

University of Tennessee, Knoxville Trace: Tennessee Research and Creative Exchange

Ecology and Evolutionary Biology Publications and Other Works

Ecology and Evolutionary Biology

January 1992

The Saurian Psyche Revisted: Lizards in Research

Neil Greenberg University of Tennessee - Knoxville, ngreenbe@utk.edu

Follow this and additional works at: http://trace.tennessee.edu/utk_ecolpubs Part of the <u>Behavioral Neurobiology Commons</u>, <u>Medical Sciences Commons</u>, and the <u>Psychology Commons</u>

Recommended Citation

Greenberg, Neil, "The Saurian Psyche Revisted: Lizards in Research" (1992). *Ecology and Evolutionary Biology Publications and Other Works*. http://trace.tennessee.edu/utk_ecolpubs/18

This is brought to you for free and open access by the Ecology and Evolutionary Biology at Trace: Tennessee Research and Creative Exchange. It has been accepted for inclusion in Ecology and Evolutionary Biology Publications and Other Works by an authorized administrator of Trace: Tennessee Research and Creative Exchange. For more information, please contact trace@utk.edu.

Adapted from a presentation at the National Conference on The Care and Use of Lower Vertebrates in Research, New Orleans, Louisiana, April 8-9, 1991

published in *The Care and Use of Amphibians, Reptiles, and Fish in Research* D.O. Schaeffer, K.M. Kleinow, L Krulish, editors. Scientists Center for Animal Welfare, Bethesda MD 1992. pp 75-91.

THE SAURIAN PSYCHE REVISITED: LIZARDS IN RESEARCH

Neil Greenberg

Department of Zoology and Graduate Program in Ethology University of Tennessee, Knoxville

PROLOGUE

This essay is intended to guide researchers interested in lizards as prospective experimental models to identify an appropriate species for their research needs and to care for lizards in a manner that will not compromise their utility. Coupled with these is a concern for critical thinking about the <u>ethical</u> dimension of lizard research, one guide for which is to consider the intersection of <u>human needs</u> and <u>lizard needs</u>.

Before proceeding further, several arbitary premises must be made clear:

1. While wholly deserving of study because of their intrinsic interest, I will assume that the lizard research to be undertaken is to obtain information that has generality and utility that transcends the species involved. That is, the information possess <u>external</u> <u>validity</u> potential applicability beyond the particulars of the individuals under study and the study environment; such data would contribute to the solving of more general problems.

2. We are concerned with <u>animal welfare</u> rather than <u>animal rights</u>. The failure to distinguish these two issues, concerned respectively with the reduction of pain and suffering on one hand and the possession by animals of rights comparable to those of humans, is a significant source of confusion (**Schmidt 1990**).

3. We are concerned with <u>research</u> rather than <u>testing</u>: the popular view of the scientist often confuses white_coated testers of toxicity with researchers in basic science. We are trying to attain original insights and advance basic knowledge, not set the agenda for commercial development or the limits for safe implementation.

Because of the great diversity of lizards and their life_styles, much of this review necessarily deals in generalities anchored in the specifics of my experience with a few iguanid species.

LIZARD NEEDS

The Species with the Right Stuff

Since traits do not exist in isolation, we seek the profile of a species that prominantly manifests the trait of interest while still being

manageable (see **Martin and Bateson 1986**:8_9). At the outset we must ask some key questions about our prospective research species: are they available? safe? visible? tolerant? reliable? (**Table 1**).

Table 1. ATTRIBUTES THAT DETERMINE THE UTILITY OF A SPECIES

LIFE HISTORY TRAITS (Is it diurnal or nocturnal? What is its structural habitat? Does it need cover or hibernacula? What habits vary diurnally, seasonally? Are there unusual nutritional or climatic needs? Does it live long enough?)

CONSISTENCY (Will the animals manifest the phenomena of interest under controlled conditions in a repeatable manner?)

GENETICS (Are the patterns of heritability of traits understood? Will it breed in captivity?)

AVAILABILITY (Is it accessible or available? Is it rare, "locally abundant," or common. At all seasons?)

SAFTY (Is the species aggressive? does it have offensive or defensive traits that intrude betweeen it and the researcher? Would it be dangerous if it escaped into the laboratory or local environment?)

VISIBILITY (Can it be seen easily, is it cryptic? secretive? Can it be discriminated from other individuals? can it be marked)

TOLERANCE (Is it tolerant of captivity, handling, or observation?)

MORHPOLOGY (Will it fit?)

ETHOLOGY (Can the psychological well being of a lizard and the normal expression of its life history attributes be accomodated by our research environment? Can needs for activity and exercise be met? Are there significant social needs?)

Once a lizard species has been identified as an appropriate model, we must consider a hierarchy of needs from basic physiology through safety, sociality, and reproductive success (**Table 2**). Researchers generally focus on only a fragment of an animal's life history, but animal needs are now understood to be so interwoven that we are generally aware that compromising one might invoke a stress response that could compromise all of them. This is particularly true in physiological research. Although a rapidly developing field, a valuable starting point is the excellent review by **McDonald** (**1976**). Husbandry practices for ectothermic vertebrates have been extensively reviewed by **Pough** (**1991**).

<u>Stress</u>. If one provided only the minimum conditions necessary to keep a lizard apparently healthy, many other dimensions of lizard biology might still be seriously compromised. The fundamental preliminary to all other needs is physiological homeostasis: the maintenance of an internal state that is stable within the range of variation an animal can experience before the physiological stress (adrenal activation) response is triggered. Within this range, animals can compensate with little or no energetic expediture, and the range is different for each of the many physiological processes that an animal must balance to maintain homeostasis. This range is also known as <u>physiological scope</u> and is to some extent subject to developmental and experiential modification. When internal or

environmental stressors force any of the animal's systems beyond its capacity to compensate, a comprehensive physiological stress response is engaged which involves an ensemble of coordinated physiological responses (**Greenberg 1990**). Clearly, a failure to provide for one stress_sensitive variable can affect other variables as the stress response ramifys throughout the organism. The stress response is energetically demanding and if sustained could lead to death, but it cannot always be assumed to be a deadly threat. Many elements of the physiological stress response are necessary parts of other essential systems, serving both somatic and neurobehavioral (psychoactive) functions (**Greenberg and Wingfield 1987**). The distinction between dangerous or potentially life_threatening stress and constructive uses of at least selected elements of the stress response is represented by the terms "distress" and "eustress."

Commonly, stressed animals can compensate for specific stressor by adopting a new behavioral or endocrine "tone" or baseline state involving changes in synthesis, secretion, binding, or receptiveness of target organs to stress_sensitive hormones. Examples would be the altered but stable endocrine profile of subordinate green anoles, <u>Anolis carolinensis</u>, (**Greenberg 1990**), or lizards subjected to frequent handling (**Meier et al. 1973**). Because of the responsiveness of dermal chromatophores to stress_sensitiove hormones, body color in many retilian taxa can provide important clues about internal state and its regulation (**Cooper and Greenberg 1991**, **Greenberg 1990**, **Hadley and Goldman 1969**).

Table 2. A HIERARCHY OF REPTILIAN NEEDS*

HOMEOSTASIS (Thermoregulation, nutrition, water balance)

SAFETY (predator evasion, hibernacula)

SOCIALITY (Is it social? When (daily, seasonally) does it engage in various activites (predatory behavior, social and reproductive behavior, migration for food or reproductive sites, torpor)

SOCIAL DOMINANCE (Does the animal manifest priority of access to valued resources?

REPRODUCTIVE SUCCESS (Fitness: how many offspring? how many successful relatives?)

*With apologies to Abraham Maslow

1. PHYSIOLOGICAL NEEDS

Homeostasis refers to the dynamic balance of mutually influencing physiological processes that is needed to maintain a stable inner environment. Key variables in this endeavor are nutrition and water, microclimate, and exercise.

Nutrition and Water

Most knowledge of lizard feeding habits is derived from gastric or scat analyses (for example, **Fitch 1954**; **Blair 1960**) and occasional observations of predatory encounters. There is only scant information about such habits, possibly because these aspects of a lizard's life are among the most sensitive to the "observer effect."

Blue spiny lizards are more likely to feed or forage during perching than basking (**Greenberg 1976**<u>a</u>). In the absence of moving prey, they may forage spontaneously, alert to prey that would otherwise be ignored. For example a motionless mealworm, <u>Tenebrio</u>, pupae, would be nudged until it twitched, and *then* quickly eaten (**Greenberg 1977**<u>a</u>). A foraging lizard will attack moving prey.

Social feeding. 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 stimulated by the activity 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 may 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 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 compensenate 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**).

Microclimate.

Light. 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) and 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, Rosenblatt, and Lehrman 1974), and possibly population density.

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, 1967, with mice; Regal 1967, with lizards). Dim light may cue a lizards'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 1976<u>a</u>), while other apparently rely on the penetration of morning warmth into their shelters (McGinnis and Falkenstein 1971; Bradshaw and Main 1968).

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**), particularly in hatchlings. Licht (1973) has found evidence of an influence of the spectral quality of light on testicular recrudesence in green anoles. Other possible influences of the spectral quality of visual light are discussed by **Regal (1978**). Further, light and heat may inreact in their influence on internal state (**Licht 1967**).

Temperature

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 using a diverse array of behavioral acts. In many resepcts, thermoregulation has become a model for approaching many kinds of regulatory processes (Greenberg 1978b) (Table 3). There is not, however, an "ideal" temperature for a lizard. Keeping some lizards cool for extended periods does not necessarily compromise their health (Regal 1968) whereas housing them at their "preferred" temperatures may lead to thyroid hypertrophy

Table 3. ELEMENTS OF THERMOREGULATORY STRATEGIES

BASIC THERMOREGULATORY STRATEGY

a. Conformer (conforms to external temperature)b. Regulator (seeks to alter internal temperature)

CONSTANCY OF BODY TEMPERATURE

a. Poikilothermy (variable)b. Homeothermy (constant)

THERMAL TOLERANCE

a. Eurythermic (broad tolerance)

b. Stenothermic (narrow tolerance)

REGULATORY HEAT SOURCE

a. Ectothermic (outside source)

- b. Endothermic (internal source)
- c. Heterothermic (regulation selectively suspended)

ECTOTHERMIC REGULATION

a. Microhabitat selection (seeks appropriate microhabitat)b. Postural Change (seeks appropriate posture to alter heat exchange)

ENDOTHERMIC REGULATION

a. Non_Energetic (adjustments in rate of heat exchange)

b. Energetic (adjustments in rate of metabolism)

ENERGETIC HEAT SOURCE

a. Bradymetabolic (low metabolic rate)b. Tachymetabolic (high metabolic rate)

HETEROTHRMIC REGULATION

a. Temporal Heterothermy (suspension of regulation at special times)

b. Regional Regulation (suspension of regulation in special parts of the body)

The thermoregulatory strategy of a species is a combination of several interrelated dimensions. In reptiles, as in mammals and birds, all of these strategies are utilized in various combinations and proportions.

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 (**Cabanac 1971**). Light, temperature, and their interaction are the organizing influences on the reroductive biology of many lizards (**Licht 1971**, **Pearson**, **Tsui**, **and Licht 1976**). But the reproductive state of some lizards is known to affect their selection of body temperature (**Garrick 1974**). 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. This indicated that after an initial "warming up," behavioral thermoregulation would not compete with or complicate subsequent activites. 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 are elevated to levels conducive to both maximum alertness and action.

<u>Humidity</u>. Relative humidity may be a comfort variable for most taxa, but it is very significant for the reproductive activities of many lizards. Reproduction is correlated with the onset of the rainy season in several anoline species (Licht and Gorman 1970). Moist soil is necessary for egg laying of <u>Anolis aeneus</u> (Stamps 1976) and high ambient humidity appears a prerequisite for reproduction in female green anole (Crews and Garrick 1980) and <u>Anolis sagrei</u> (Brown and Sexton 1973). Indeed, oviductal growth in green anoles is known to be arrested by experimetally induced low humidity (Summers 1988), probably associated with a disordered adrenal corticosteroid rhythm (Summers and Norman 1988)

<u>Wind</u>. The effect of wind gusts on the activity of <u>Sceloporus</u> was observed by **Jackson** (**1974**). These lizards apparently change perching sites to increase their predatory surveillance area and they make these site changes during gusts of wind when they may be less subject to predation because their movements would be less conspicuous. A comparable strategy would be reasonable for the small arboreal green anole, but in fact site changes were unaffected by wind and foliage movement although changes in posture were significantly increased as was the rate of air_licking. Interestingly, animals mildly stressed by handling prior to an observation period air_licked significantly more frequently than unstressed animals (**Greenberg 1985**).

Activity

Lizards manifest characteristic activity patterns in which different necessary activities are allocated differing levels of energetic investment. However, a simplistic economic metaphor is misleading because energy must be invested where there is a reasonable prospect of an appropriate payback, which could be something as subtle as maintenance of endocrine tone. Indeed, abnormal behavior has been associated with the artificially induced inactivity that attends freedom from the need to search for food in some small captive animals (**Kavanau 1967**).

<u>Predatory activity</u>. The predatory needs of most lizards are served by varying species_typical ratios of foraging and "sit_and_wait" predation. While herbivorous lizards such as <u>Iguana iguana</u> actively forage, for many lizards, the the central element in their predatory behavior is the apparently inactivity of perching. 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.

Depending on the objective, lizard researchers should provide a variety of prey types (and prey behaviors) to induce lizards to explore their habitats in a natural way. In green anole habitats, the use of loose sphagnum moss gives crickets sufficient cover to require lizards to maintain a naturalistic level of arousal in order to feed.

2. SAFETY NEEDS

Lizards need provision for individual security, for protection from real or potential threats from climatinc extremes or predators, including the <u>perceived</u> predatory threat of the researcher.

<u>Shelter</u>. 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. There are apparently readily available alternative behavioral strategies: individuals excluded from preferred crevices will bury themselves in loose substrate (**Greenberg 1977a**).

Such patterns of shelter utilization appaer to reflect social dominance relationships (**Greenberg 1979**). Some lizards were consistently exposed while others hid. Such "covert" behavior is well known in other species such as <u>Gehyra</u> (**Bustard 1967**), <u>Dipsosaurus dorsalis</u> (**DeWitt 1971**), and even in the usually arboreal <u>Anolis nebulosis</u> (**Jenssen 1970b**). Clearly, in research concerned with activity levels, one must also consider activity that may occur in microhabitats normally concealed from the observer.

3. SOCIAL NEEDS

<u>Group living</u> can be fortuitous in species that do not maintain territories or individual distance thresholds. Alternatively, other stimuli may override territorial dispositions. For example, many lizards that are mutually intolerant under normal conditions will aggregate in the presence of predators, during adverse weather or at night (for example, in <u>Coleonyx</u>, **Evans 1967**, <u>Anolis cyanogaster</u>, **Curry_Lindhal 1956**, or <u>Klauberina</u>, **Regal 1968**); or at sites having an atypical abundance of prey (**Evans 1951** in <u>Ctenosaura</u>; **Fitch 1940**, in <u>Cnemidophorus</u>; **Norris 1953** in <u>Dipsosaurus</u>).

<u>Social space</u>. Lizards differ strikingly in their social dynamics in ways apparently related to their sensory capacities and life history attributes. Beyond the physical, climatic, microhabitat, and ecological aspects of a study habitat, the <u>perceptual</u> space can have important effects on lizards. Some of these effects can be attributed to exposure to social stressors, recently found to be capable of eliciting elements of the physiological stress response (**Greenberg and Crews 1983**) which can profoundly affect a large number of physiological and behavioral variables. In green anole, social distances and related behavioral patterns control the synchronization of reproductive cycles (**Crews, Rosenblatt, and Lehrman 1974**).

In some cases small enclosures in which lizards are continually exposed to one another will diminish interactions. **Mayhew (1963)** observed that although a large and a small <u>Amphibolorus pictus</u> would cohabit peacefully in a small enclosure, when 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 a similar phenomenon in both the rainbow lizard and the blue spiny lizard.

Apparently, males continually exposed to the tonic stimulus of social dominants have altered physiological tone related to chronic stress. The inhibitory effects of this altered state may then abate under less restrictive conditions in which the smaller lizard may develop territorial habits that elicit aggressive responses in the dominant.

The response to social density can be exploited: In his study of <u>Anolis nebulosus</u> ethoecology, **Jenssen** (1970) 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.

Where sociality is a significant consideration, the comprehensive checklist of potentially significant variables developed by McBride (1976) is a valuble starting point (Table 4).

Table 4. ASPECTS OF SOCIALITY*

TEMPORAL VARIABILITY

a. Circadian

b. Circalunar

c. Circannual

SPECIALIZED SUBSYSTEMS

a. Casteb. Social phase (temporary role)

GROUP STRUCTURE

a. Cohesive social unitsb. Integration and cooperationc. Relation to outsiders

ORGANIZATION OF SPACING

a. Territoriality

b. Home ranges

SPACING WITHIN GROUPS

a. Individual distanceb. Dominance relationshipsc. Relatedness

SEXUAL BEHAVIOR

a. Dominant sexb. Division of labor

PARENT_OFFSPRING BEHAVIOR

a. Oviposition/birthing

*following McBride (1976).

4. SOCIAL DOMINANCE NEEDS

In social animals, relative status generally involves eventual fitness. The key element in social dominance is "priority of access to a limited resource." The resource might be a life_sustaining necessity such as food, warmth, or a refuge from predation, a variable that enhances energetic efficiency, mates, or egg_laying/birthing sites. In several species observed in the field where resources appear locally abundant, social dominance relationships may be quickly formed, in others, such as the green anole, dominance relationships have been seen only in the laboratory

An understanding of the dynamics of relative social status is important to researchers because both the behavioral patterns and their physiological determinants and consequences can be markedly different for individuals of different status and at different points in the establishment of status relationships (**Greenberg and Crews 1990**). The key neuroendocrine system in the establishment and maintenance of dominance relationships is the hypothalamic_pituitary_adrenal axis, involving most of the hormones associated with the physiological stress response. All the hormones involved also have psychoactive properties, and in this situation, they primarily act through neurobehavioral mechanisms, although somatic processes are involved and sometimes quite observable, as in changes in body color (**Cooper and Greenberg 1992**).

5. REPRODUCTIVE SUCCESS

An assessment of the constraints on the utility of a lizard follow the converging categories of ethological research supplemented by purely practical considerations. While various fragments of an animal's life might serve a given research need, an "entire" life reaches its biological "fulfillment" in the expression of individual (or inclusive) fitness. Fitness in terms of offspring (or genes) transmitted to the future is the "bottom line" of lizard life. The physiological and behavioral elements of reproduction are also remarkably conservative and vulnerable to disturbance. The necessary coordination of many processes thus makes reproduction a valuble index of overall "well being." **Murphy and Collins (1980)** have edited a volume with several fine papers on the reproductive biology and diseases of reptiles.

HUMAN NEEDS

Once we have identified a species with which to collaborate in the solving of a research problem, we need to identify and devise a means of accommodating its needs for "physical and psychological well_being." But our decisions must also be guided by a clarity of vision of our <u>own</u> needs (Table 5). This is important not only to structure the mechanics of research around the model species, but because <u>our</u> needs will profoundly affect our thinking about the cost to the <u>lizard's</u> well being that we are able to ethically accept.

Physiological and Safety Needs: Survival

<u>Medicine</u>. Many lizards possess biological attributes that, once understood, can be shared, exploited, or adapted to correct or ameliorate our own dysfunctions or diseases. To the medieval mind that identified earthly natural forms as representations of an unseen order in heaven, lizards also had a medicinal function. Licking them would confer wound_healing powers, burying them would cure fever, some of their products would cure impotence in aged men.

Ecology. In common with all taxa, we need to avoid predators, acquire prey, and compete for resources. In these cases our knowledge of specific reptiles may be useful (the Komodo dragon, the tasty iguana). Some lizards are the enemies of our enemies and have thus become friends, albeit occasionally begrudgingly (vermin-eating geckos).

<u>Models</u>. Modeling is a central mission of experimental science: it is the extrapolation from the known to the unknown and the discovery of regularities in the world that permit us to predict the consequences of our actions. Of course we and our models share at least general survival needs and sometimes we solve our problems in comparable ways, in other cases we have found alternative but comparably effective solutions, adapted to our particular circumstances. The distinction of these particulars is the key to the utility of an animal model. The proper use of this key involves potential homologies between the structure or function as represented in our subject and in us (**Greenberg 1978c**, **Senn 1976**), along with a consideration of the limits of inference (**Cranach 1976**).

Further, the more thoroughly we know lizards, the more we will learn of analogous traits and thus the more useful they will become as exemplars of alternative adaptive tactics. Several specific uses of reptile models and their utility have been elaborated in a recent review (Greenberg <u>et al</u>. 1989), and perspectives on their unique virtues have been discussed in several other reviews (Gans and Dawson 1976, MacLean 1978)

Sociality and Self Actualization

<u>Myth and religion</u>. Once our physiological and safety needs are met, sociality emerges as a compelling need, and systems of myth and religion often serve to facilitate social cohesion (**Rappaport 1971**). A key dimension of our relationship with other species is our perception of shared and valued attributes, from appearance (<u>big brown eyes</u>) to habits (<u>caring for young</u>). Lizards are not prominant players in the socially binding systems of organized thought about our relationship to the world, its origin and destiny. The ancient Romans depicted them on grave monuments as symbols of hope and medieval Christians sculpted them as symbols of rebirth and resurrection (**Armstrong 1970**).

Table 5. A HIERARCHY OF HUMAN NEEDS SERVED BY SCIENTIFIC RESEARCH

PHYSIOLOGICAL (we need to maintain homeostasis and protect the stability of our physiological functions, we must tolerate, compensate for, or overcome dysfunctions and diseases of cells, tissues and organs)

SAFETY (we need to meet challenges to the integrity and stability of the whole organism)

SOCIAL (we need to be in the company of others for enhanced protection from physical or predatory threats, to locate or produce food, for resource defense, to faciltate the efficiency of division of labor, for a richer learning environment, and for reproduction)

SOCIAL ESTEEM (we need to have our possession of traits valued by our social group recognized, partly because our group is thus more likely to protect us or our access to needed resources)

SELF-ACTUALIZATION (we need to attain our maximum biological or cultural potential, a state characterized in humans by a unique and ineffible epiphenomenal harmony with one's self and environment)

The Conduct of Research

The steps in the effective pursuit of a scientific inquiry can be viewed as hierarchically arrayed, beginning with a clear articulation of a question or problem specified in terms amenable to a scientific solution ______that is, in an objective and empirically verifiable, usually quantitative way. The process culminates with an accumulation of data which, guided by feedback loops at many steps, is selected and focused to most effectively address the original question or problem and, when fully analyzed, can answer or solve it. A consideration of the needs that must be met to conduct useful research (**Table 6**) also helps us identify the corresponding capacities of our research subject to meet those needs. Framing the question is the key step in selecting a level of analysis (**Sherman 1988**).

Table 6. A HIERARCHY OF RESEARCH NEEDS

1. NEED TO IDENTIFY A QUESTION OR PROBLEM

- a. Species Oriented (central phenomena or range of variation)
- b. Concept oriented (selection of appropriate species)

2. NEED TO FORMULATE A TENTATIVE ANSWER/MAKE PREDICTIONS

Hypotheses that are empirically verifiable

3. NEED TO SELECT THE APPROPRIATE LEVEL OF ANALYSIS

- a. Ecological
- b. Population
- c. Organismic
- d. Physiological
- e. Cellular
- f. Biochemical

4. NEED TO IDENTIFY THE RELEVANT VARIABLES

- a. Dependent variables
- b. Independent variables

5. NEED FOR PRELIMINARY OBSERVATIONS OR EXPERIMENTS

- a. Select most effective technology
- b. Laboratory
- c. Field
- d. Sample size.

6. NEED FOR DATA

- a. Validity (specificity and accuracy -- freedom from systematic errors)
- b. Reliability (sensitivity, resolution, consistency and precision--freedom from random errors)

7. NEED FOR INTERPRETATION

- a. Select appropriate statistic to explore data and test hypothesis
- b. Accept or reject hypothesis
- c. Replicate
- d. Revise hypothesis
- e. Identify further questions

Field versus Laboratory

A fact so obvious that it is often neglected is that the traits and attributes manifested by our prospective animal model evolved in a complex environmental matrix. Not only is it unreasonable to have a complete knowledge of the present ecology, but many traits exist in their present form as responses to conditions that no longer exist. Observing an animal in the field may provide confidence that some necessary ecological variable has not been inadvertantly compromised by moving the animal to a more convenient location, but that is often impractical. The profusion of potentially important ecological variables is intimidating, but a reasonable empirically-derived compromise that effectively replicates the ecological elements that are relevant to the biological phenomenon of interest is to identify and quantify key variables in the life of the species in its natural environment and then create a simulation of the natural environment, however complex, in the laboratory in which comparable quantities and <u>relationships</u> of these life-history variables are <u>spontaneously</u> expressed. Once such a state has been attained, the laboratory environment can be gradually reduced in complexity as the subjects are watched for indications that a removed variable was, in fact, important to the expression of the behavioral patterns of interest (**Greenberg 1978c**).

Experiments: Natural and Artificial

What we know of nature and the relationships between its elements we know from observation, but when nature cannot or does not provide the events to observe, we must resort to "artificial" experiments, which are, as **J.S. Mill** put it, an extension of 'pure' observation that "enables us to obtain innumerable combinations of circumstances which are not to be found in nature and so add to nature's experiments a multitude of experiments of our own" (in *A System of Logic*, Book II). The essence of an exoperiment is the selective control of relevant variables. And occasionally, the alert observer detects a naturally occuring experiment, such as when circumstances subject separated populations of a species to altered environmental conditions. The circumstances that we have maneuvered into a combination appropriate for answering particular question or solving a particular problem are, of course, selected representations of nature, and in that selection ______ that abstraction from the greater whole______ is the art of the scientist. But it is an art that thrives only when nature is seen for what it is and is not colored by subjectivity and anthropomorphism. It is

precisely this selective representation of an an attribute of interest that makes an animal model useful to us.

Objectivity and Anthropomorphism

Anthropomorphism is the attribution of human traits to other objects or organisms; ultimately, it is an extrapolation from a source of confident knowledge to one of relative ingnorance. It is understandable in light of our need for order and our intolerance of mystery, but it is also a common source of profound error. This need for order is often at odds with the practical if not ultimate limitation on our knowledge of other species. Complete knowledge is not possible and would not be practical if it were. What is needed is a <u>selective</u> representation of the attributes that interest us ___attributes that can help us answer our question or solve our problem___ in concert with a resonable measure of confidence that these attributes are not subject to forces outside our understanding if not control. But this necessary incompleteness of our measures of other species must not demoralize or inhibit our effective use of them to advance our cause. To the extent that our empathy with other creatures implies an unavoidable anthropomorphism, we must endeavor to *at least* be critical in its application, particularly when evaluating animal suffering in the laboratory (**Morton, Burghardt, and Smith 1990**).

The effectiveness of research utilizing lizards requires an understanding of their ethological constraints. We must be cognizant of the biological forces that affect the taxon, a particular genus, or even an individual under our scrutiny. Because of the many variables that must inform our use of animals, there is a relativism that cannot be reduced to a single ethical guideline, although a clear sense of where we stand in a complex moral landscape will emerge from reflecting on where we really <u>want</u> to stand. In the end it is usually innocent thoughtlessness and thoughtless prejudice that perverts our purpose. As **Donnelly** put it, "Our fundamental moral persuasions and responsibilities run deeper than our knowledge" (**1990**). For example, we are often deeply affected by traits we appear to share with lizards (Burghardt and Herzog, 1980). The point is, human and animal needs necessarily intersect. The perceived point of intersection, however informed by our ethical sensibilities, then determines our selection of research procedures that might affect lizard welfare (**Table 7**). Several factors that should affect the decision to proceed with animal experimentation were identified by **Orlans (1990**). Two of Orlan's factors, the purpose of the experiment and the extent of animal pain can be associated with our scale of human and animals needs. Additional factors included, the perceived "sentience" of the model, the competence of the investigator, good faith efforts to identify an alternative experimental model, the quality of the facility where the work is to be done, and public accountability.

Table 7. ETHICAL CONSIDERATIONS IN ANIMAL RESEARCH*

NEED TO KNOW (What human needs are served by this research? Reducing competition for resources? Safety and avoiding danger? Testing? Recreation?)

VIABLE ALTERNATIVES (Is the use of an animal really needed?)

NECESSARY NUMBERS OF ANIMALS (Can the number of animals used be reduced?)

PAIN and DISTRESS (Any evidence of trauma? Are there significant distortions of behavior? Any uniquely stressful variables?)

a. Minor or short_term pain or stress? (indwelling catheters, implants, minor post_surgical discomfort)

b. Significant but unavoidable pain or stress? (significant post_surgical discomfort; unavoidable noxious stimuli or behavioral stressors)

c. Severe pain at, near, or above the pain tolerance of unanaesthetized, conscious animals? (generally prohibited by national policy, may cause revocation of federal funds or USDA registration.)

DO THE ENDS JUSTIFY THE MEANS?

ENDANGERED STATUS?

COLLECTING/BREEDING (Are the sources reputable, reliable, licensed?)

HEALTH and HANDLING (Is there long_term impairment of overall health? Is handling distressing or comforting?)

DEGREE OF ORGANISMIC INVASIVENESS (Injections, implants, minor surgery, major surgery: Is the extent of the intrusion into the animal warrented?)

DEGREE OF ECOLOGICAL INVASIVENESS (Is removal from the natural habitat or the extent of the deprivation of normal environmental cues warrented?)

RELEVANT LEGISLATION (What is the law?)

*adapted from Guidlines of the Ethical and Animal Care Committees of the Society for the Study of Animal Behavior and the Animal Behaviour Society and SCAW Newsletter 8(3).

Lizards, like all other species, deserve our respect unconditionally, uncritically, without reservation. But even in the spirit of enlightened self_interest, respect is <u>the</u> safest foundation upon which a useful relationship can can be built. Our needs for a relationship exist at many levels from the romantic Gaian to the pragmatics of predation, and from spiritual symbolism to their possession of attributes that make them suitable models for life-enhancing research.

ACKNOWLEDGEMENTS

I am grateful to Gordon Burghardt, Sandy Echternacht, and Katherine Harris Greenberg for their helpful reading. This essay was adapted in part from earlier essays (Greenberg 1978<u>a</u>, 1978<u>c</u>).

REFERENCES CITED

Armstrong, E.A. 1970. Lizard. in: , Encylopedia of Man, Myth & Magic. R. Cavendish, ed. New York, NY: Marshall

Cavendish, pp 1638_1639.

Bartholomew, B.A. 1966. A field study of temperature relations in the Galapogos marine iguana. Copeia 1966(2):241_250.

Berk, M.L. and J.E. Heath 1975. Effects of preoptic, hypothalamic and telencephalic lesions on thermoregulation in a lizard, *Dipsosaurus dorsalis. J. Therm. biol.* 1:65_78.

Bernheim, H.A., and M.J. Kluger. 1976. Fever: Effects of drug_induced antipyresis on survival. Science 193:237_239.

Blair, F. 1960. The Rusty Lizard: A Population study.. Austin TX: Univ. Tex. Press.

Boycott, B.B., and R.W. Guillery 1959. Environmental temperature and the reptilian nervous system. Nature. 183:62_63.

Boycott, B.B., E.G. Gray, and R.W. Guillery 1961. Synaptic structure and its alteration with environmental temperature: A study by light and electron microscopy of the central nervous system of lizards. *Proc. Royal Soc.* **154(b)**:151_172.

Bradshaw, S.D., and A. R. Main. 1968. Behavioral attitudes and regulation of temperature in *Amphibolurus*. lizards. J. Zool. Lond. 154:193_221.

Brattstrom, B.H. 1974. The evolution of reptilian social behavior. Amer. Zool. 14:35_49.

Brattstrom, B.H. 1978. Learning studies in lizards. *in: Behavior and Neurology of Lizards*. N. Greenberg and P.D. MacLean, eds. Bethesda, MD: NIMH. Pp. 173_182.

Brown, K.M. and O.J. Sexton 1973. Stimulation of reproductive activity of female *Anolis sagrei* by moisture. *Physiol. Zool.* 46:168_172.

Burghardt, G.M. 1977. Learning Processes in reptiles. in: *Biology of the Reptilia, Vol. 7*, C. Gans and D.W. Tinkle, eds. New York, NY: Academic Press. pp 555_681

Burghardt, G.M. 1984. On the origins of play. in *Play in Animals and Humans*, P.K. Smith, ed. Oxford, England: Basil Blackwell. pp. 5_41.

Burghardt, G.M. and Herzog, H.A. jr. 1980. Beyond conspecifics: Is Brer Rabbit our brother? BioScience 30(11):763_768.

Bustard, H.R. 1967. Activity cycle and thermoregulation in the Australian gecko, *Gehyra variegata*. *Copeia* 1967:753_758. Cabanac, M. 1971. Physiological role of pleasure. *Science*. 173.:1103_1107.

Christian, J.J. 1980. Endocrine factors in population regulation. In: *Biosocial Mechanisms of Population Regulation*. Cohen, M.N., Malpass, R.S. and Klein, H.G., eds., New Haven, CT: Yale University Press. pp. 55_115.

Cooper, W.E. Jr. and N. Greenberg. 1992. Reptilian coloration and behavior. in: *Biology of the Reptilia, Vol. 18, Physiology and Behavior*, C. Gans and D. Crews, eds, Chicago IL: University of Chicago Press,

Cowles, R.B., and C.M. Bogert 1944. A preliminary study of the thermal requirements of desert reptiles. *Bul. Amer. Mus. Nat. Hist.* 83(5): 261_296.

Crews, D. and Garrick, L.D. 1980. Methods of inducing reproduction in captive reptiles. In: *Reproductive Biology and Diseases of Captive Reptiles*, J.B. Murphy and J.T. Collins, eds, pp. 49_70. Soc. Stud. Amphib. Rept., Miami University, Oxford, Ohio.

Crews, D., J.S. Rosenblatt, and D.S. Lehrman. 1974. Effects of unseasonal environmental regime, group presence, group composition and males' physiological state on ovarian recrudescence in the lizard, *Anolis carolinensis*. *Endocrinology* 94 (2):541_547.

Curry_Lindahl, K. 1956. Behavior of the tropical rock lizard *Agama cyanogaster* (Ruppel) in hot environments. *Ann. Soc. Royale Zool. Belg*.87:45_74.

DeWitt, C.B. 1971. Postural mechanisms in the behavioral thermoregulation of a desert lizard, *Dipsosaurus dorsalis*. *Physiologie* **63**(3):242_245.

Donnelley, S. (1990). Animals in science: The justification issue. in: *Animals, Science, and Ethics*. S. Donnelley and K Nolan, eds, *Hastings Center Report*, May/June Supplement pp. 8_13

Evans, K.J. 1967. Observatons on the daily emergence of *Colenyx variegatus* and *Uta stansburiana*. *Herpetologica* **23** (3):217_222.

Evans, L.T. 1951. A field study of the social behavior of he black lizard *Ctenosaura pectinata*. *Amer. Mus. Novitates* **1493**:1_26.

Fitch, H.S. 1940. A field behavior study of the growth and behavior study of the growth and behavior of the fence lizard. *Univ. Cal. Publ. Zool.* 44(2):151_172.

Fitch, H.S. 1954. Life history and ecology of the 5_lived Skink, *Eumeces fasciatus*. Univ. Kansas Publ., Mus. Nat. Hist. 8 (1):11_156.

Fox, W., and H.C. Dessauer, 1957. Photoperiodic stimulation of appetite and growth in the male lizard, *Anolis carolinensis*. J. *Experimental Zool*. 134:557_57.

Fox, W., and H.C. Dessauer. 1958. Response of the male reproductive system of lizards (*Anolis carolinensis*) to unnatural day lengths in different seasons. *Biol. Bull.*, 115(3):421_438.

Gans, Carl, and Dawson, W.R. 1976. Reptilian physiology: an overview. In: *Biology of the Reptilia: Volume 5, Physiology A*. Carl Gans and Wm. R. Dawson, eds. New York, N.Y.: Academic Press, pp. 1_17

Garrick. L.D. 1974. Reproductive influences on behavioral thermoregulation in the lizard, *Sceloporus cyanogenys. Physiol. & Behav.* 12:85_91.

Greenberg, N.. 1976a. Thermoregulatory aspects of behavior in the blue spiny lizard, *Sceloporus cyanogenys* (Sauria, Igunidae). *Behaviour* 59:1_21.

Greenberg, N. 1976b Observations of social feeding in lizards. *Herpetologica* 32(3):349_352.

Greenberg, N. 1977a An ethogram of the blue spiny lizard, *Sceloporus cyanogenys* (Sauria, Iguanidae). J. Herpetology 11 (2):177_195.

Greenberg, N.. 1977b. A neuroethological study of display behavior in the lizard *Anolis carolinensis* (Sauria, Iguanidae). *American Zoologist* 17:191_201.

Greenberg, N.. 1978a. Probing the saurian psyche: Ethological constraints on the activity of captive reptiles. *Proc. Amer. Assoc. Zoo Veterinar*. pp. 197_294.

Greenberg, N.. 1978b. Physiological and behavioral thermoregulation in living reptiles. in: . A Cold Look at the Hot_Blooded Dinosaurs. RDK Thomas and EC Olson, eds. Washington, DC: AAAS, pp. 141_166.

Greenberg, N. 1978c. Ethological considerations in the experimental study of lizard behavior. in: , *Behavior and Neurology of Lizards*. N. Greenberg and P.D. MacLean, eds. Bethesda, MD: NIMH, pp. 203_226.

Greenberg, N.. 1985. Exploratory behavior and stress in the lizard, *Anolis carolinensis*. Zeitschrift fur Tierpsychologie 70:89_102.

Greenberg, N.. 1990. The behavioral endocrinology of physiological stress in a lizard. *J. Experimental Zoology*, Supplement 4:170_173.

Greenberg, N.. and David Crews. 1983. Physiological ethology of aggression in amphibians and reptiles. In: *Hormones and Aggressive Behavior*. B. Svare, ed., New York, NY: Plenum Press. pp. 469_506.

Greenberg, N.. and David Crews 1990. Endocrine and behavioral responses to aggression and social dominance in the green anole lizard, *Anolis carolinensis. General and Comparative Endocrinology*, 77:1_10.

Greenberg, N. and J. Wingfield. 1987. Stress and reproduction: Reciprocal relationships. In: *Reproductive Endocrinology of Fish, Amphibians, and Reptiles*. D.O. Norris and R.E. Jones, eds., New York, NY: Plenum Press. pp. 461_503.

Greenberg, N., Gordon Burghardt, David Crews, Enrique Font, Richard Jones, and Gerald Vaughan. 1989. Reptile models for biomedical research. In: *Animal Models in Biomedical Research*. Woodhead, Avril D., ed., New York, NY: CRC Press. pp 289_308.

Hadley, M. E. and Goldman, J.M. 1969. Physiological color changes in reptiles. American Zoologist 9(2), 489_504.

Harris, V.A. 1964. The life of the rainbow lizard. London, England: Hutchinson Tropical Monographs, Hutchinson & Co.

Heath, J.E. 1962. Temperature_independent morning emergence in lizards of the genus Phrynosoma. Science 138:891_892.

Jackson, J.F. 1974. Utilization of periods in high sensory complexity for site changes in two lizards. Copeia 1974(3):785_787.

Jenssen, T.A. 1970. The ethocology of Anolis nebulosis (Sauria, Iguanidae). Herpetologica 4(1_2):1_38.

Kavanau, J.L. 1962. Twilight transitions and biological rhythmicity. Nature 194:1293_1294.

Kavanau, J.L. 1967. Behavior of captive white_footed mice. Science 155:1623_1639.

Kleinholz, L.H. 1938. Studies in reptilian color change III. Control of light phase and behavior of isolated skin. J. exp. Zool. 15, 492_499.

Kluger, M.J., D.A. Ringler, and M.R. Anver 1975. Fever and survival. Science 188:166_168.

Leach, M. 1950., ed., Dictionary of Folklore, Mythology and Legend. Funk and Wagnells, N.Y. Vol 2, pp 637_638.

Licht, P. 1967. Environmental control of annual testicular cycles in the lizard *Anolis carolinensis*. I. Interaction of light and temperature in the initiation of testicular recrudescence. *J. Exp. Zool.*, 165, 505_616.

Licht, P. 1971. Regulation of the annual testis cycle by photoperiod and temperature in the lizards, *Anolis carolinensis*. *Ecology*, **52** 240_252.

Licht 1973. Influence of temperature and photoperiod on the annual ovarian cycle in the lizard *Anolis carolinensis*. *Copeia* 1973 (3):465_472.

Licht, P. and G.C. Gorman 1970. Reproductive and fat cycles in Caribbean *Anolis* lizards. Berkeley, CA: Univ Calif. Press. 52pp.

MacLean, P.D. 1978. Why brain research on lizards. in: *Behavior and Neurology of Lizards*. N. Greenberg and P.D. MacLean, eds, NIMH, Bethesda, MD, pp.1_10.

Martin, Paul and Patrick Bateson 1986. *Measuring Behavior: An Introductory Guide*. New York, NY: Cambridge University Press. 200 pp.

Maslow, Abraham. 1962. In: D. Krech, R. Cruchfield, E.L. Ballacher, eds, *The Individual in Society*. New York, NY: McGraw Hill.

Mayhew, W.W. 1963. Observations on captive Amphibolorus pictus an Australian Agamid lizard. Herpetologica 19

(2):81_88.

Mayhew, W.W. 1964. Photoperiodic responses in three species of the lizard genus Uma. Herpetologica 20:95_113.

McDonald, H.S. 1976. Methods for the physiological study of reptiles. In: *Biology of the Reptilia: Volume 5, Physiology A*. Carl Gans and Wm. R. Dawson, eds, New York, N.Y.: Academic Press. pp. 19_126.

McGinnis, S.M. 1965. Thermal ecology of the western fence lizard, *Sceloporus occidentalis*. Ph.D. thesis, Univ. of Calif., Berkeley.

McGinnis, S.M. and M. Falkenstein 1971. Thermoregulatory behavior in three sympatric species of iguanid lizards. *Copeia* 1971:552_554.

McBride, Glen. 1976. The study of social organizations. *Behaviour* 59(1_2):96_115.

McDonald, Harry S. 1976. Methods for the physiological study of reptiles. In: *Biology of the Reptilia: Volume 5, Physiology A*. Carl Gans and Wm R Dawson, eds. New York, N.Y.: Academic Press. pp. 19_126

Meier, A.H., Trobec, T.N., Haymaker, R., MacGregar, R. III, and Russo, A.C. 1973. Daily variations in the effects of handling on fat storage and testicular weight in several vertebrates. *J. Exp. Zool.* 184, 281_288.

Moehn, L.D. 1974. The effect of quality of light on aganistic behavior of iguanid and agamid lizards. *Herpetologica* 8 (2):175_183.

Morton, D.B., Burghardt, G.M., Smith, J.A. 1990. Critical anthropomorphism, animal suffering, and the ecological context. In: *Animals, Science, and Ethics.* S. Donnelley and K. Nolan, eds, *Hastings Center Report*, May/June Supplement. pp. 13-19.

Murphy, James B. and Jos. T. Collins. 1980. eds, *Reproductive Biology and Diseases of Captive Retiles*. SSAR "Contributions to Herpetology, No. 1; 277pp.

Norris, K.S. 1953. The ecology of the desert iguana, Dipsosaurus dorsalis. Ecology 34(2):265_287.

Orlans. F.B. 1990. Policy issues in the use of animals in research, testing, and education. In: *Animals, Science, and Ethics.* S. Donnelley and K. Nolan, eds, *Hastings Center Report*, May/June Supplement. pp. 25_30.

Pearson, A.K., Tsui, H.W. and Licht, P. (1976). Effect of temperatures on spermatogenesis, on the production and action of androgens and on the ultrastructure of gonadotropic cells in the lizard *Anolis carolinensis*. J. Exp. Zoo., 195, 291_304.

Pough, F.H. 1991. Recommendations for the care of amphibians and reptiles in academic institutions. ILAR News 33(4):S1-S21.

Rand, A.S. 1964. Inverse relationship between temperature and shyness in the lizard Anolis lineotopus. Ecology 45:863_864.

Rappaort, R. 1971 The sacred in human evolution. Annual Review of Ecology and Systematics 2:23_44.

Regal, P.J. 1967. Voluntary hypothermia in reptiles. Science 155:1551_1553.

Regal, P.J. 1968. An analysis of heat_seeking in a lizard. Ph.D. Dissertation. Los Angeles, CA.: UCLA

Regal, P.J. 1978. Behavioral differences between reptiles and mammals: An analysis of activity and mental capabilities. In: *Behavior and Neurology of Lizards*. N. Greenberg and P.D. MacLean, eds, Bethesda, MD: NIMH pp. 183_202.

Reichenbach_Klinke, H. and E. Elkan 1965. Diseases of Reptiles. New York, N.Y.: Crown Pub.

Roth, J.J. and C.L. Ralph 1976. Body temperature of the lizard (*Anolis carolinensis*): Effect of parietalectomy. *J. Exp. Zool.* 198(1):17_28.

Schmidt, R.H. 1990. Why do we debate animal rights. Wildlife Soc Bull. 18(4):459_461.

Sherman, Paul W. 1988 The levels of analysis. Animal Behavior 36(2):616_619

Spellerberg, I.F., and K. Hoffman 1972. Circadian rythm in lizard critical minimum temperature. *Naturwissenschaften* 59 (11):517_518.

Stamps, J.A. 1976 Egg retention, rainfall and egg laying in a tropical lizard, Anolis aeneus Copeia 1976:759_764.

Summers, Cliff H. 1988. Chronic low humidity_stress in the lizard *Anolis carolinensis*: Effects on ovarian and oviductal recrudescence. *J Exptl. Zool.* 248:192_198.

Summers, Cliff H. and M.F. Norman 1988. Chronic low humidity_stress in the lizard *Anolis carolinensis*: Changes in diurnal corticosterone rhythms. *J. Exptl. Zool.* 247:271_278.

Webster, R. and N. Greenberg. 1988. Territoriality and social dominance in the green anole lizard. *American Zoologist*. 28 (4):381.

Wilhoft, D.C. 1958. The effect of temperature on thyroid histology and survival in the lizard, *Sceloporus occidentalis*. *Copiea* 1958:265_276.

last major draft: April 23, 1991/8:49 AM last review/revision: