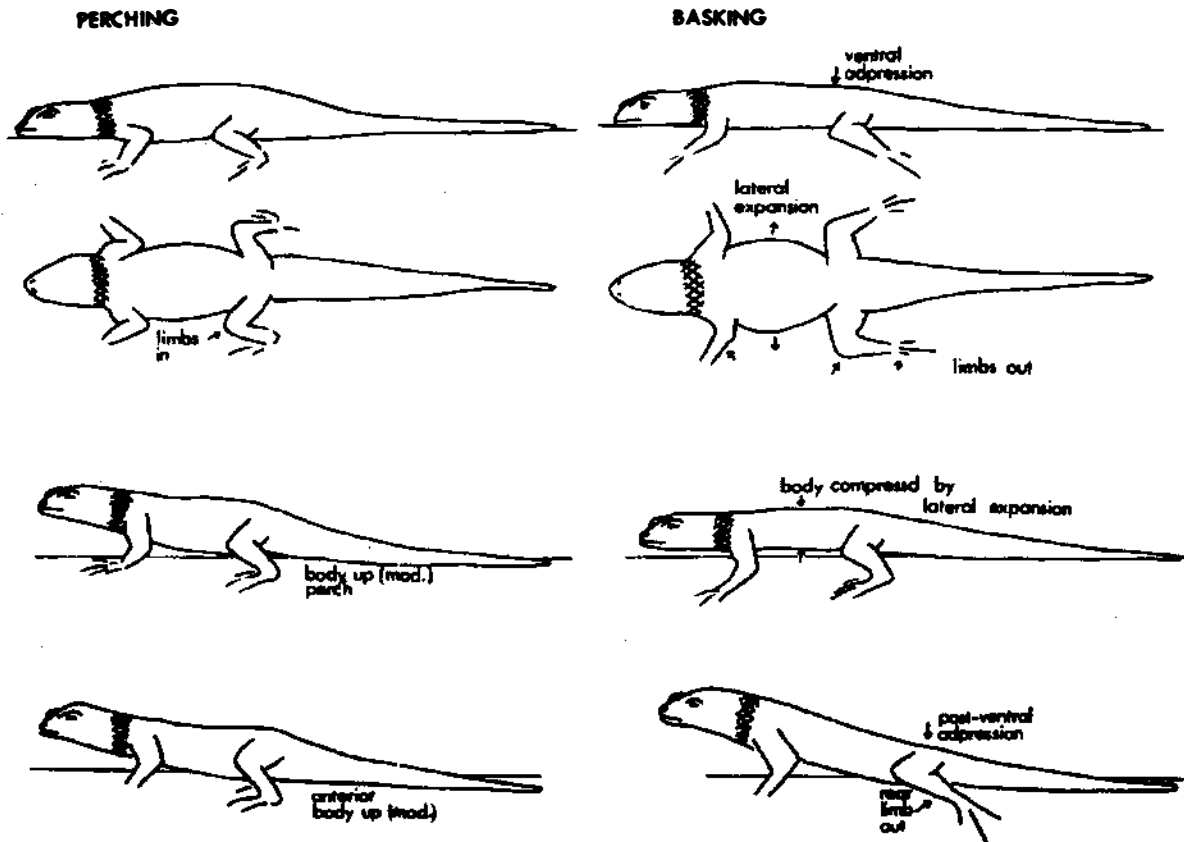
Figure 9. Basking and perching postures in the blue spiny lizard have been operationally defined. When basking, the profile of the body is expanded and the legs are out; in perching, the limbs are closer to the body in a way that suggests readiness for rapid action.

animals (Kavanau, 1967). in my present studies, lizards in colonies are initially fed a variety of prey. *Tenebrio* larvae, pupae, and adults, crickets, sweep-net contents, and an occasional neonatal mouse are provided on an irregular schedule in order to provide a variety of prey types (and prey behaviors) to induce lizards to explore their habitats in a natural way.

Sceloporus cyanogenys are more likely to feed or forage during perching than basking (Greenberg, 1973b, 1976a). Feeding episodes that are initiated from the perch occur when a lizard perceives prey (or another lizard) moving in its surveillance area. At times, in the absence of moving prey, a blue spiny lizard will spontaneously begin a foray, alerting it to prey that would otherwise be ignored. For example, nonmoving *Tenebrio*

pupae would be nudged until they twitched, and then quickly eaten (Greenberg, 1977a). A foraging lizard will always attack prey.

Another consideration in the interpretation of predatory aggression is social feeding (Greenberg, 1976b). In some situations, perching lizards, watching each other as well as looking for prey, will be guided to a feeding site by the activity of congeners, or be stimulated to search their habitual feeding sites by the sight of a feeding congener. Food stealing is a common social interaction at feeding sites and may be a source of information about novel prey. Large prey will be shared when attempted stealing results in a pulling contest that rends the prey.

Deference to dominants at a feeding site, or an apparent reluctance to be active near a dominant, can compromise the activity of
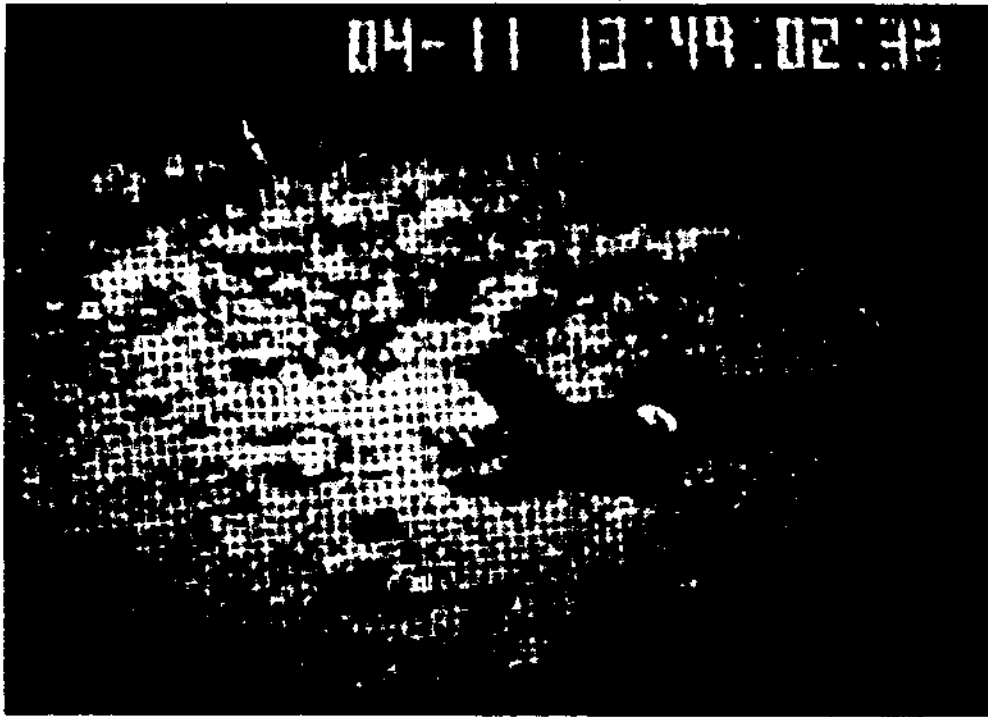
Figure 10.   Photo of CCTV frame of the legs-out component of the basking posture in *Agama*.

some lizards. Juveniles, however, rarely show such reluctance and may in fact be the initiators of a feeding episode.

Dietary supplements are often employed to compensate for the deficiencies inherent in diets of limited prey types. Of these supplements, calcium may be the most important. Changes in activity may occur because of inadvertant dietary deficiencies. For example, there is an increase in activity observed in fowl deprived of calcium and sodium (Hughes and Wood-Gush, 1973).

Use of Shelters

The shelter appears to be more than a mere site of sequestered rest, a hiding place from potential predators or aggressive conspecifics, or protection from environmental extremes. The availability of shelter has been shown to have a function in the normal expression of circadian thermal activity (Regal, 1968). At certain times, the crevice-

dwelling blue spiny lizard will defend a crevice as a territory. Excluded individuals have been observed burying themselves in loose substrate (Greenberg, 1973a).

Blue spiny lizards will occasionally bask inside their shelter, sometimes orienting to a thin shaft of light and at other times pressing their backs to a warm overlying rock shelf. Such "covert basking" is not uncommon; it has also been observed in *Gehyra* (Bustard, 1967), *Dipsosaurus dorsalis* (DeWitt, 1971), and even in the usually arboreal *Anolis nebulosis* (Jenssen, 1970a). Perching just inside the threshold of a shelter, alert for prey or social activity, was often observed. The pattern of shelter utilization seemed to reflect the social organization of the population. Some lizards were consistently more exposed than others.

These data indicated that observations of activity within a shelter would be of value. To make such observations of the blue spiny lizard, the "shelter column" enclosure was developed. This habitat was constructed to

Table 1: The context in which blue spiny lizards fed, foraged, or were aware of prey but made no move to feed. Based on 238 observations of a four lizard population in a large complex habitat. The ratio of daily time spent in basking versus perching is about 1:3, but the ratio of feeding episodes initiated during basking versus perching is about 1:5, and for foraging the ratio is about 1:10

	BASKING full-body	BASKING anterior body up	COVERT PERCHING	PERCHING	FORAGING	OTHER	(n)
DOMINANT MALE							
FEEDING	6.5	4.3	19.6	56.5	13.1	0	(46)
FORAGING	6.2	3.2	25.0	62.5		3.1	(32)
AWARE OF PREY	25.0	0	0	75.0	0	0	(4)
SUBORDINATE MALE							
FEEDING	16.7	12.5	0	54.2	16.7	0	(24)
FORAGING	0	9.4	3.1	84.4		3.1	(32)
AWARE OF PREY	11.1	11.1	11.1	55.6	0	11.1	(9)
FEMALE							
FEEDING	9.5	9.5	9.5	42.9	28.6	0	(21)
FORAGING	0	9.4	3.1	84.4		3.1	(14)
AWARE OF PREY	22.2	0	22.2	55.6	0	0	(9)
FEMALE							
FEEDING	0	11.1	5.5	72.2	11.1	0	(18)
FORAGING	8.3	4.2	16.7	62.5		8.3	(24)
AWARE OF PREY	20.0	40.0	0	40.0	0	0	(5)
CUMULATIVE							
FEEDING	8.3	8.3	11.0	55.9	16.6	0	(109)
FORAGING	3.9	4.9	14.7	71.6		4.9	(102)
AWARE OF PREY	14.8	14.8	11.1	55.5	0	3.7	(27)

reveal in an ant-nest fashion the inner recesses of a saurian shelter (Fig. 11).

The findings depicted in Figure 12 suggests that only the dominant male conforms to the often reported—almost classic—activity profile for diurnal lizards; the subordinate male and female were more variable in their behavior. It is also important to note that there were no overt agonistic social interactions that led to this pattern, and the environmental temperatures never reached aversive levels.

Lizards typically "slept" with their heads wedged tightly into the angles of the crevices (Greenberg, 1971). Animals were generally more alert on the wider parts of shelves. This apparent alertness seemed to follow a diurnal pattern suggesting a circadian variation in thigmotaxic tendency (Fig. 13).
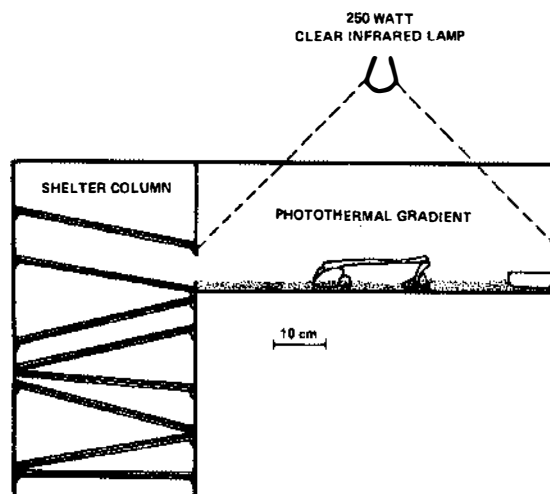

Figure 11. This habitat reveals in bee-hive fashion the inner recesses of a shelter. Observations suggested important differences in the way different members of the population utilized their space.
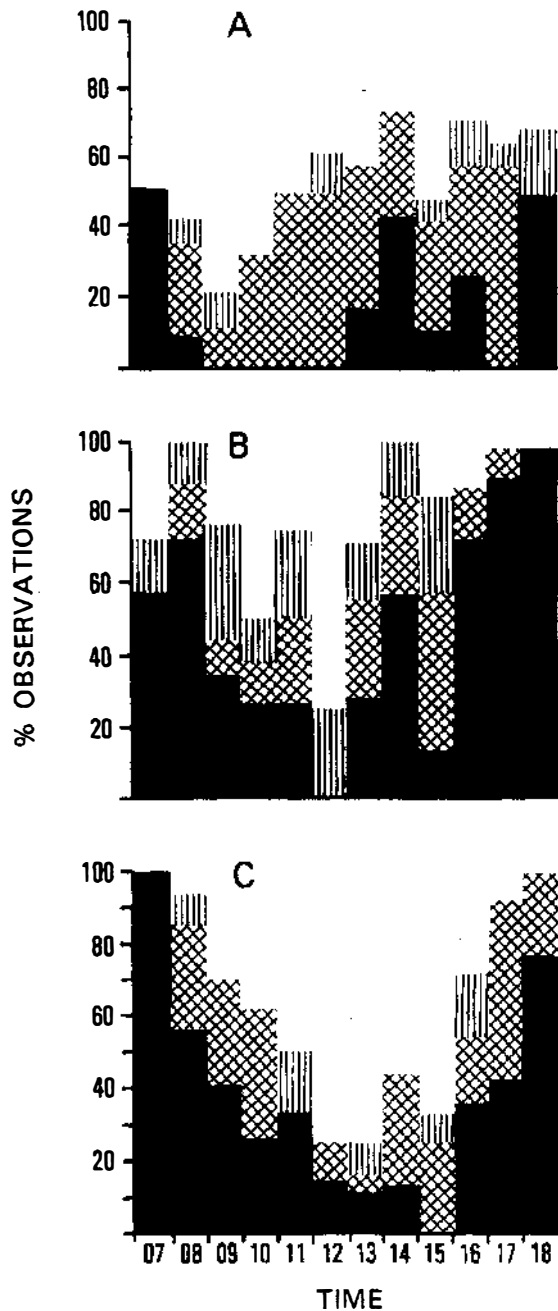
Figure 12. The proportions of the kinds of activities observed within the shelter for subjects A (female), B (subordinate male), and C (dominant male). The dark portion of each bar = sleeping or quiescent animals; the hatched portion = animals are active on or between shelves; the striped portion = time spent surveying the habitat from within the shelter ("covert perching").

These observations make it clear that, in an experimental design concerned with activity levels, one must also consider activity that may occur in microhabitats normally concealed from the observer.

Social Behavior

In his study of *Anolis nebulosus* ethoecology, Jenssen (1970a) used crowded conditions to "catalyze" social interactions. He was confident that the motor patterns exhibited under these conditions were essentially the same as those seen in nature, although the frequency of displays was probably abnormal.

The behavioral or perceptual space of a laboratory habitat can affect some lizards in unexpected ways. In some cases small enclosures in which lizards are continually exposed to one another will diminish interactions. Mayhew (1963a) observed that a large and a small *Amphibolorus pictus* cohabited peacefully in a small enclosure, but when both were transferred to a larger vivarium, the large male vigorously pursued the smaller animal. Mayhew proposed that the small enclosure inhibited the normal expression of territoriality.

I have observed the same phenomenon in a colony of *Agama agamas*. Harris (1964) observed that some *Agama* males are "repressed" by the presence of a dominant male, made conspicuous by its bright red head. Perhaps such a "repression" exists in small laboratory habitats where lizards are continually exposed to dominants. Repression may then abate under less restrictive conditions in which the smaller lizard may develop territorial habits that elicit aggressive responses in the dominant.

In nature, environmental influences on aggression in lizard populations are not uncommon. Many lizards that are mutually intolerant under normal conditions will aggregate during adverse weather or at night (Evans, 1967, in *Coleonyx;* Curry-Lindahl, 1957, in *Agama cyanogaster;* and Regal, 1968; in *Klauberina*), or at sites hav-
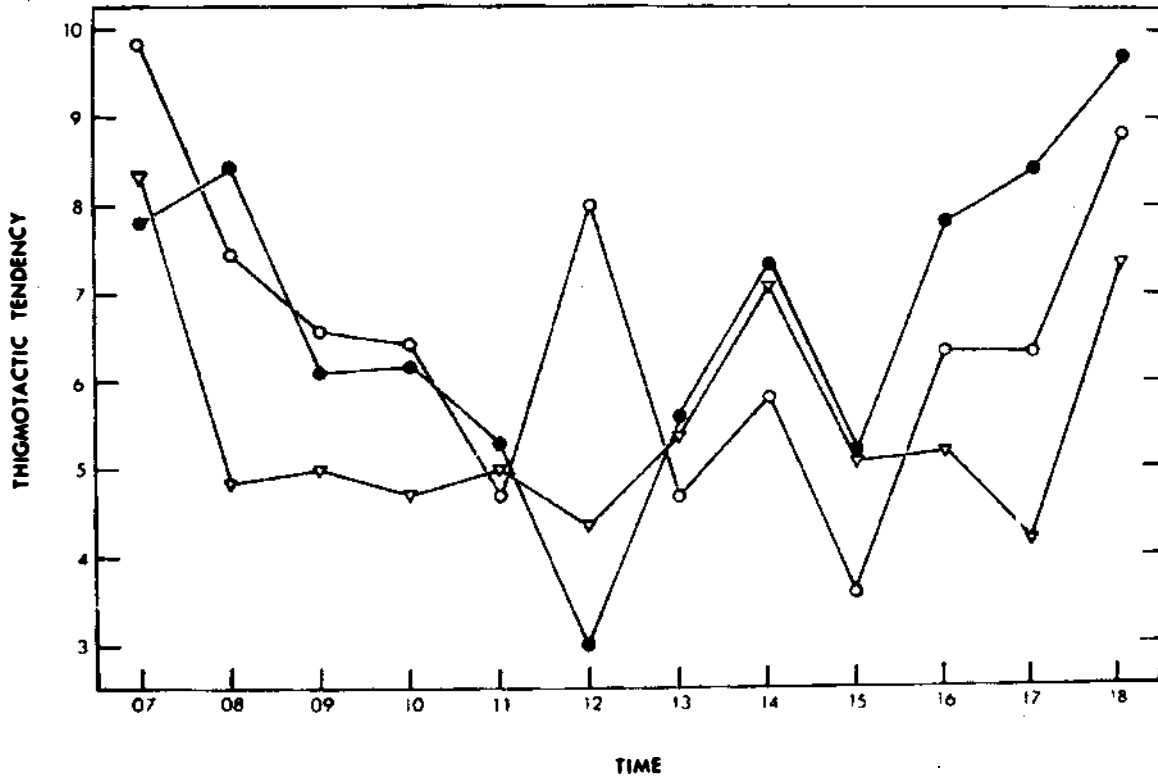
Figure 13. The curves for three lizards suggest a diurnally varying thigmotactic tendency. Lizards were scored on the basis of posture and activity—with the highest score going to sleeping animals with their heads wedged into crevices. Triangle = female, closed circle = subordinate male, and open circle = dominant male.

ing an abundance of prey (Evans, 1951; Fitch, 1940; Norris, 1953).

Social behavior has received much attention by students of saurian behavior—possibly because of the early attention drawn to the work of Noble and Bradley (1933) by Lorenz (1935). Since Carpenter's (1962) introduction of the "display action pattern" analysis display activity has been subject to intense research (Jenssen, this volume).

Context is of importance in an interpretation of either arousal (operationally defined by postures and activities) or the communicative significance of a display. W.J. Smith (1969) points out that since there are more functions served by displaying than there are displays, recipients of displays must rely heavily on contextual information. The possibility of a discontinuity in the physiological causation of superficially simi-

lar displays that appear in various contexts must be considered.

A prevalent view is that the bobbing displays of iguanids include two types which represent a continuum of "intensity" (Carpenter, 1967). These displays are designated "assertive" and "challenge"; the former is performed in social and nonsocial situations and may be elicited by a broad range of stimuli; the latter is performed as part of ritualized territorial defense. The possibility of a gradient between these displays recalls Moruzzi's suggestion that different responses are possible at different arousal levels (cited by Andrew, 1974). Stamps and Barlow (1973) have analyzed the display behavior of *Anolis aeneus* and observed that while some components may indicate a gradient of "intensity" between displays, in general, no smooth continuum exists between the

"challenge" display (Gorman, 1968) and the lower intensity "fanbob" that they observed.

In my observations of blue spiny lizards, a discontinuity of display "motivation" was suggested by the finding that assertive displays varied greatly in intensity and were often performed with much more vigor than many challenge displays.

An analysis of the conditions in which assertive displays occur suggests that the only thing that they all have in common is a clearly elevated level of arousal—at least in terms of sensitivity to peripheral stimuli (Table 2).

The appearance of an assertive display during foraging illustrates the importance of the experimental habitat for the eliciting and subsequent functional interpretation of social displays.

SOCIAL CLUES ABOUT THE CAUSATION OF BEHAVIOR

Manning (1967) regards the species differences in the head-bobbing patterns of *Sceloporus* described by Hunsaker (1962) as an elegant example of gene control of

changes affecting thresholds within the nervous system. An analysis of display behavior may be of value in suggesting hypotheses about the neurophysiology of displays if sufficient information about different species is obtained to suggest how displays have evolved.

Display is often the most dramatic behavioral pattern with which ethologists deal. It is probably at the end of a continuum of homologous behavioral patterns that begins with less striking behavior, such as locomotor intention movements (Daanje, 1950) or somatic or autonomic responses (Morris, 1956). We may ask with Barlow (1968:227) —do shared effectors mean shared central nervous system mechanisms? If we think that they might, ideas about the different functions of homologous behavioral patterns might yield important clues about the neural aspects of ritualized behavior.

Consider the head nodding of an iguanid in terms of conflicting components of autonomic stimulation. I have observed an exchange of signals in blue spiny lizards (Greenberg, 1973a, 1977a) that suggests that the nod may represent an alternating pattern of fear and aggression: Every time a dominant

Table 2: The contexts in which the "assertive" display of the blue spiny lizard is observed. About 75 percent of the display were in nonsocial contexts.

	Female	Male	% of Total Assertive Displays	(n)
NON-SOCIAL				
SPONTANEOUS	100.	00.0	09.0	(7)
AFTER MOVEMENT DURING FORAGING	52.6	47.4	25.3	(19)
AFTER ATTAINING PERCH	14.8	85.2	36.0	(27)
DURING EMERGENCE	00.0	100.	02.6	(2)
SOCIAL				
RESPONSE TO ACTION OR APPEARANCE OF ANOTHER LIZARD	80.0	20.0	20.0	(15)
IMMEDIATELY AFTER SOCIAL INTERACTION	00.0	100.	06.7	(5)

raised its head, revealing its signal blue color, the subordinate lowered its head in apparent submission. In other species also, dominant lizards characteristically elevate their heads when aroused, and subordinate lizards lower their heads to the substrate (Carpenter 1967:99). These are the same patterns seen in lizards when exploring or when making themselves inconspicuous.

Or consider the origin of the profile changes of an aggressive lizard in terms of thermoregulation—the expansion of the surface area of the body and hence the solar interface. *Phrynosoma* (Milne and Milne, 1950), *Uma* (Carpenter, 1963), *Amphibolorus barbatus* (Brattstrom, 1971), and *Leiolepus belli* (Regal, personal communication) use a similar kind of posture in thermoregulation as in a show of aggression.

The tail-lashing "attention-getting" of the female blue spiny lizard is remarkably like that of the tail-to-side reflex in mating (Fig. 14). It recalls the "rejection" movements of *Sceloporus undulatus* (Carpenter, 1962), the tail lashing of "excited" *Amphibolorus* (Mayhew, 1963a), and the stalking of *Anolis* lizards (Ruibal, 1967; Jenssen, 1970a). How

are such motor patterns brought under more and more specific stimulus control?

Might the tail-in-the-mouth minuet of the blue spiny lizard (Fig. 15) be related to the
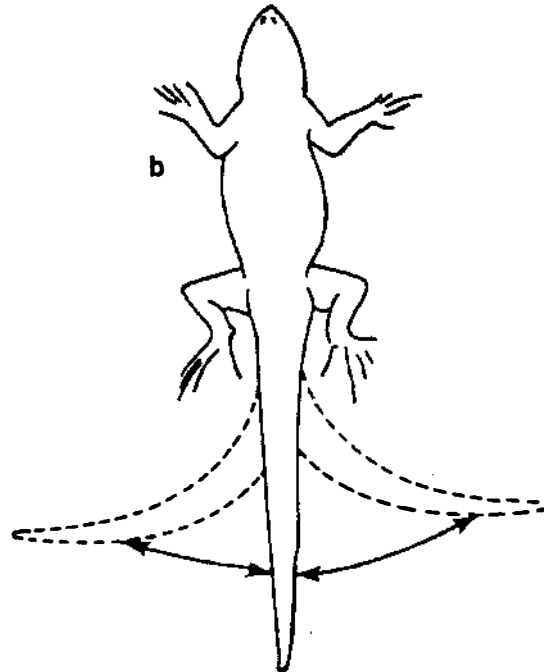

Figure 14.   The tail-lash pattern of the female blue spiny lizard.
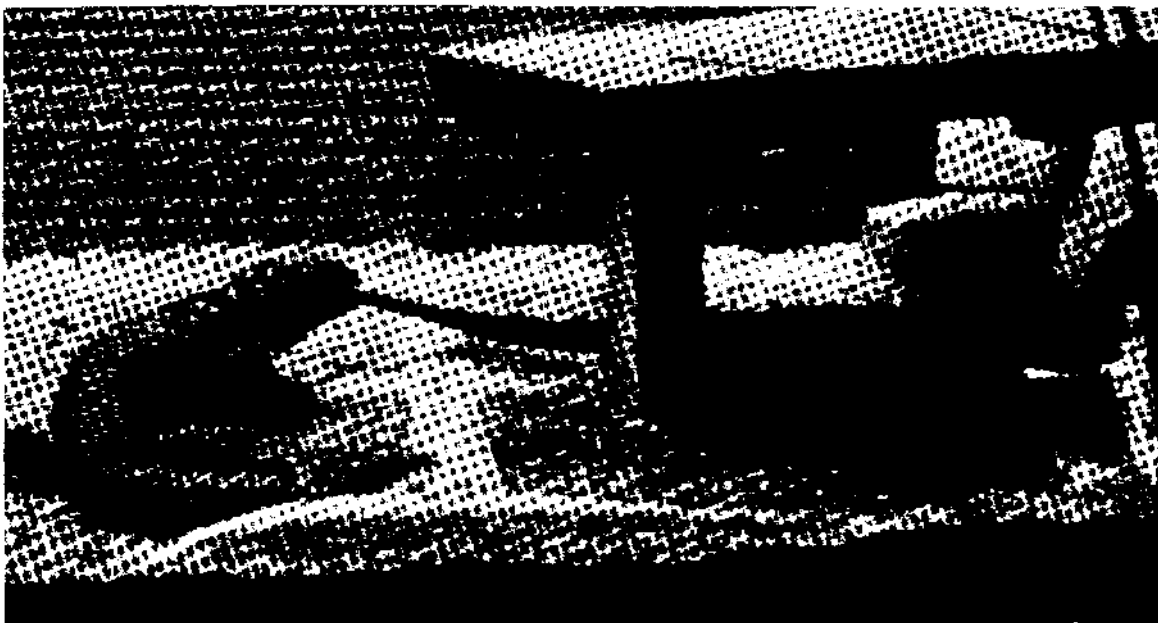

Figure 15.   The tail-grip courtship ritual of the blue spiny lizard.

tail-biting aggression so familiar to observers of iguanids, or to the tail-tasting form of sexual discrimination employed by *Coleonyx* (Greenberg, 1943)?

I have observed an increase in the frequency of "exploratory" tongue-touching of *Anolis carolinensis* when in a new habitat. This is much like the tongue-touching of the substrate by *Sceloporus iarrovi* in novel situations (DeFazio et al., 1976). Might the tongue-touching seen in other species under other conditions be a "displacement" derivative of such behavior—for example, the tongue-touching used in the reinforcement of social status by the *Amphibolorus barbatus* (Brattstrom, 1972) or the tongue-touching that I have seen during the aggressive display of *Agama agama?*

Anolis carolinensis are occasionally observed engaging in social grooming during shedding (Fig. 16). Might this behavioral pattern be comparable to the ectoparasite "grooming" of young *Iguana* (Burghardt, 1975) or to the food-stealing so often observed during social feeding of blue spiny lizards (Fig. 17) and green anoles (Greenberg, 1976b)?

Although these suggested relationships are hypothetical, they may be of value in providing clues about the underlying organization of behavior. Particularly, the mechanisms by which autonomic reflexes and fragments of motor patterns become elaborated and progressively brought under the control
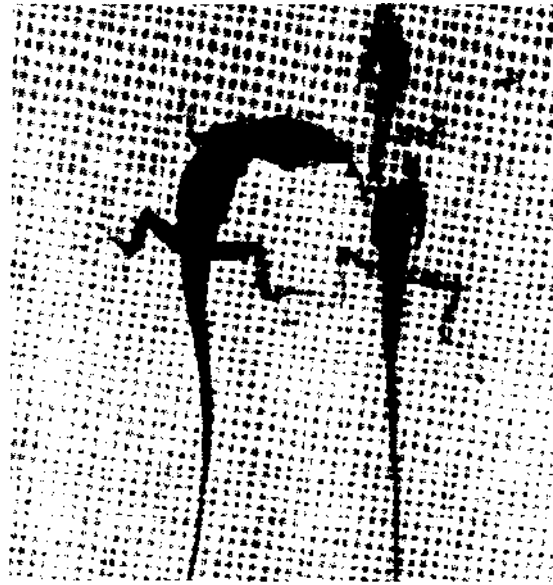

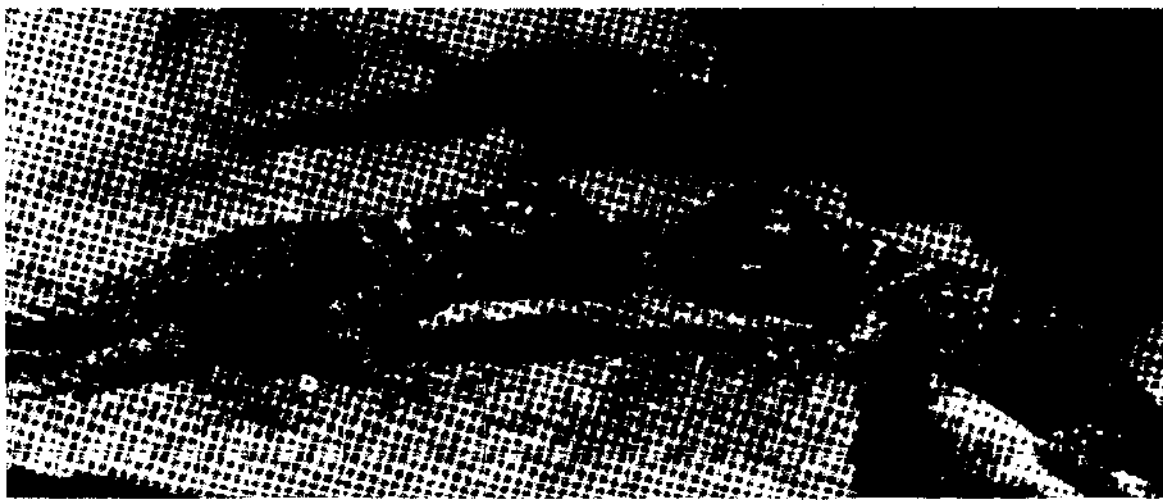Figure 16. *Anolis carolinensis* allogrooming.

Figure 17. Blue spiny lizard hatchlings tug-of-war with mealworm.

of higher neural structures and more specific external stimuli. They also illustrate the diversity and complexity of the behavioral patterns of lizards that make these animals such fascinating subjects for ethological investigations. A researcher need only shed his preconceptions to appreciate the uniqueness of each species and its exquisitely tuned eco-evolutionary adaptations.

ACKNOWLEDGMENTS

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DISCUSSION

PETERSON to GREENBERG: Regarding naturalistic settings, it is important to realize that there are some problems that only a simplified laboratory setting can deal with. For example, natural settings exaggerate the possibility that an experimental effect may be overlooked. This is because in a complex environment the brain can compensate for some kinds of deficits, but in an unnatural laboratory setting the animal may be compelled to live in a certain way and this can be very revealing. For example, Schneider's tectal lesioned hamsters looked normal in some environments but an important deficit showed up in others. There is also the possibility of misinterpreting a deficit. For example, in 1970 Humphrey (BBE 3:320–337) dispelled the old belief that primates with striate cortex lesions are blind. In an unnatural setting he was able to show that the deficit is really one of recognition.

GREENBERG: your point is good about the difficulty of interpreting behavior in complex settings. The main thing is to have a reasonable idea of the normal behavior of the animal. Without such an idea you may find yourself investing considerable effort in investigating a laboratory-induced pathology of relatively limited interest. Once a naturalistic overview is obtained one could successively simplify experimental habitats until an appropriate one for the experiment is obtained. Also, naturalistic observation may reveal behavioral patterns that you might otherwise be totally ignorant of.

REGAL to CREWS: This research contributes to our understanding of the process of sexual selection. I think the difference between emergence of males and females might relate to the fact that it is to the female's advantage to let the subordinate males get "weeded out" so that, when the female finally selects a male, it is a male with a superior genetic constitution (a territory-holding male) who has possibly selected a better habitat. In any event, the chosen male has won out in some sort of competition and presumably would give her superior male offspring, etc.

CREWS: I believe females are presented with two different types of choices in terms of sexual selection. First, when the female emerges from winter dormancy, she must establish a home range; this choice is probably determined by a combination of habitat preferences and some aspect of the male in whose territory she will reside. Second, male choice is perhaps more important for the transient female who moves about the habitat. This would be especially important when the female has a large, preovulatory ovarian follicle—which male does she choose to mate with?

MacLEAN to CREWS: Can you keep animals cycling year round with the environmental conditions you have described?

CREWS: Female *Anolis carolinensis* will go through at least three complete ovarian cycles (ovarian quiescence, recrudescence, breeding, and regression) under this environmental regimen in a one-year period. Within each reproductive phase, females will usually go through at least ten estrous cycles and sometimes lay up to 15 eggs before the ovaries regress.

MACLEAN: What other lizards have this sort of an estrous cycle?

CREWS: Most temperate species that I am aware of are single or multiple-clutch layers; that is, they only exhibit one or two estrous cycles, after each of which they lay a clutch of eggs. All anoline lizards, however, exhibit the pattern of ovarian activity I have described here.

GARRICK to CREWS: Is there any evidence for hormone-brain interactions in some of these behaviors that you observed?

CREWS: We have recently begun an investigation of the neural and hormonal determinants of sexual behavior in reptiles.

PETERSON: I would like to expand on a point raised by Dr. Brattstrom, namely, that learning may play a more important role in the normal behavior of lizards than has heretofore been suspected. One gets the impression, both from remarks made at this conference and from an examination of the behavioral literature, that data on lizards gathered from the learning laboratory are

somehow irrelevant to the behavior of these animals in the wild. I believe that such an attitude may be misguided. Over the last 10 years, a body of literature has emerged from the learning laboratory which indicates quite clearly that lizards are capable of a wide variety of learned behaviors. It is difficult for me to understand just how the ability could have evolved in the first place were it not exhibited by animals in the wild.

In this connection, it is important to understand that the paradigms studied by comparative psychologists are not simply laboratory curiosities but are, at least in many cases, representative of situations encountered routinely by animals in their normal habitats. For example, the paradigm known as passive avoidance learning refers to a situation in which an animal learns to withhold a response—under certain stimulus conditions—which otherwise has a high probability of occurring. This is precisely the kind of behavior which underlies the putative success of the Batesian mimic. Another example would be the capacity for "latent learning" as discussed by Dr. Brattstrom. Recently, Philabosian has suggested that this type of behavior may occur in *Anolis cristatellus*. The point is that one cannot safely ignore the implications of these laboratory studies on lizards—that is, that learning may play a significant and unsuspected role in the naturally occurring behavior of this very successful vertebrate group.

I would also like to suggest that it may be productive to think of learning ability (or, more properly, abilities—since there are many different types of learning) as an evolutionary strategy which may affect the survival of a species just as, for example, the tendency to develop digital lamallae or species-specific displays. Like any character, certain lineages should exhibit more highly developed learning capabilities than others —and it may be possible to relate this differential distribution of learning ability to either taxonomic status or type of niche utilization. For example, large predatory lizards, especially opportunistic hunters such as *Varanus komodoensis* described by Dr. Auffenberg might be expected to rely more heavily on learned behaviors than lizards which occupy a highly structured, relatively invariant, behavioral niche. Whatever the distribution of learning ability across lizard species, it is reasonable to expect that such a capability will play a role in the naturally occurring behavior of lizards and in the adaptive success of certain Saurian taxa.

HEATH to REGAL: Why couldn't a reptile just develop an unusually large heart for its size? Reptiles are generally small-hearted. This is a path that they could follow. Increased perfusion of the tissues can be accomplished by increasing capillary diameters as well.

REGAL: Increasing size will not increase efficiency, and efficiency is what might count in competition between two or more otherwise comparable species. I would have to have data on what the benefits would be of enlarging an "inefficient" heart relative to the costs. We lack the data to answer your question.

GANS: At an equivalent temperature, reptiles have a lower metabolic rate than birds or mammals. So one could raise a larger herd of dinosaurs on a pasture of land than a herd of cows. Ectotherms can maintain more mass on an equivalent energy input.

REGAL: Yes, I agree that there are distinct advantages to ectothermy just as there are to endothermy and I believe that we should spell these out.

GANS: Crocodilians have essentially four-chambered hearts, and yet their metabolic rates are still low. This illustrates that there are advantages to ectothermy. Reptiles can maintain a larger biomass than mammals on an equivalent amount of food as long as it is possible for them to get away with paying the price, which may be resigning themselves to basking or sit-and-wait predation, or whatever.

REGAL: Yes. I see no reason why endothermy should *automatically* be selected for because of a four-chambered heart. The heart simply *allows* selection for intense activity strategies to proceed and the species may be superior in competition of the appropriate sort.